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Habitat Use and Movement of the Endangered Arroyo Toad (*Anaxyrus californicus*) in Coastal Southern California

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Abstract.—Information on the habitat use and movement patterns of Arroyo Toads (*Anaxyrus californicus*) is limited. The temporal and spatial characteristics of terrestrial habitat use, especially as it relates to upland use in coastal areas of the species' range, are poorly understood. We present analyses of radiotelemetry data from 40 individual adult toads tracked at a single site in coastal southern California from March through November of 2004. We quantify adult Arroyo Toad habitat use and movements and interpret results in the context of their life history. We show concentrated activity by both male and female toads along stream terraces during and after breeding, and, although our fall sample size is low, the continued presence of adult toads in the floodplain through the late fall. Adult toads used open sandy flats with sparse vegetation. Home-range size and movement frequency varied as a function of body mass. Observed spatial patterns of movement and habitat use both during and outside of the breeding period as well as available climatological data suggest that overwintering of toads in floodplain habitats of near-coastal areas of southern California may be more common than previously considered. If adult toads are not migrating out of the floodplain at the close of the breeding season but instead overwinter on stream terraces in near-coastal areas, then current management practices that assume toad absence from floodplain habitats may be leaving adult toads over-wintering on stream terraces vulnerable to human disturbance during a time of year when Arroyo Toad mortality is potentially highest.

The Arroyo Toad (*Anaxyrus californicus*) is a federally endangered amphibian species in both the United States and Mexico (USFWS, 1994; Poder Ejecutivo Federal, 2008). It inhabits cismontane rivers and streams draining to the Pacific Ocean along the west coast of North America, from Monterey County, California (Salinas River) to Northern Baja California, Mexico (Rio Santa Maria; Gergus et al., 1997), as well as transmontane rivers that drain to the Mojave Desert from the north side of the Transverse Ranges (i.e., San Bernardino and San Gabriel Mountains) of southern California (Price and Sullivan, 1988; Grismer, 2002; Mahrdt et al., 2002, 2003; Mahrdt and Lovich, 2004). The toad is associated with low-gradient, intermittent streams and rivers with extensive terrace systems, braided channels, and large areas of fine sediment deposits periodically reworked by flooding (Stebbins, 1951; Cunningham, 1961; Sweet and Sullivan, 2005). Reproduction is dependent upon the availability of shallow and slow moving water typical of flood-disturbed environments from which breeding, egg laying, and larval development occur (Sweet, 1992; Jennings and Hayes, 1994). Arroyo Toads are generally active from the first substantial rains in January to March through August or September, depending on latitude and elevation (Sweet and Sullivan, 2005; Brehme et al., 2010). Adult toads are nocturnally active, remaining underground in sandy stream-sides and stable terraces during the daytime, emerging to engage in foraging and breeding activity at night (Stebbins, 1951). The Arroyo Toad, formerly widespread, has been extirpated from much of its historical range largely because of urban and agricultural development and the channelization and impoundment of streams and rivers (USFWS, 1994). Jennings and Hayes (1994) consider the toads present in 22 river systems, representing 24% of their historical range. Subsequent discoveries of new localities and remnant populations have increased this figure to about 35% (Sweet and Sullivan, 2005).

In addition to occupying washes, arroyos, sandy riverbanks, and other riparian habitats, the use of uplands (areas of low topographical relief outside of the floodplain) is also recognized as a key component of the Arroyo Toad's life history in near-coastal areas of its range (USFWS, 1999, 2009). The temporal and spatial characteristics of terrestrial habitat use of adult toads, especially as it relates to upland use in coastal areas, however, has not been well defined and remains poorly understood (Griffin and Case, 2001; Sweet and Sullivan, 2005). Holland and Sisk (2000, 2001) found evidence of upland dispersal by Arroyo Toads in coastal areas of San Diego County, California. During their multiyear study (1998 through 2001) at the U.S. Marine Corps Base (USMCB) Camp Pendleton, Holland and Sisk (2000, 2001) trapped adult toads (through the use of drift fences and pitfall traps) within floodplain habitats, but also several hundred meters outside of the floodplain in grassland and sage scrub habitats prior to, during, and after the breeding season. Other than the studies by Holland and Sisk (2000, 2001), however, little additional evidence exists on the use of upland habitats by Arroyo Toads. A radiotelemetry study of Arroyo Toads completed at USMCB Camp Pendleton failed to find evidence of upland dispersal at the close of breeding but, instead, described habitat-use patterns (i.e., male and female toad activity concentrated in the stream channel and terrace habitats during and after breeding) known from other areas of the species' range (Griffin, 1999; Griffin and Case, 2001). In their species ecology review, Sweet and Sullivan (2005) substantiate a pattern of observations that suggest Arroyo Toads are present in stream channel and terrace habitat year-round, with the possible exception of near-coastal areas of the species' range, where proximity to the marine environment provide for milder terrestrial conditions in the summer and fall allowing for the possibility of dispersal by Arroyo Toads into upland habitats at the close of breeding.

Uncertainty regarding the movement of adult Arroyo Toads in coastal areas can lead to conflicting conclusions regarding species dispersal patterns and ultimately affect how the species is managed. In southern California, despite a limited amount of supporting evidence, an upland-dependent life-history model has gained wide acceptance for the Arroyo Toad (Atkinson et al., 2003). The life-history model, developed to inform Arroyo Toad management and monitoring efforts throughout the region, suggests adult toads make extensive movements between riparian and upland environments at the close of breeding. This view of a seasonal migration of toads, based largely on the findings by Holland and Sisk (2000, 2001), runs counter to the stream channel and terrace hypothesis described by Sullivan and Sweet (2005), wherein toads remain in the

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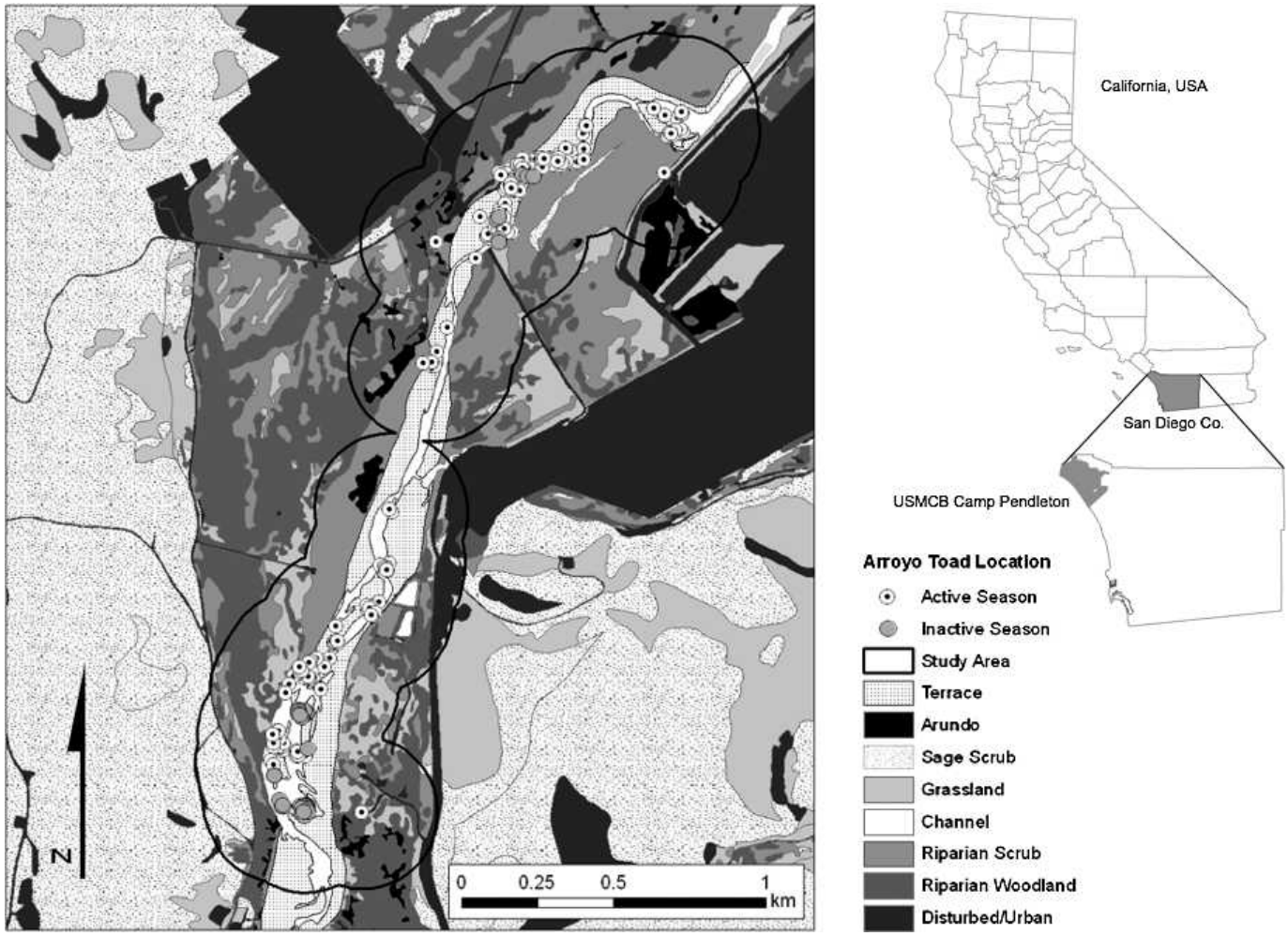

FIG. 1. Active and inactive season Arroyo Toad locations and major land cover types present within the study area located along the Santa Margarita River at USMCB Camp Pendleton, California in 2004. Study area is delimited by a 250-m buffer of all toad locations. Disturbed and urban areas include the Marine Corps Air Station Camp Pendleton located east of the study site and a rifle range occupying the square parcel of land immediately west of the study site.

floodplain year-round. Because adult toads are presumed to become hyper-dispersed upon moving into adjacent upland habitats under the upland-dependent model of life history, management of the Arroyo Toad has the potential to become ''relaxed'' during the fall and winter seasons, with toad-specific management protection provided to floodplain habitats suspended until the following breeding season. If adult toads are not migrating out of the floodplain at the close of the breeding season in mass, but instead overwintering on stream terraces, as is understood to be the case across most of their range, then an upland-dispersal management model for coastal southern California would leave the toad population vulnerable to human disturbance during the fall and winter seasons, a time when Arroyo Toad mortality is presumed to be high (Sweet, 1993). To minimize uncertainty regarding Arroyo Toad life history, additional information on the spatial ecology of the toad is needed, especially information that adds to our understanding of terrestrial habitat use of adult toads in coastal areas of the species' range, both during and outside the period of breeding activity.

We examine terrestrial habitat use and movements of adult Arroyo Toads in coastal southern California. We present analyses of radiotelemetry data from 40 individual adult toads tracked at a single site between March and November. The objectives of this study, using radiotelemetry data, were to (1) quantify adult Arroyo Toad habitat use during and after the breeding season; (2) quantify Arroyo Toad movements, comparing movement patterns between male and female adult toads; and (3) interpret results from the study in the context of Arroyo Toad life history, to better inform year-round management strategies for the toad.

MATERIALS AND METHODS

Study Area.—We conducted radio-tracking studies along the Santa Margarita River on the U.S. Marine Corps Base Camp Pendleton, California (33°18′N, 117°21′W; Fig. 1). The intermittent river drains an approximately 1,922 km^2, largely inland, watershed to the Pacific Ocean and typically ceases surface flow by early fall. Within the boundaries of the base, the lower stretches of the river lie within a broad 500–1,500 m wide floodplain, bounded on either side by upland areas dominated by sage scrub and grassland habitats of low to moderate relief. Substrate within the channel is composed almost entirely of sand, with scattered cobbles and boulders. Vegetation in the channel is sparse and largely limited to patches of emergent vegetation in the form of watercress (*Rorippa nasturtium-aquaticum*), cattails (*Typha* spp.), and sedges (*Carex* spp.), concentrated along stream edges. The alluvial terraces bordering either side of the channel approximately 0.5–1.0 m above the stream bed are of varying widths, undergoing periodic scouring during high flows that limit

vegetation to early-succession stage riparian represented by clover (*Melilotus* sp.) and cocklebur (*Xanthium strumarium*), with occasional mulefat (*Baccharis salicifolia*) and willow (*Salix* spp.) also present. Dense clumps of the invasive giant reed (*Arundo donax*) are also encountered occasionally along the terrace, with individual sprigs scattered throughout. Riparian scrub dominated by coyote bush (*Baccharis pilularis*), mulefat, and scattered willow, and riparian woodland comprised of willows, elderberry (*Sambucus mexicana*), sycamores (*Platanus racemosa*), cottonwoods (*Populus fremontii*), and oaks (*Quercus agrifolia*), are intermixed throughout the floodplain. Disturbed and developed areas bordering sections of the river near the study area include a rifle range, military airfield, and paved and unpaved roads along the edge of the riparian wash. Collectively, the streams in USMCB Camp Pendleton have been surveyed since the mid-1980s and are considered to be among the more productive sites for Arroyo Toads throughout their range (USFWS, 1999, 2005; Brehme et al., 2010). Precipitation totals for the 2004 water year (1 October 2003 through 30 September 2004) were approximately half the average rainfall total (30 cm; NOAA, 2006) for the study region. Rains occurring in October 2004 were significant, totaling 8–9 cm, and signaling the start of a new water year (2005), in which total rainfall was more than twice the annual average.

Methods.—We conducted direct searches for toads along the stream edge and adjacent alluvial terraces at night beginning in March and extending through the end of June and then again in October through November of 2004. In the fall, surveys were conducted on nights with high humidity and ambient temperatures above 10°C. We captured encountered toads by hand. Following capture, we attached cryptically colored radio transmitters (model BD-2, Holohil Systems, Ontario, Canada) to adult toads (minimum of 55 mm snout–urostyle length). Transmitters weighed 1.8 g, averaging 7% of the toads' total body mass (range: 3% to 10%), with a reported life span of 14–20 weeks. We clipped antennas on the transmitters from the factory size of 120 mm to 90 mm to reduce the chance of detection by predators. We attached the transmitters to each toad using a custom-fit belt of 1.65-mm microbore silicon tubing, following Richards et al. (1994). We used silicone tubing because it appears to cause significantly less abrasion and injury than other belt materials (Griffin and Case, 2001). Toads were fitted with belts sized to allow 2–3 mm of slack to avoid constricting the toads while preventing excessive movement of the transmitter and reducing abrasions from rubbing (Griffin, 1999). After the transmitter was attached, we fit toads with an AVID Identification Systems (Norco, CA) Passive Integrated Transponder (PIT) following Hitchcock et al. (2004). We used the PIT tags to identify individuals after radio tracking ceased and transmitters were removed or in case the toads dropped their transmitters prior to the end of the study (Muths, 2003).

Radio tracking was conducted during daytime hours when the chiefly nocturnal toads were most likely in burrows (i.e., daytime retreat sites, largely consisting of loose alluvium) and not active on the surface. We used a portable receiver (model TR-4, Telonics, Mesa, AZ) and hand-held three-element Yagi antenna to locate radio-tagged toads every two to three days to monitor movements. At the onset of a tracking period, we attempted to locate each toad within two days of attaching the transmitter to assess individual welfare. Following the initial welfare check, we repeated checks every two weeks to examine the physical condition of the toads. The biweekly welfare checks allowed us to better monitor the toads in an effort to prevent injuries associated with the transmitter and included removal of the toad from its burrow, brief examination of the toad, and reburial in the same burrow as per Griffin and Case (1999).

We recorded GPS coordinates of burrowed Arroyo Toads using a handheld unit (model 12XL, ~5.0 m accuracy, Garmin International, Olathe, KS) positioned directly above the burrow location. In addition to obtaining coordinates for each animal following relocation, we collected information on behavior (i.e., if a toad was active on the surface or burrowed), burrow depth, distance to stream, vegetation, and substrate type. A toad was considered burrowed if it was found to be completely or partially buried below the surface of the ground. We recorded burrow depths only during animal welfare checks to limit stress and desiccation of tracked animals. Burrow depths were measured as the distance from the surface of the substrate to the top of the buried toad. We measured the locations of the toads relative to the nearest section of flowing stream using rangefinders (Yardage Pro; Bushnell, Overland Park, KS). In cases where the active stream channel was not clearly visible, we determined distances using topographical maps. We characterized each location site by vegetation type by identifying the tallest type of vegetation, if any, within a 30-cm diameter circle directly over the sampled point. We classified substrates into four categories that we regularly encountered at the study site: silt (very fine particles intermediate in size between sand and clay); sand (sedimentary material, coarser than silt and finer than a granule); organic soil (typically dark, soft soil rich in organic matter, as is common in woodlands and dense shrublands); and leaf litter (fallen leaves, matted grasses, seeds, fruits, or any other loose vegetative debris). Substrate type was recorded at each location site by identifying the substrate within a 10-cm diameter circle centered on the toad's location. In addition to collecting microhabitat information at each toad location, at the close of 2004 we also sampled microhabitat conditions at 123 randomly selected points located within 250 m of a known toad location. Points were selected first by using GIS to generate random locations throughout the study area and second by selecting only those locations that fell within 250 m of a known toad location.

Statistical Analyses.—We estimated four distinct components of movement for each individual toad tracked a minimum of 10 days during the ''active'' season (Sweet and Sullivan [2005] defined this season to be the months of January through July, although toads in many years do not become active until late February or early March): (1) home-range size; (2) distance of movements; (3) frequency of movement; and (4) net displacement. We used the Spatial Analyst extension in ArcGIS 9.1 (ESRI, Redlands, CA) to estimate home-range size. We calculated home-range size as 100% minimum convex polygon (MCP). To calculate the distance of movements, we first measured the mean distance traveled per day to estimate an overall rate of movement. Distance traveled per day, recommended by Gregory et al. (1987), was measured across a sequential pairs of fixes (the distance traveled between two fixes divided by the number of days between the two fixes) producing a distribution of distances (Diffendorfer et al., 2005). Mean distance of movements (i.e., mean distance traveled per move) was identical to the mean distance traveled per day, except movements of zero were excluded. Because the accuracy of our GPS unit was ~5.0 m, we defined movements as a sequential pair of fixes resulting in a net displacement 10 m or more. We estimated the frequency of movement by calculating the proportion of fixes resulting in moves for each individual. We calculated the net displacement of individual toads in two ways. First, we calculated ''net displacement,'' which is simply a measure of the linear distance between an individual toad's initial location and final location. We used one-way *t*-tests to sequentially test for displacements greater than 25 m (25 m, 50 m, 75 m, etc.), stopping at a point where the test was no longer returned significant.

Second, we calculated ''net displacement (stream),'' which is a measure of the difference in linear distance an individual

TABLE 1. Results from hierarchical linear modeling analyses comparing the effects of different hypotheses (e.g., sex, weight, and their interaction, or sex, season, and their interaction) on the response variables describing Arroyo Toad movement, burrow location, and burrow depth.

Response variable[a]	Model[b]	ΔAICc[c]	w_i[d]	K[e]
MCP home-range size[1,2]	Sex × weight	0.0	0.88	6
	Weight	4.9	0.08	4
	Null	6.3	0.04	3
	Sex	9.1	0.01	4
Mean movement distance[1,2]	Null	0.0	0.50	3
	Weight	1.1	0.29	4
	Sex	2.8	0.12	4
	Sex × weight	3.4	0.09	6
Movement frequency[1]	Weight	0.0	0.53	4
	Null	1.1	0.31	3
	Sex	2.5	0.15	4
	Sex × weight	6.9	0.02	6
Net displacement[2]	Null	0.0	0.63	2
	Weight	2.4	0.19	3
	Sex	2.7	0.17	3
	Sex × weight	8.0	0.01	5
Net displacement (stream)	Null	0.0	0.60	2
	Weight	2.4	0.18	3
	Sex	2.5	0.18	3
	Sex × weight	5.1	0.05	5
Distance to stream[2,3]	Sex × season	0.0	0.67	6
	Sex	1.5	0.33	4
	Null	12.6	0.00	3
	Season	14.0	0.00	4
Burrow depth[3]	Season	0.0	0.56	4
	Sex × season	2.2	0.19	6
	Null	2.6	0.15	3
	Sex	3.3	0.10	4

[a] Key: [1]Number of toad locations included as a covariate in all models. [2]Dependent variable log-transformed. [3]Individuals included as a random effect in all models.
[b] Null model includes the intercept plus a random effect of individuals or a fixed effect of number of locations as a covariate, if applicable. The explanatory variables include the fixed effects of sex, weight, and their interaction or sex, season, and their interaction.
[c] Difference in AICc-values between each model and the low-AICc model; when comparing the relative fits of a suite of models, differences in AICc-values among models indicate relative support.
[d] AICc-model weight; weights have a probabilistic interpretation. Of these models, w_i is the probability that model i would be selected as the best-fitting model if the data were collected again under identical conditions.
[e] Number of parameters in the model.

toad was from the nearest section of flowing stream between their first and last locations. If a toad's final location was closer to the stream relative to their capture location, the distance was negative. If the toad's final location was further away from the stream, the distance was positive. We used this second measure of displacement to test for the migration of toads away from the stream during the active season. Because toads were captured at the stream edges, we would expect these values to be positive and potentially large, if they were leaving the stream for upland habitat following breeding activities. The limited number of toads ($N = 3$) tracked for more than 10 days in the fall, precluded us from testing for the effects of season on individual movement parameters. In general, because adult toads were tracked during the day while they were largely inactive in burrows, home-range estimates and movement rates could be biased low.

Next we employed hierarchical linear modeling (HLM, sensu Raudenbush and Bryk, 2002; a.k.a. mixed model or multilevel modeling) in SYSTAT 12 to model the effects of sex, weight, and their interaction on the estimated movement parameters. We also used HLMs to model the effects of sex, season, and their interaction on burrow depth (''burrow depth'') and the distance of individual burrow locations relative to the stream (''distance to stream''). To account for the within-individual correlation structure of the data, we included ''individual'' as a random effect along with the fixed effects in the HLM modeling of burrow depth and distance to stream. Because of the strong positive relationship between the number of locations and home-range size, we included number of locations as a covariate in our HLMs of ''MCP home-range size,'' ''mean movement distance,'' and ''movement frequency.'' To account for excessive skew, we log-transformed affected response variables (see Table 1). We evaluated and weighted all mixed models using the corrected Akaike's Information Criterion (AICc; Burnham and Anderson, 2002) to assess the multiple hypotheses (i.e., effects of sex, weight, season, etc.) for each response variable. We included a null model (intercept plus individual random effect or number of locations covariate, depending on the response variable) in the model set to evaluate the explanatory power of the variables relative to a mean value.

Habitat Selection (Burrow Selection).—We investigated macro- and microhabitat selection by male and female toads during the active season by identifying habitat features (i.e., major habitat types and local-scale vegetation and substrate) used in greater proportion than expected based on their availability to the animals (Thomas and Taylor, 2006). We partitioned the study area into eight distinct, major habitat or land cover types: (1) channel, (2) terrace, (3) arundo, (4) riparian scrubland, (5) riparian woodland, (6) sage scrub, (7) grassland, and (8) disturbed/urban. With the exception of Terrace, which we defined using 2003 aerial images, habitat types were classified based on land-cover types identified by 2003 GIS vegetation data (USMCB Camp Pendleton). To define microhabitat use, we defined 10 local-scale vegetation types present at the location sites (listed in order of frequency detected in the study area; from most to least frequent): willow and mulefat, mustard (*Brassica* spp.), hemlock (*Conium maculatum*), none, other exotics (e.g., *Ricinus communis*, *Carduus pycnocephalus*), grass (both native and exotic), native perennials (e.g., *Eriogonum fasciculatum*, *Heterotheca grandiflora*), arundo, cocklebur, and aquatic and semiaquatic plants (e.g., *Cyperus* spp., *Scripus* spp., *R. nasturtium-aquaticum*).

We determined selection of each type of macrohabitat, local-scale vegetation, and substrate for male and female toads by

comparing use of each land-cover type or habitat feature with their corresponding availability (Thomas and Taylor, 2006). We assessed selection of macro- and microhabitat at one scale, second-order selection (Johnson, 1980). For purposes of assessing macrohabitat selection, we compared the proportion of each land-cover type within the individual 100% MCP home range (use) to the proportion of that type of cover within the study area (availability). We assessed second-order microhabitat selection by comparing the proportion of individual toad locations (use) within each vegetation and substrate type to the proportion of that type of vegetation or substrate within the study area (availability). We described availability of microhabitat features by calculating the proportion of locations selected randomly from throughout the study area within each of the vegetation and substrate types. We calculated selection ratios (i.e., proportions used vs. per the proportion available) for each individual and habitat type (Manly et al., 2002; Alldredge and Griswold, 2006). If there was no selection, we expected mean ratios of selection across individuals to be near one. Furthermore, if there was no partitioning between sexes, we expected mean ratios to be similar for males and females (Horne et al., 2009). We defined the boundaries of the study area (for purposes of estimating habitat availability) as the total collective area located within a 250-m buffer of individual toad locations.

Results

Tracking was initiated in late March and lasted until late November of 2004. We heard the first calling males at the end of March and captured 36 adult Arroyo Toads between 30 March and 28 April. With the onset of precipitation in October, we again initiated nighttime visual surveys for toads, capturing eight toads between 18 October and 22 October. We tracked 19 male and 21 female Arroyo Toads. In general, male toads (mean length [SD]: 56.1 mm [1.5]; mean weight: 20.6 g [2.4]) were smaller than female toads (mean length: 61.4 mm [4.3]; mean weight: 30.8 g [8.0]). Of the 40, we relocated 33 (16 males and 17 females) adult toads during the spring and summer a collective 248 times over a 117-day tracking period. Of the 33 toads, 23 (males = 14; females = 9) retained their radios for more than 10 days. For these 23 toads, both the mean number of days tracked (mean [SE]: 39.5 [4.5]) and number of locations (9.9 [1.0]) did not differ between males and females (number of days tracked: $t_{21} = 1.678$, $P = 0.108$; number of locations: $t_{21} = 1.630$, $P = 0.118$). During the fall, we tracked seven toads, three males and four females, locating them a total of 47 times over a period of 45 days. Of these seven, two female toads and one male toad retained their radios for more than 10 days, with tracking periods lasting between 13 and 44 days. In general, trouble securing the transmitters to the toads limited the duration of tracking. Of the 40 toads tracked, all 40 eventually escaped from the belt and transmitter system; 26 of these escaped in less than 20 days. Griffin and Case (2001), who also used an identical system of transmitter attachment, show similar results of frequent toad escapes, indicating a need to improve the technique used to attach transmitters to Arroyo Toads.

Movement.—After accounting for the differences in the number of locations among individuals, we found the interaction of sex (i.e., gender) and weight influenced the response variable MCP home-range size more than weight alone (Table 1). For both sexes, heavier toads maintained smaller home ranges than did lighter toads. The negative effect of weight on the log of MCP area, however, was greater for male versus female toads (Fig. 2). We found no influence of weight or sex on mean movement distance (Table 1), which averaged 13.1 m (SD = 7.7) per day per move. Similar to home-range size, weight had a negative effect on movement

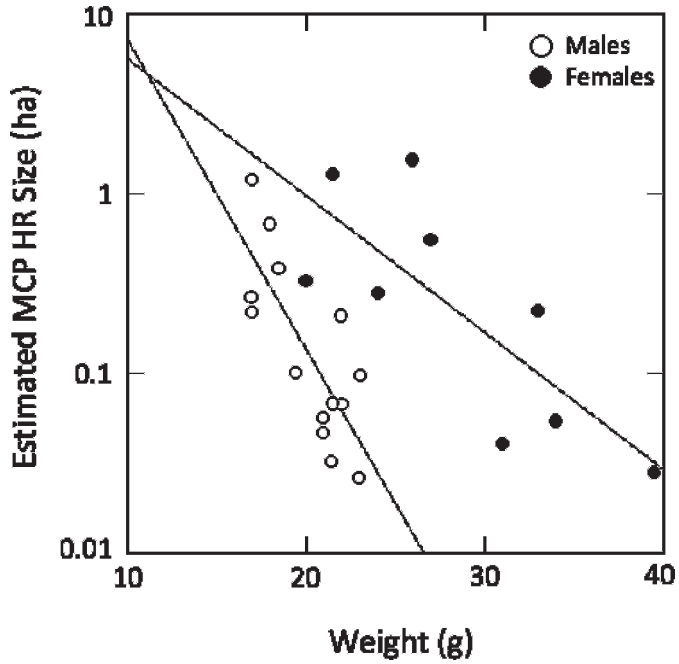

FIG. 2. Estimated 100% MCP home-range size (ha) by weight (g) for active season male and female Arroyo Toads. Estimates of MCP control for number of locations. Estimated Log-MCP for males = 1.784 − 0.168 × (weight) + 0.082 × (locations); and females = −0.55 − 0.038 × (weight) + 0.082 × (locations).

frequency (Table 1) with heavier adult toads moving less frequently than did lighter adult toads (estimated movement frequency = 1.0 − 0.013 × weight[g]; adjusted $R^2 = 0.79$).

The log of net displacement was significantly greater than 25 m (one-sample *t*-test mean = 25.0 m: $t_{22} = 3.082$, $P = 0.005$) but not 50 m (one-sample *t*-test mean = 50.0 m: $t_{22} = -0.107$, $P = 0.916$), indicating a modest shift in location by the toads away from their initial capture location during the active season ($N = 23$, max = 202.0 m, min = 9.0 m, mean = 77.8 m, median = 54.0 m, SD = 69.9 m). With respect to the toads' location relative to the stream, we saw little net positive movement away from the stream (one-sample *t*-test with mean = 0.0 m: $t_{22} = 2.034$, $P = 0.054$), with the average value of net displacement (stream) only 8 m ($N = 23$, max = 56.0 m, min = −30.0 m, SD = 18.9 m). Neither measures of displacement were influenced by sex, weight, or their interaction (Table 1). We did not include the number of locations as a covariate in the HLMs for both of these measures because we found no evidence of a positive linear relationship between the number of locations and the net displacement ($t_{22} = -0.867$; $P = 0.396$) and net displacement (stream) ($t_{22} = 0.277$; $P = 0.784$).

After accounting for the random effects of individuals on burrow locations, we found the interaction of sex and season influenced the log of distance to stream more than did sex alone (Table 1). In the active season, male burrows were located, on average, approximately 11 m closer to the stream ($N = 124$, max = 76.0, min = 0.1, mean = 8.7, SD = 12.7) than were female burrows ($N = 122$, max = 135.0, min = 0.3, mean = 20.0, SD = 23.4; Fig. 3). In the inactive season (i.e., fall) females shifted their location about 45 m further from the stream channel ($N = 34$, max = 109.0, min = 10.0, mean = 64.4, SD = 25.5), whereas the small number of locations for male toads did not show a difference between seasons ($N = 8$, max = 15.0, min = 0.1, mean = 5.3, SD = 4.2). The response variable, burrow depth was influenced by season, not sex, after accounting for the random effect of individuals on burrow location (Table 1), with toads burrowing on average 54 mm below the surface in the active season ($N = 95$, max = 135.0,

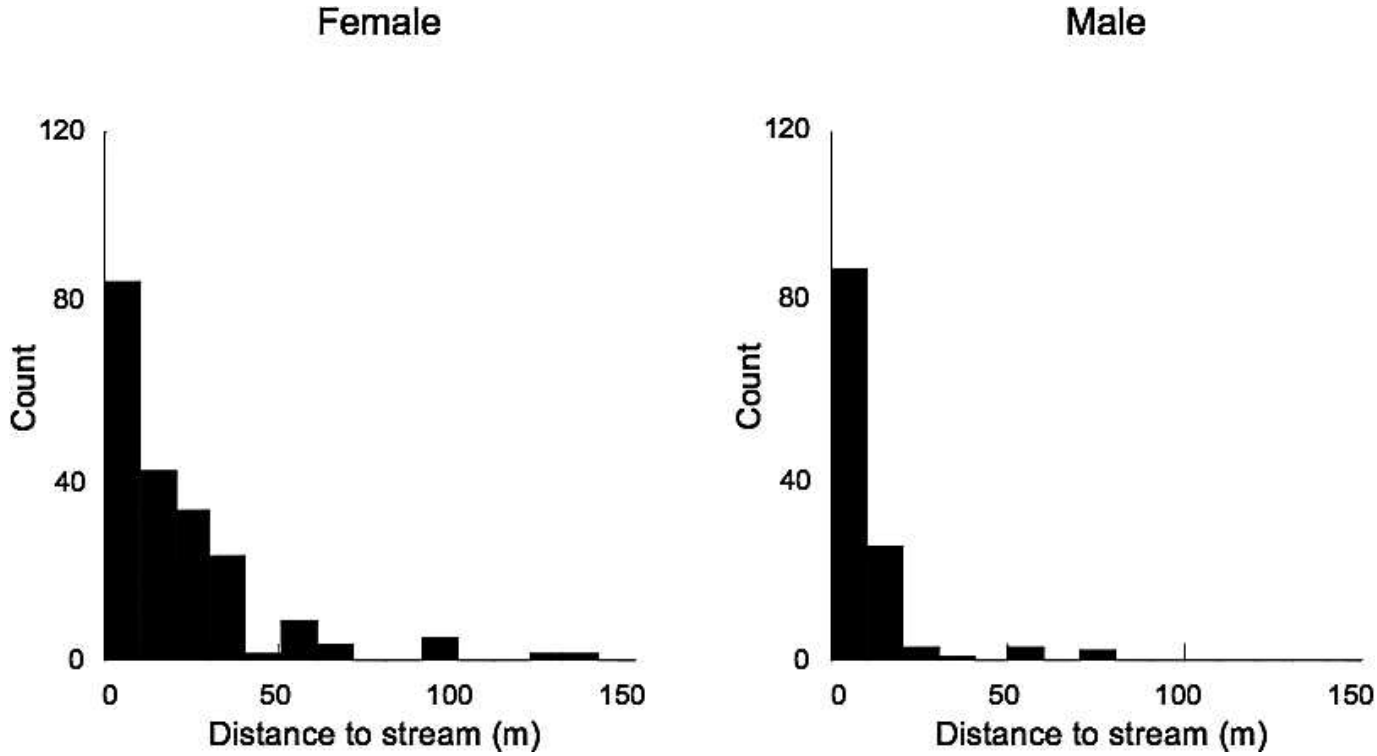

FIG. 3. Distance (m) of male and female Arroyo Toad burrow locations from nearest flowing section of the stream during the active season.

min = 10.0, mean = 53.6, SD = 23.9) compared to 67 mm in the inactive season (N = 20, max = 112.0, min = 30.0, mean = 67.0, SD = 22.2).

Habitat Selection.—When we compared proportions of each land-cover type present within home ranges to proportions in the study area, we found that land-cover types were used nonrandomly (disproportionately to their availability). Selection ratios varied by land cover type (repeated-measures ANOVA: $F_{6,16}$ = 552.818, $P < 0.001$; Fig. 4a) with Terrace and Channel habitats selected (i.e., used significantly more than available with selection ratios greater than 1). Regardless of their overall availability, all other land-cover types (riparian scrub, riparian woodland, disturbed/urban, grassland, arundo, and sage scrub) were avoided (i.e., used significantly less than available). Although selection ratios across land-cover types did not vary by sex ($F_{6,16}$ = 0.983, P = 0.468), pairwise comparisons of male and female use of channel and terrace habitats revealed male toads used channel habitat more than they did terrace habitat (paired t-test: $t_{13} = -3.591$, P = 0.003), whereas female toads showed no preference ($t_8 = -1.071$, P = 0.315). Similar to land-cover types, microhabitat conditions (local scale vegetation types) were used nonrandomly by the toads at the level of second-order selection (Fig. 4b). Selection ratios varied by vegetation type ($F_{8,23}$ = 24.874, $P < 0.001$) but not by sex ($F_{8,23}$ = 0.677, P = 0.707) with 90% confidence intervals indicating positive selection (i.e., not overlapping 1) for willow and mulefat, and cocklebur vegetation types. The vegetation types, none, grass, arundo, and aquatic plants showed no selection by toads as confidence intervals overlapped one. Toads avoided mustard, hemlock, other exotics, and native perennials vegetation types as indicated by selection ratios less than one. Although the proportion of random locations within the study area with sandy soil was 37% (of a total of 123 locations), male and female toads were found to burrow exclusively in sandy soils (195 of 195 toad burrow locations) avoiding silt (23% of random locations), organic soil (17%), and leaf litter (23%) as burrowing substrates.

DISCUSSION

The findings of our study provide novel information on the terrestrial habitat use and movement of Arroyo Toads, highlighting the likely importance of floodplain landforms to the persistence of Arroyo Toads, not just during times of breeding but through all seasons in near-coastal areas of the species' range. Although our study was limited in both geographic and temporal scope, the observed patterns of habitat use and movement are consistent with other studies of Arroyo Toad ecology and raise important questions concerning the dynamics of the movement of adult toads between riparian and upland habitats in coastal areas.

The duration of tracking during the active season in 2004 lasted for just over three months, beginning in early April and ending in July. During this time we tracked individual adult toads, on average, for approximately 35 days and saw very little movement away from the stream channels and elevated terraces, with both male and female toads engaged in activity at the edge of the stream during and after breeding activity, which concluded at USMCB Camp Pendleton on May 10 (as recorded by Brehme et al. [2010]). Although both adult male and female toads occupied generally similar environments, we did find subtle differences between the sexes in habitat use at the level of second-order selection (Johnson, 1980) as well as in burrow location during the spring and summer. In our study, male toads used (as measured by 100% MCP) channel habitat more intensively than terrace habitat, whereas female toads showed no difference in use between the two habitat types. In support of these findings, males constructed burrows that were on average ~10 m closer to the stream than were the burrows constructed by females. Similar results for both measures were reported by Griffin and Case (2001) and may relate to differences in male and female behavior related to breeding activity, with males maintaining higher densities in the immediate vicinity of the stream channel to maximize breeding opportunities and females distributed more evenly over both channel and adjacent terrace. In October and November,

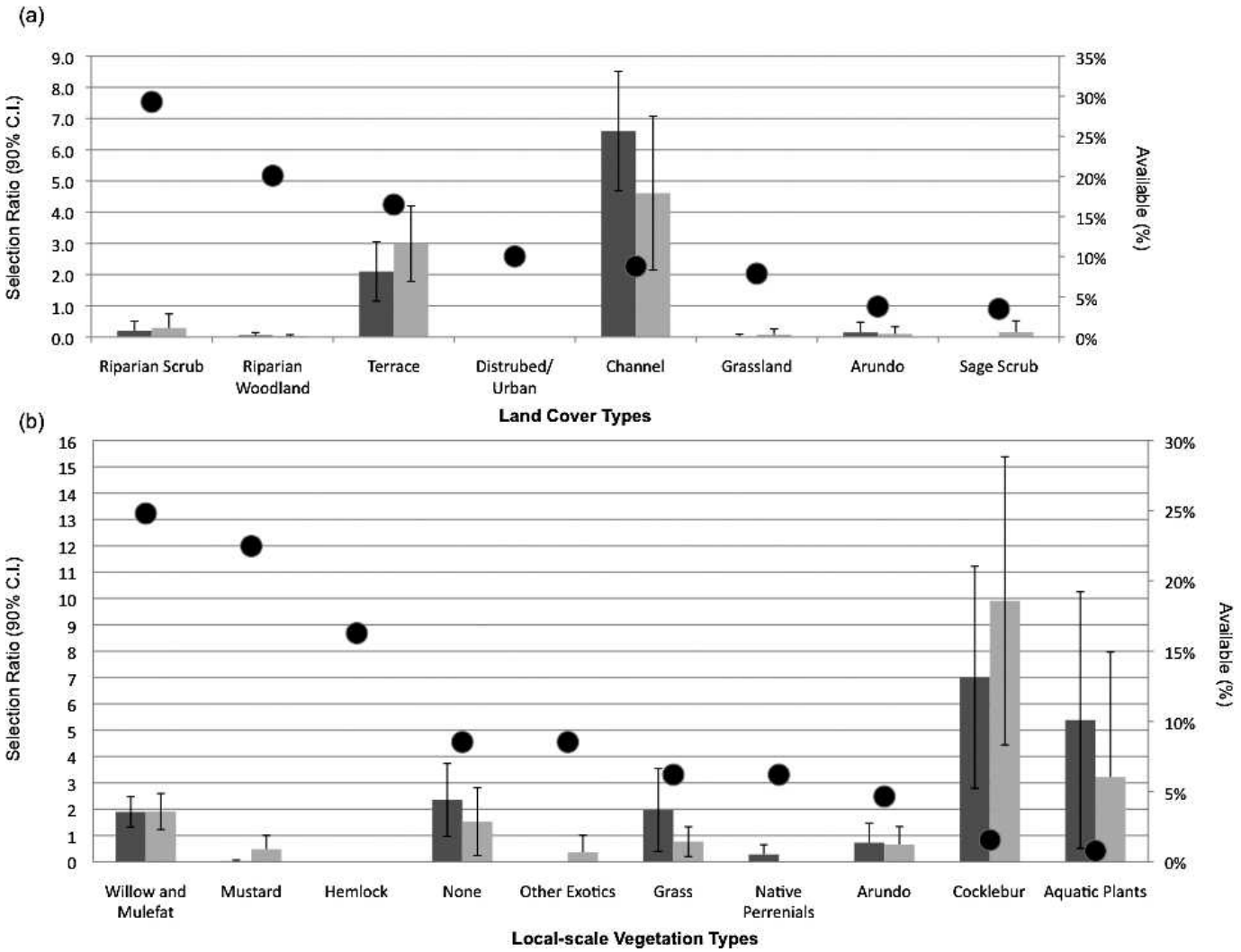

FIG. 4. Mean selection ratios (proportions used per the proportion available; 90% CI) for the active season male (dark bars) and female (light bars) Arroyo Toads. Dark circles indicate percentage of the study area represented by individual land cover or vegetation type. Ratios greater than one indicate selection. (a) Land cover availability was determined by the proportion of each land cover type within the study area, and use was determined by the proportion of each land cover type within the 100% minimum convex polygon home range of an individual. (b) Availability of local-scale vegetation types was determined by the proportion of randomly selected locations associated with each vegetation type within the study area, and use was determined by the proportion of locations for an individual toad associated with each vegetation type.

tracked toads dug slightly deeper burrows in the elevated stream terraces, possibly escaping the drier conditions on the surface, with females shifting their location further away (~45 m) from the stream channel.

Microhabitats used by adult toads during the spring and summer, as measured by local-vegetation type and substrate, varied from what was available in the study area. Both male and female toads used sandy substrates exclusively within which to construct their shallow daytime retreats and favored retreat sites associated with cocklebur, willow, and mulefat. Avoidance of organic soils, silt, and leaf litter, as well as other vegetation types associated with later-succession riparian or upland habitat, is not surprising given the observed macrohabitat preferences of the toads. The favored open, sandy flats associated with the stream edges are largely derived from periodic flood events that scour the near-shore environment and are typical of the localities where Arroyo Toads have historically been known to occur throughout the southern California region (Stebbins, 1951; Cunningham, 1961; Sweet and Sullivan, 2005).

Interestingly, home-range size and the frequency of movement during the spring and summer varied as a function of body mass, as heavier toads moved less frequently and maintained smaller home ranges than toads of lesser mass. The difference in strength of the effect of mass on MCP area between the sexes appears to simply reflect the larger and more variable size of adult females relative to males. Other studies (Sweet, 1992, 1993) have also shown differential movement based on body mass in Arroyo Toad populations. In more northern populations, both adult males and females become sedentary with increasing size (Sweet, 1992). In these populations, site fidelity for the same breeding pool within the same season or between successive years is common in large adult males and females, respectively. In general, smaller adults, presumed to be younger and thus less experienced, are likely to spend more time searching for suitable foraging and breeding sites than larger adults who are more familiar with the spatial arrangement of resources and thus more likely to occupy the best locations earlier in the season. In southern California, stream hydrology is exceptionally variable from year to year (Mount, 1995; White and Greer, 2006); thus, the location of suitable breeding and foraging sites are equally less predictable. Because of this, wandering by young toads along the stream channel during the breeding season, characterized

as ''drift'' by Sweet and Sullivan (2005), is likely to be even more pronounced.

The absence of detected variation in movement between males and females, as well as the minimal total displacement and net displacement as measured relative to the nearest section of flowing-stream, suggests that offsite dispersal (i.e., dispersal outside the most active areas of the floodplain) by adult toads within the sampled population during and after breeding is rare or uncommon. Instead, the concentration of both sexes within the stream channel and terraces throughout the spring and summer study period suggests there are likely other benefits to occupying the channel and terrace environment beyond reproduction. Stream margins are important habitat for foraging juvenile Arroyo Toads (Sweet and Sullivan, 2005). We suspect that the high density of arthropod prey provides significant foraging opportunities for adults and juvenile toads. The prey type is preferred by species in the genus *Bufo* (Clarke, 1974a) and is available on the open stream terraces during the spring and summer months. Such opportunities, in addition to reproduction, drive both adult female and male toads to use the near-stream environment throughout the breeding season. In other parts of their range, the strong preference of Arroyo Toads for the tree ant, *Liometopum occidentale*, is known to influence where females occur during the active season and where males occur principally after the breeding season concludes (S. Sweet, pers. comm.).

The results from fall surveys revealed the presence of adult toads on the stream terraces at the study site in October, several months following the cessation of breeding activities. Given that the reappearance of toads on the terraces immediately followed (within 24 h) the return of precipitation to the study region after an approximately six-month dry period (which is not unusual for the Mediterranean-type climate of coastal southern California), we suspect the toads were already present in the floodplain prior to the October rainstorm and likely never left following the close of near-stream surface activity in mid- to late summer as would be predicted by the stream channel and terrace model of Arroyo Toad life history, which predicts year-round occupancy of the near-stream environment. Subsequent radio-tracking of the captured toads showed that the adult toads used the stream terrace and channel habitats exclusively during the days and weeks that followed their capture. Previous to the October storms, the Santa Margarita River had ceased to flow by the middle of August (USGS, 2004) leaving the stream channel dry at the study site for about a two-month period.

Although we were unable to track individual toads continuously throughout the active season, our results provide evidence of widespread stream channel and terrace use during the fall in addition to the spring and summer following breeding activity. If toads were dispersing to the upland habitats outside of the floodplain following breeding in near-coastal areas as predicted by the upland-dependent model of life history described by Atkinson et al. (2003), then we would expect to see evidence of upland dispersal in May, June, or July, a period of time in which we did not observe any evidence of dispersal. Although dispersal into upland habitat may have occurred later in the season when we did not have any active transmitters on toads, the longer toads wait to disperse after the close of breeding, the worse the environmental conditions become for overland movement, suggesting that the likelihood of toad dispersal into upland habitat decreases with increasing time since breeding.

Surface conditions are driest in coastal southern California, as measured by both Live Fuel Moisture (LFM) and precipitation, in late summer through mid-fall. Live Fuel Moisture is a measure of the moisture content of sampled vegetation and an indicator of soil moisture and temperature (Countryman and Dean, 1979). The long-term mean annual trend for LFM of coastal chaparral in Los Angeles County, highly correlated with measures of LFM for coastal sage scrub (Peterson et al., 2008), shows that peak moisture levels in southern California are achieved in spring then decline as summer drought progresses and remain low until the onset of growth in late winter and early spring (Countryman and Dean, 1979; Peterson et al., 2008). Because of the severity of surface conditions (i.e., absence of moisture) during late summer and early fall, even with the availability of dry-season moisture (i.e., fog), it seems more likely that Arroyo Toads would experience a shutdown in activity (i.e., aestivation) in near-coastal areas during the latter summer months rather than engage in extensive upland movement out of the floodplain as predicted by the upland-dependent model of life history.

Sweet and Sullivan (2005) describe a shut down in the activity of adult Arroyo Toads range-wide from August through December, stating that adult toads become progressively less active after early July with few adults found on the surface beginning in August. Pitfall trapping data from Holland and Sisk (2001) and the USGS at USMCB Camp Pendleton (RNF, unpubl. data) show a similar drop in activity during the driest times of the year with a brief return of activity in the late fall correlated with the return of winter rains. This observed positive correlation between Arroyo Toad activity and surface moisture is expressed in other North American Bufonids (Ewert, 1969; Clarke, 1974b; Fitzgerald and Bider, 1974), which are most active in terrestrial habitats during the late winter and early spring following their emergence from hibernation or torpor.

Even though our study is limited in scope, the patterns of terrestrial habitat use and movement raise important questions concerning the dynamics of adult toad movement between riparian and upland habitats in near-coastal areas. Our results highlight the uncertainty that still exists concerning the timing and universality of adult toad dispersal out of the floodplain identified by Holland and Sisk (2000, 2001) in near-coastal areas of the species' range. Whether the population that we studied is representative of Arroyo Toad populations in other near-coastal areas of southern California and Mexico is not known. Nor is our understanding of how these observed patterns of habitat use and movement change with variation in seasonal precipitation. Griffin and Case (2001) tracked adult toads in the San Mateo River watershed on USMCB Camp Pendleton in 1998, when rainfall in the region was 2.3 times the annual average. Although the research was completed in an unusually wet year, the authors reported little evidence of upland dispersal by adult toads and conclude that channel and terrace habitats are critical for Arroyo Toads prior to, during, and after breeding. Even though there appears to be substantial agreement among studies, additional research is warranted to determine whether the space-use patterns identified by our study are representative of other populations of the toad in near-coastal areas and under differing environmental conditions.

Although uncertainty remains concerning the dynamics of Arroyo Toad terrestrial habitat use, the results of our work as well as the findings of other studies support the hypothesis that floodplain landforms are likely key to the persistence of Arroyo Toads not just during times of breeding but also through all seasons. In general, management efforts for the Arroyo Toad extends protection to breeding toads and egg masses and larval and juvenile toads occupying riparian habitat during the spring and summer months (USFWS, 2009). By not extending protection to adult toads overwintering on stream terraces, a large portion of the Arroyo Toad population is potentially left vulnerable to human disturbance during the fall and winter. High-risk activities include the controlled release of large amounts of water from dams that

can washout sandy terraces; bridge construction or maintenance; invasive plant species management involving the use of heavy machinery; recreational off-road vehicle use; and military training exercises involving heavy mechanized equipment that could potentially crush toads hibernating just below the ground surface. Mark–recapture data indicate that winter mortality rates of adult Arroyo Toads can be exceptionally high (Sweet, 1993). By not managing for an overwintering population of toads in the near-stream environment, incidental mortality caused by human activities may exacerbate rates of winter mortality in this endangered amphibian species and further jeopardize the likelihood of this species' long-term persistence in the coastal southern California landscape.

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