Herpetological Conservation and Biology 3(2):155-169
Submitted: 8 February 2007; Accepted: 30 March 2008

MOVEMENT PATTERNS OF CALIFORNIA RED-LEGGED FROGS (*RANA DRAYTONII*) IN AN INLAND CALIFORNIA ENVIRONMENT

PATRICIA J. TATARIAN

Wildlife Research Associates, 1119 Burbank Avenue, Santa Rosa, CA 95407, USA,
e-mail: trish@wildliferesearchasscociates.com

***Abstract.*—During the fall, winter, and spring of 1999-2000 and 2000-2001, I radio-tracked the movements of 49 individuals of *Rana draytonii* at a series of eight pools. Less than half of the frogs tracked (42.8%) moved away from their source pool, either terrestrially or aquatically, on at least one occasion. I observed 43 terrestrial forays by 12 frogs and 18 aquatic dispersals by 10 frogs. Frogs initiated movements after the first 0.5 cm of rain in the fall, with more terrestrial movements occurring in the pre-breeding season (57%) than in the breeding season (32%) or post-breeding season (11%). Frogs moved greater average distances aquatically (107.2 m) than terrestrially (24.4 m). They moved greater average terrestrial distances during the pre-breeding season (41.8 m) than during the breeding (13.5 m) or post-breeding (16.3 m) season, with the majority of movements occurring for only one of the 3-4 day survey periods. Frog occupied sites were significantly closer on average to the source and nearest pools and contained significantly more surface object cover and under shelter cover than randomly located plots. My data differs from studies of *Rana draytonii* in more mesic habitats along parts of the California coast. I suggest that management for the species in similar habitats should include a buffer zone with several key components, including: (1) a connection between breeding habitat and non-breeding aquatic habitat; (2) sufficient upland habitat surrounding the aquatic habitats; and (3) sufficient object cover.**

Key Words.—California Red-legged Frog; radio telemetry; *Rana draytonii*; terrestrial movement; upland habitat

INTRODUCTION

World-wide amphibian declines have been attributed to diseases (Beebee and Griffiths 2005), habitat loss and fragmentation (Fisher and Shaffer 1996), urbanization and agricultural spraying (Davidson et al. 2001), and predation by non-native amphibian and fish populations (Knapp 2004). These factors become exacerbated when coupled with other subtle or undetected effects (Green 1997; Semlitsch 2000; Kiesecker et al. 2001).

One species known to be affected by the synergism between habitat loss and competition with non-native amphibians is the California Red-legged Frog (*Rana draytonii*). Adapted to survive in a Mediterranean climate consisting of wet winters and dry summers, *R. draytonii* breeding begins in early winter (late November) and lasts until mid-spring (early April), with metamorphosis occurring between July and September (Jennings and Hayes 1994). This species breeds primarily in permanent and ephemeral ponds, or deep pools in intermittent streams (Jennings and Hayes 1994). Ponds that support breeding are typically permanent, at least 0.6 m in depth, and contain emergent and shoreline vegetation, although non-vegetated ponds and streams have been used (Jennings and Hayes 1994). Sufficient pond depth and shoreline cover are critical, because they provide means of escape from predators (Stebbins 1985). Current research focuses primarily on *R. draytonii* in mesic environments, specifically along the coast of California in San Luis Obispo County (Rathbun et al. 1993; Rathbun et al. 1997), Santa Cruz County (Bulger et al. 2003) and Marin County (Fellers and Kleeman 2007).

To understand present population requirements and identify future possible mechanisms for decline in *R. draytonii* populations, additional behavioral and ecological information is required that will provide a clearer understanding of individual movements to and from breeding pools in a xeric inland environment. I designed this study to gather quantitative information on the terrestrial movements of *R. draytonii* within a more xeric inland environment. I present results of frog movements from their summer aquatic habitat to upland areas. I examined their use of upland habitats surrounding their aquatic areas, the components of these upland habitats, and the distances frogs move in a xeric inland environment. I approached these questions using radio tracking to document the movement patterns of Red-legged Frogs and quantitatively analyzing the habitat components within the microhabitats that they used.

MATERIALS AND METHODS

The research took place from July 1999 to March 2000 and from September 2000 to June 2001. I conducted daytime surveys twice weekly between 0730 and 1200 hr during the first year; roughly twice-weekly surveys between early evening at twilight and 2300 hr during the second year. During each survey, I tracked

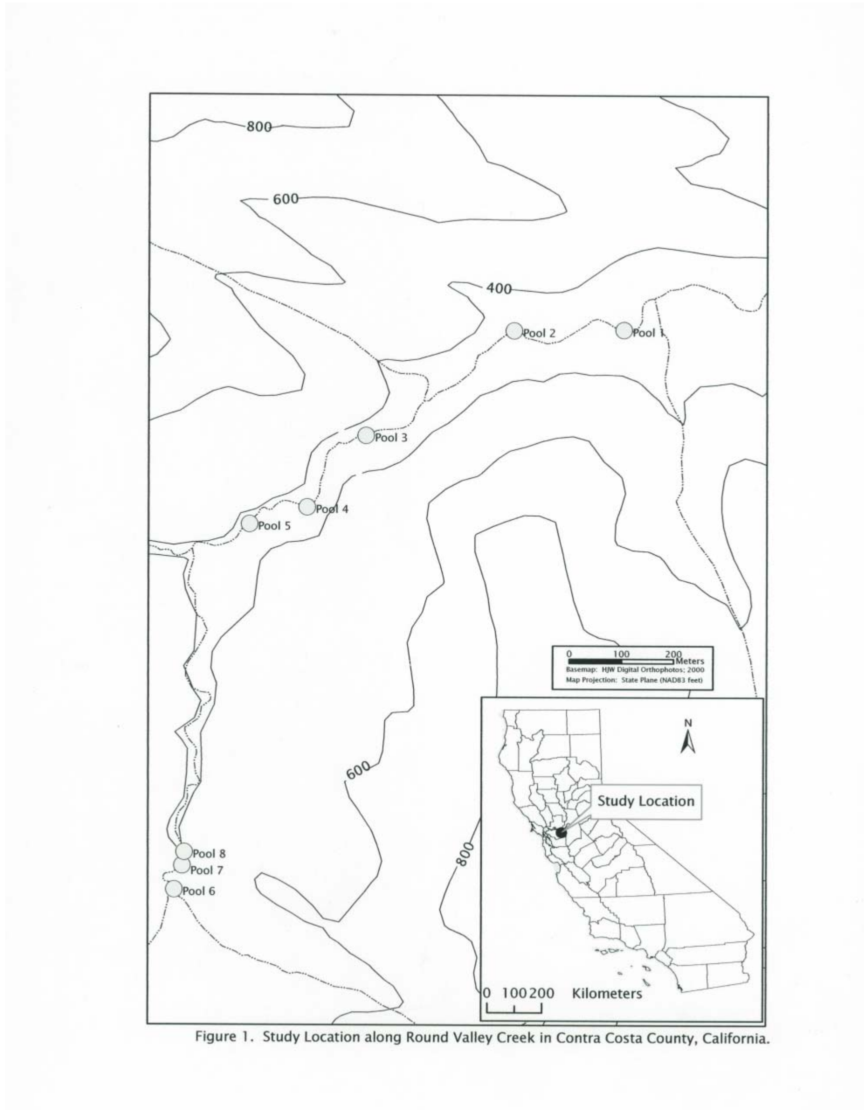

FIGURE 1. Map of study location showing pools along Round Valley Creek in Contra Costa County, California, USA, where *Rana draytonii* movements were tracked with radio-transmitters during 1999-2001.

frogs with radio-telemetry equipment. This formed an "observation period" for a particular individual.

Study site.—The study site was located in the northeastern portion of Contra Costa County, California, USA, in the Round Valley Regional Preserve (owned by the East Bay Regional Park District; Table 1, Fig. 1). Located in the foothills of the California Coast Range, within the rain shadow of Mt. Diablo, the study site receives an average of 40.13 cm of precipitation per year. I obtained climatic data from a weather station at the East Bay Regional Park Black Diamond Mines Regional Park, approximately 13.6 km northwest of the study area. Although this station is somewhat distant from the study site, the weather station receives the same rain shadow effects of Mount Diablo and the Black Hills Range located south of Round Valley as does my site.

Round Valley is aligned on a north-south axis along Round Valley Creek, which is the main drainage flowing from the Black Hills in the south, through Round Valley to the north, and into Deer Creek. Round Valley Creek, approximately 4 km in length, is an ephemeral drainage, with several pools that are perennial most years.

Plant communities within the Round Valley Regional Preserve consist of coastal and valley freshwater marsh along the edges of the creek, with freshwater plant species that include Watercress (*Rorippa nasturtium-aquaticum*), sedges (*Carex* sp.) cattails (*Typha* sp.) and rushes (*Juncus* sp.) in areas where the water level is constant, and Salt Grass (*Distichlis spicata*) in some places along the upland portion of the creek. A sparse riparian woodland occurs in discrete areas along the creek, consisting of willows (*Salix* sp.) and Cottonwoods (*Populus fremontii*), among other species. The majority of the site is vegetated with non-native grassland, which consists of oats (*Avena* sp.), brome (*Bromus* sp.), barley (*Hordeum* sp.), quaking grass (*Briza* sp.), and ryegrass (*Lolium* sp.), along with other invasive plants such as Yellow Star Thistle (*Centaurea solstistialis*), Red-stem Filaree (*Erodium cicutarium*), and Black Mustard (*Brassica nigrica*). Blue Oak (*Quercus douglasii*) savanna occurs mainly on north-facing slopes and is interspersed with California Buckeye (*Aesculus californica*). Interior Live Oak (*Quercus wislizenii*) occurs sparsely on south-facing slopes.

Round Valley Creek consists of distinct perennial and ephemeral pools that lay along an otherwise summer-dry channel. Six of the eight pools were perennial and Pool 5 was the largest perennial pool, with a surface area of 88 m^2. Pools 1 and 2 were ephemeral and Pool 1 was the larger of the two at 125 m^2. The average size of the perennial pool was 33 m^2 with an average maximum depth of 1.0 m.

Frog tracking methods.—To determine movement patterns, I attached Holohil Systems Ltd. model BD-2G radio transmitters (Carp, Ontario, Canada) to frogs and tracked them using a Wildlife Materials TRX 1000S receiver (Murphysboro, Illinois, USA) with a Wildlife Materials three–element Yagi antenna (Murphysboro, Illinois, USA). I attached transmitters to an aluminum beaded chain that I individually fitted around each frog's waist (Rathbun and Murphey 1996). To correct for numerous early failures of transmitter attachment, I modified the method of chain attachment by using marine-grade epoxy to cement a small monel wire loop to the transmitter and then placed the keychain through this loop. Transmitter weight was always < 10% of the animal's body mass (Richards et al. 1994).

I attached transmitters to the first adult frogs (> 70 mm snout to vent length, "SVL") captured in pools with the highest number of frogs (pools 2, 3, 4 and 6). Adults fitted with transmitters had a mass between 49-152 g. I used the presence or absence of a nuptial thumb pad to identify males and females. We considered frogs with an SVL >95 mm and lacking toe pads as females. All sex determination was double-checked during the third year and corrected as needed. In each year (29 attachments in Year 1, 20 in Year 2), I attempted to attach transmitters to equal numbers of males and females; however, in Year 2, many captured frogs did not meet the size criterion, which resulted in my capturing only five adult males. The transmitter batteries supplied continuous power for approximately 20-weeks. I recaptured most frogs and replace exhausted transmitters as needed to extend the duration of the study. Six transmitters were lost at the beginning of the season.

I identified individuals by using Passive Integrated Transponder (PIT) tags (Destron Model 8101D, Boulder, Colorado, USA). Due to equipment limitations, I used PIT tags but not transmitters in only one survey of 20 frogs in Pool 3 during Year 1. During this year, I assumed that the each of the 15 different males and 14 females with transmitters were all unique individuals.

TABLE 1. Distance between pools and pool dimensions at Round Valley Creek, Contra Costa County, California, USA. Distances were measured from GIS on a 2002 aerial photograph.

Pool	Width (m)	Length (m)	Max. Depth (m)	Direct Distance from Previous Pool (m)	Habitat Description
1	4.8	26	1.8	-	Intermittent with undercut banks and underlain by bedrock
2	3.8	7	1.8	209.9	Intermittent with undercut banks and underlain by bedrock. Aquatic rocks have ground squirrel burrows when pool is dry.
3	1.5-3.6	8.2	0.8	346.9	Perennial with waterfall and undercut banks and a ledge ~ 1.9 m in length, 22.8 cm in width and 43 cm below the top of bank. Downstream area supports freshwater marsh.
4	3.6	5.8	0.9	178.5	Perennial with a 0.8 m high bank located on the northwestern edge. Upstream area supports freshwater marsh. 70% tree canopy cover.
5	3.5	25.1	0.8	114.8	Perennial with of a 4.3 m vertical bank on the southeastern side and undercut banks. Downstream area supports freshwater marsh. 90% tree canopy cover.
6	1.2	4.5	0.8	643.6	Perennial with banks 3.5 m in height. 95% tree canopy cover.
7	8.3	3.0	0.8	26.2	Perennial with a 3.4 m high bank located on the western side. 90% tree canopy cover.
8	2.4	12.7	0.6	48.8	Perennial with undercut bank along eastern side. 95% tree canopy cover.

TABLE 2. Number and sex of tracked individual California Red-legged Frogs (*Rana draytonii*) at Round Valley Creek, Contra Costa County, California, USA.

Year	Tracked frogs Total	Males	Females
1 (1999-2000)			
Pool 1	0	0	0
Pool 2	2	1	1
Pool 3	25	13	12
Pool 4	0	0	0
Pool 5	2	1	1
Totals		15	14
2 (2000-2001)			
Pool 2	2	1	1
Pool 3	14	3	11
Pool 4	1	0	1
Pool 5	0	0	0
Pool 6	3	1	2
Pool 7	0	0	0
Pool 8	0	0	0
Totals		5	15

During Year 2, I used PIT tags to identify any frog in hand during transmitter attachment, resulting in 17 transmitters placed on 20 frogs (5 males and 15 females, Table 2).

Whenever I found a radio-tagged frog on land, every effort was made to determine its location without disturbing it or its surroundings. If no movement occurred after two survey periods (~ six days), I carefully verified that the transmitter was still attached to the frog. I assumed that all frog movements were linear between the source pool and the observed location. I used metric measuring tapes to determine the distance from the source pool and to known landmarks to map locations of frogs in Year 1. In Year 2, I recorded locations with a Garmin GPSMAP 76 WAAS global positioning unit (Olathe, KS, USA), with a nominal sub-3-meter accuracy. In both years, I recorded data on the landscape features used by frogs. I assumed that any transmitter that became separated from a frog was carried by the individual to the location from which I recovered it.

Microhabitat sampling procedure.—To determine frog terrestrial habitat use, I sampled a number of variables within plots used by frogs and plots randomly selected within the same area. I defined an "occupied" plot to be an 8 m x 8 m area centered on each terrestrial capture location. Within this area I characterized woody cover, plant cover, and number of burrows at each location. I characterized both small and large cover, such as logs. More than one frog used two of the plots, so the number of occupied plots is smaller than the number of terrestrial forays.

To locate the random plots within an area relevant to occupied plots, I calculated the average distance of the occupied plots in a direction perpendicular to the creek and calculated the 95% confidence limit for this value. This yielded a value of 44.3 m as the outer limits for the random sampling. Using the creek as a "y-axis" along the 2,200 m length within my study area, I chose one plot at random from 0-44.3 m perpendicular to the creek (an x-value) at each 50 m point along the creek. I established plots on alternate sides of the creek, starting 50 m from the upstream end of the study area, with the first location (east or west) determined at random.

I used measuring tapes to lay out plots on the ground. I measured slope, aspect, direction to source pool, direction to nearest pool, direction to creek, distance to source pool, distance to nearest pool, and distance to creek. I measured the distance from the creek to the plot with a measuring tape and using a range finder, and measured the horizontal distance. I estimated tree canopy visually from the center of the plot.

I measured other variables by positioning measuring tapes from north to south at the 1-7 m points of each plot and then recorded the data using a line intercept method. I recorded cover data, such as bark, fencepost, root, rock, bare ground, burrow, duff, herb and water, as well as; branch (up to 10 cm diameter), small log (11-25 cm in diameter), and large log (26-50 cm in diameter). Crisafulli (1997) served as the basis for these woody-debris categories.

The categories used for analysis comprised percentage cover data (canopy, bare ground, burrow, duff, herb and water), cover of surface objects (e.g. rock cover, woody cover [bark, fence post, root, branch, small log, and large log], and miscellaneous cover [barn door, metal can and cement block]). I measured the area of the cavity underneath an object and identified it as shelter cover that provided refuge and included woody shelter cover, other shelter cover and total shelter cover (woody shelter cover plus other shelter cover). I measured the diameter of the exposed openings of subterranean cover, which included burrows of California Ground Squirrels (*Spermophilus beecheyi*), crevices, and microtine burrows to obtain an area of cover. Subterranean count was the number of available openings of burrows.

To determine if frogs favored a specific hillside aspect (north-facing versus south-facing), I converted the aspect of a hillside at all plots into an arbitrary code for easier analysis, with north being the aspect with a reduced solar exposure, equaling the highest value of 2, and south equaling the lowest value of –2. West and east each received a value of 0, southwest and southeast received each a value of –1, and northeast and northwest each received a value of 1.

Analysis of data.—I used parametric statistics when assumptions of normality were met, based on the Shapiro-Wilk test, and non-parametric tests when they were not. I performed statistical tests and associated properties of the data with JMP Version 4 (SAS Institute, Inc). Data evaluation involved t-tests and Kruskal-Wallis test. For all habitat components, I

TABLE 3. Summary of total tracking days of individual frogs. "F" denotes female; "M" denotes male. One survey period = 3-4 days. A * denotes lost signal.

Frog I.D.	Weight (grams)	Tracking Initiated	Total Tracking (days)	Total Survey Periods
		Year 1		
F1	107	27 Aug. 1999	4	1*
F2	148	27 Aug. 1999	162	41
M3	84	27 Aug. 1999	50	13
M4	61.6	27 Aug. 1999	13	2
M5	73	7 Sept. 1999	12	5
F6	107.5	7 Sept. 1999	118	28
F7	152	13 Sept. 1999	134	40
F8	118	27 Sept. 1999	12	3
F9	149	8 Oct. 1999	7	5
F10	139	15 Oct. 1999	3	1
M11	111	18 Oct. 1999	39	12
M12	93	18 Oct. 1999	112	28
M13	90	18 Oct. 1999	79	20
F14	112	18 Oct. 1999	10	3
F15	122	18 Oct. 1999	35	11
M16	87	18 Oct. 1999	25	6
F17	115	18 Oct. 1999	21	7
M18	NA	28 Oct. 1999	102	25
M19	85	19 Nov. 1999	79	22
F20	102	22 Nov. 1999	4	1
M21	86	26 Nov. 1999	15	4
F22	141	29 Nov. 1999	14	5
M23	NA	5 Jan. 2000	73	16
M24	57	18 Feb. 2000	28	7
F25	90	18 Feb. 2000	58	11
M26	58	21 Feb. 2000	14	6
M27	64	21 Feb. 2000	14	6
M28	69	7 Mar. 2000	32	7
M29	66	17 Mar. 2000	7	2
		Year 2		
F30	115	28 Sept. 2000	162	32
M31	73	28 Sept. 2000	145	31
M32	71	28 Sept. 2000	140	31
F33	114	28 Sept. 2000	53	22
F34	105	4 Oct. 2000	135	30
F35	120	4 Oct. 2000	112	25
F36	120	20 Oct. 2000	147	28
F37	95.5	23 Oct. 2000	130	27
F38	133	7 Nov. 2000	132	25
M39	96	7 Nov. 2000	134	14
F40	117.5	20 Nov. 2000	92	17
M41	80	20 Nov. 2000	98	22
F42	110	21 Dec. 2000	78	19
F43	114	1 Feb. 2001	48	12
F44	118	26 Feb. 2001	25	8
F46	99	12 Mar. 2001	87	11
M47	74	12 Mar. 2001	35	3*
F48	142	15 Mar. 2001	35	9
F49	116	26 Mar. 2001	24	5

transformed each variable to natural logs and conducted a t-test between the two types of plots, frog and random. I compared habitat use and water temperature with a Pearson correlation. Comparisons between occupied frog plots and random plots were made using a paired z-test when different averages and standard deviations occurred in each sample. For all averages, I provided the standard deviation (mean ± SD).

Definitions.—Several terms hereafter describe my tracking results. A "survey period" was a 3-4 day interval during which I found each frog. An "observation" was a frog location during one survey period (i.e. 20 frog observations occurred during one survey period). A "movement" was an event in which one frog moved to a new location since the previous survey period. A "tracking unit" was a single frog location determined by a transmitter signal in one observation period. I used "tracking rate" to depict the number of times I found an individual. Terrestrial movements between the source pool and upland habitat were "forays." "Dispersal movements" were aquatic movements, movements between pools, or relocation from a source pool to a new breeding pool.

RESULTS

The total number of frogs observed in each pool varied by year and among pools (Table 2). Of the 15 males and 14 females radio-tagged in Year 1, I obtained 59 observations and 345 tracking units. In Year 2 I had 45 observations and 386 tracking units. Transmitter retention averaged 43 days in Year 1 and 98 days in Year 2. The number of tracking units ranged from 2-41 per individual in Year 1 and from 1-32 per individual in Year 2.

Size comparisons of moving and non-moving frogs.—More than half of the 49 radio-tagged frogs (57%) remained at their source pools, whereas 21 frogs (12 females and 9 males) moved to upland habitat or to new pools. I evaluated associations between frog size and movement behavior. During the two years, I obtained body mass (BM) and snout-vent lengths (SVL) of 28 females (BM = 118 g ± 16.7.) and 18 males (BM = 77.82 g ± 14.3). There was no significant difference between the BM of the females that moved and those that did not (Table 4), nor was there a significant difference between the SVL of the moving and non-moving females (Table 4). There also was no significant difference for males' BM and SVL (Table 4) between frogs that moved and those that did not. There was no significant difference between those frogs that moved and those that did not ($t = 0.68$, df = 46, $P = 0.002$).

Seasonal patterns of movements.—All movements of frogs from their source pool began after the first 0.5 cm of rain during fall months (between September and November; Fig. 2). For both years combined, I observed 43 terrestrial forays. Thirty-six movements were pool-to-land, or land-to-pool, and seven were land-to-land movements. There were 18 aquatic movements (pool-

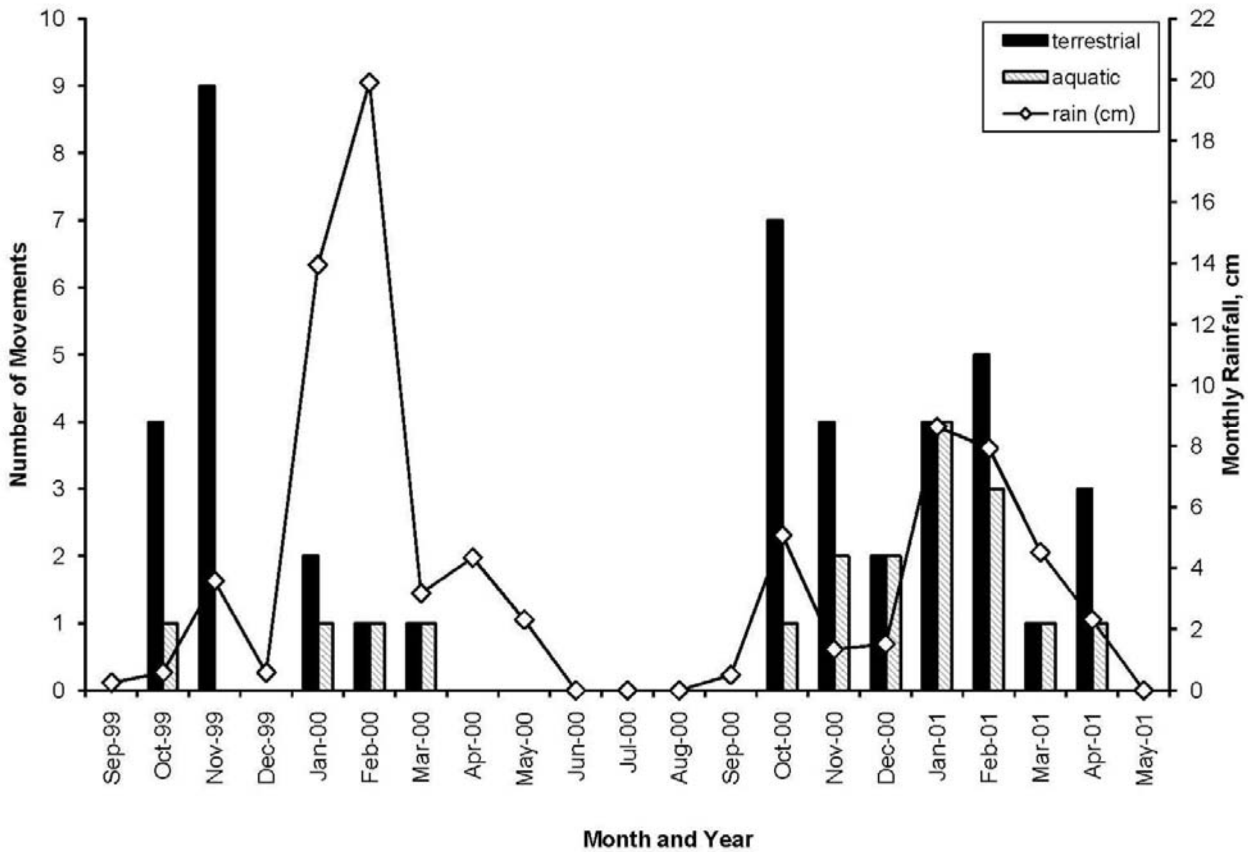

FIGURE 2. Number and seasonal timings of terrestrial movements of radio-tagged *Rana draytonii* at Round Valley Creek, Contra Costa County, California, USA, shown with rainfall amounts between September 1999 and May 2001.

to-pool or pool-to-creek). Twenty-four of the 43 terrestrial forays (which counts a round trip as two movements and includes multiple movements by the same individual) were made during the fall rains by 12 individuals (seven females and five males, all of which moved back to their sources pools; often the nearest pools), during the same season (Table 3). Terrestrial forays occurred more frequently during fall rains (57%) than during winter (between December-February; 32%) or spring rains (March-April; 11%).

Four of the 18 aquatic movements (22%) occurred during the fall, and involved three individuals. Seven individuals accounted for eleven aquatic movements (61%) during the winter. Only three aquatic movements (16%) occurred in the spring. Irrespective of season, eight movements were relocations to new pools. The latest seasonal movements occurred in February of Year 1 and April of Year 2.

Spatial patterns of terrestrial movements.—The majority of the terrestrial movements occurred for a single observation period and consisted of single forays from the source pool to land and then back. Frogs used 16 terrestrial sites that are identified as "occupied plots" in the Habitat Analysis. In the fall of the first year, I tracked six frogs to six different sites (numbers 3, 4, 5, 6, 7, and 11); I tracked four frogs to seven different sites (numbers 9-10, and 12-15) in the fall of the second year, and three frogs to three sites (numbers 1, 8 and 16) in the winter of the second year. One frog used one plot (number 2) in the spring. One female used four different sites (numbers 1, 12, 13, and 14), two females used the same sites at two different occasions (numbers 2, 11), another female used two different sites (numbers 15 and 16), while three males used Plot 8, and two males used Plot 10. Most movements originated from pools 3 and 6. Ten frogs from Pool 3 moved to eight independent plots (Fig. 3) and two frogs from Pool 6 moved to six independent plots (Fig. 4).

Terrestrial microhabitats chosen by the frogs were quite variable. These included a barn door laying on the ground that had what appeared to be a ground squirrel burrow under it; five different ground squirrel burrows (one occurring under a boulder and the others were at the bases of trees); and two large logs (including an erosion control log jam). Of the eight sites occurring in non-

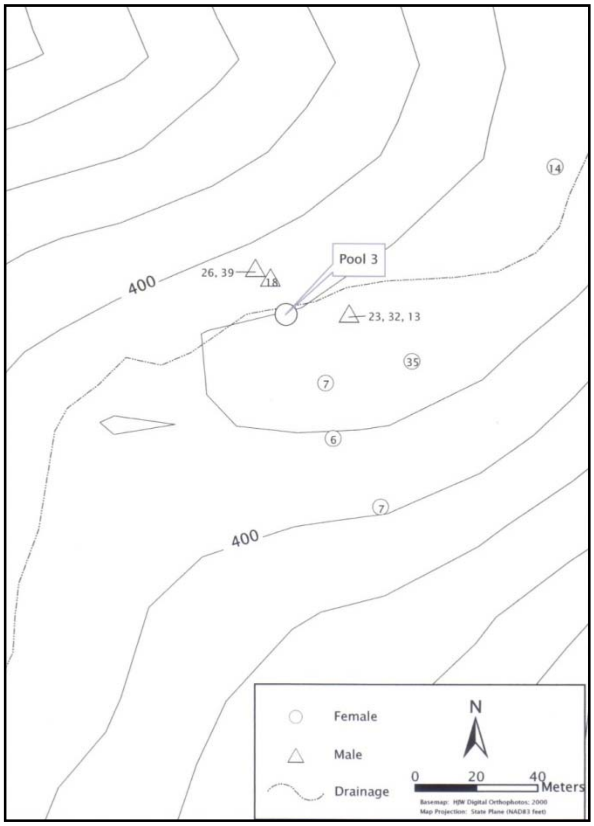

FIGURE 3. Terrestrial movement patterns of individual *Rana draytonii* away from Pool 3 within Round Valley Creek., Contra Costa County, Callifornia, USA. Numbers denote individual frogs, with males identified as triangles and females identified as circles. Multiple numbers at one location shows more than one frog using the site.

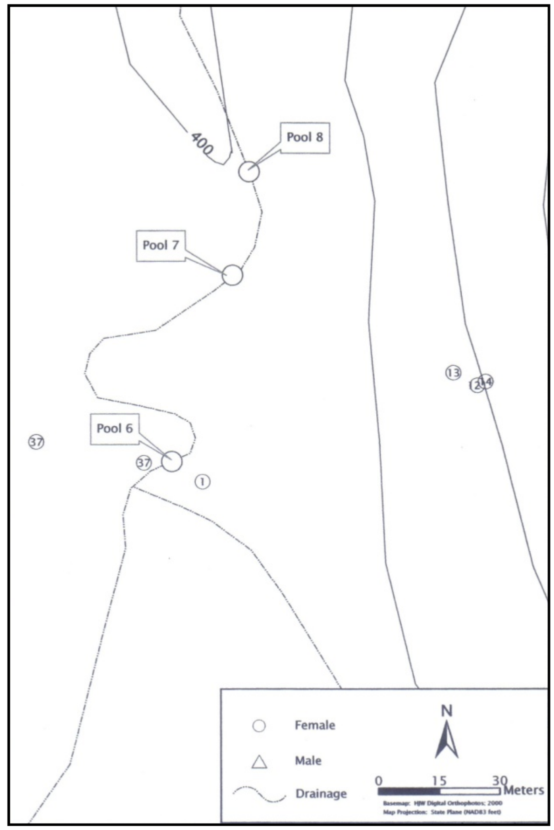

FIGURE 4. Terrestrial movement patterns of female *Rana draytonii* away of Pool 6 within Round Valley Creek, Contra Costa County, California, USA. Numbers identify individual frogs that moved from Pool 6.

native grassland, one had a frog in a cow hoof print, another had a frog underneath a thatch of grass and one had a frog in a crevice in the ground. Other sites in grasslands lacked any shelter.

TABLE 4. Mean (SD) of weight and length comparisons of *Rana draytonii* between movers and non-movers for all years and test results between movement types.

	N	Weight (g)	Length (mm)
Females			
Move	11	115.8 (18.08)	103.0 (3.00)
Non-move	18	121.5 (14.01)	105.1 (5.59)
		t = 0.882 df = 27 P = 0.3854	Z = -0.843 s = 146 P = 0.3989
Males			
Move	5	83.4 (20.01)	92.8 (4.43)
Non-Move	13	76.0 (21.33)	89.5 (6.52)
		t = -0.953 df = 16 P = 0.3548	t = -1.045 df = 16 P = 0.3117

Distances of movements.—Average terrestrial distances were larger during the pre-breeding season (41.8 m) than in the breeding season (13.5 m) or post-breeding season (16.3 m), with greater distances travelled in the second year (Fig. 5). The average terrestrial distance moved was 24.38 ± 20.74; range 1-71 m) and the average aquatic distance moved was 107.2 ± 152.08 (range 11-661.4 m).

Females moved 21 different times terrestrially with an average distance of 37.3 ± 32.8 m (range 2-94 m). Males made six terrestrial movements, with an average distance of 14.4 ± 5.8 m (range 4.57-19 m). Females made 15 aquatic movements with an average distance of 52.98 ± 63.10 m (range 3.65-269.3 m). Most of these were pool to creek movements; only two females moved from one pool to another. Most males with transmitters (72.2%, 13/18) stayed at their source pool. However, the three males that did move made larger aquatic excursions than females, with males moving an average distance of 180.7 ± 277.06 m (range 11.9-661.4 m). This greater average distance appears to reflect relocation to breeding pools, and without an observed

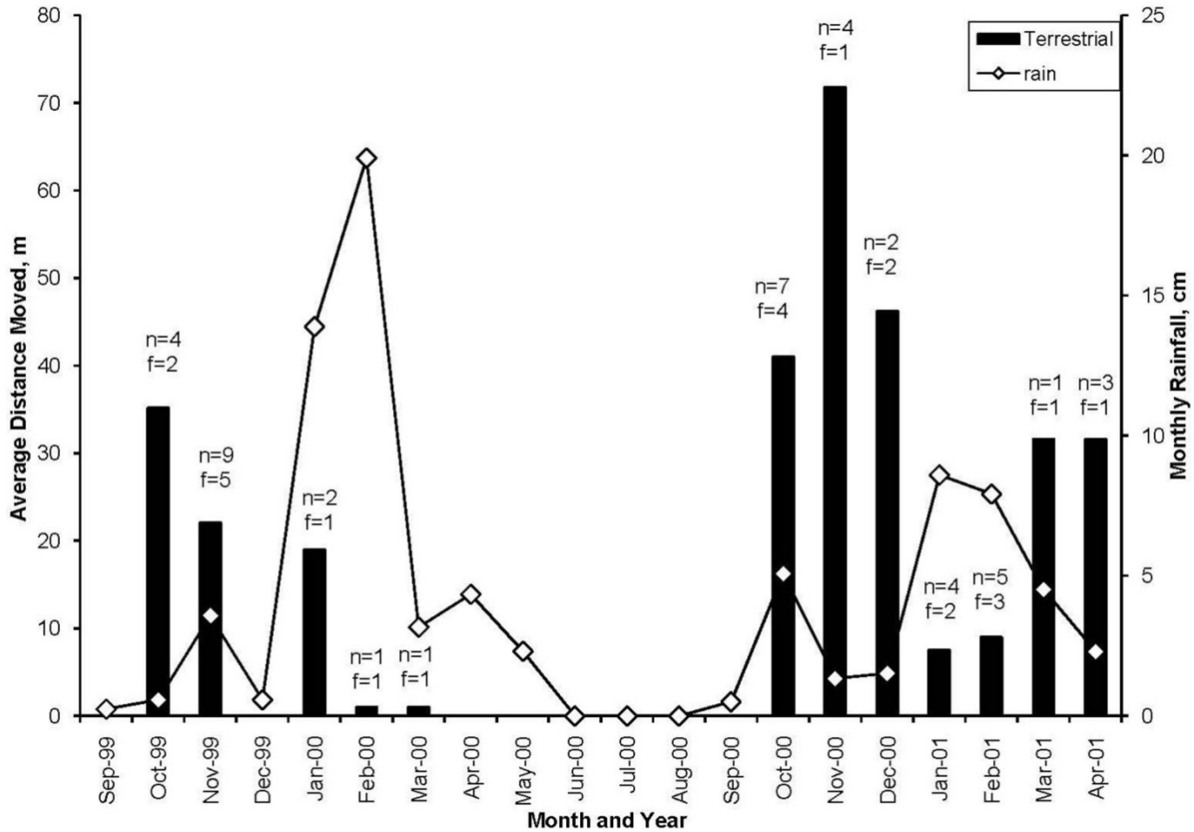

FIGURE 5. Average distances of terrestrial movements of *Rana draytonii* by month shown with monthly rainfalls between September 1999 and May 2001. For each month n = number of movements, f = number of frogs involved in these movements.

return trip. Two radio-tagged males moved to new pools in Year 1, one 200 m downstream (from Pool 5 to Pool 4), the second 661 m downstream (from Pool 3 to Pool 1).

Duration of terrestrial movements.—Data on the time frogs spent away from their source pool or creek imply that individuals in this population do not leave their summer aquatic habitat for new over-wintering habitat. Time spent on land away from the source pools in Year 1 ranged from 1-4 days (one survey period). The time spent on land in the second year was 3-28 days (1-9

survey periods). Eleven of the 16 frogs (five females, six males) moved terrestrially for only one survey period, returning to water the following survey period. Some frogs exhibited this single-period pattern several times. Males stayed on land from 1-4 days. Two females made terrestrial forays that encompassed two different survey periods. One female stayed in upland habitat for up to 50 days (eight survey periods) in Year 2, beginning from the first rains in October. She remained in grassland habitat until December, when she relocated to a pool downstream from her source pool. Then she moved from the pool into a ground squirrel burrow in January and stayed there until February (nine survey periods) before relocating to her source pool (Fig. 6).

Microhabitat use and site fidelity in pools.—I made qualitative observations on some microhabitats used during this study. Prior to the first rains, as many as 18 frogs simultaneously used a ledge that was at, or slightly above, the water level of Pool 3. An overhanging bank protected this ledge. Prior to the first rains, frogs in Pool 3 used other microhabitats included smaller ledges and cavities underneath rocks at the water's edge. After the first rains, many of these ledges were below water and frogs did not use them for the rest of the winter season. The swift current and high water levels may preclude frogs from using these potential refuges because they used cavities under rocks at the water's edge and at the bottom of the pool when they were flooded. Frogs at other pools (pools 1, 2, 4, 5, and 6) also used ledges before the water rose. Similar to Pool 3, frogs used other shelters including overhanging branches at the water level or under overhanging grass along the bank.

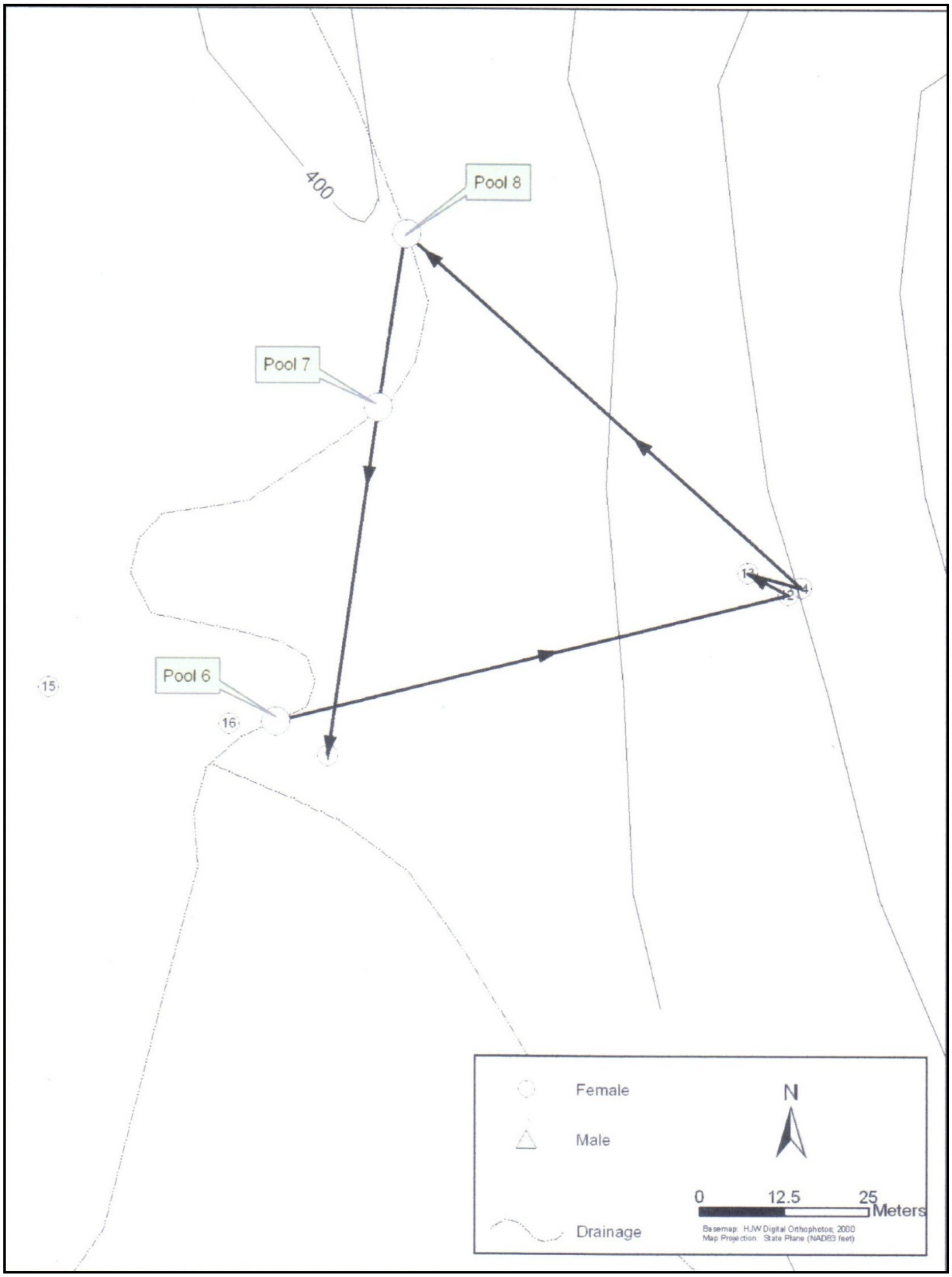

FIGURE 6. Movement patterns of female *Rana draytonii* #36 away from pool 6 to upland habitat, to pool 8, and into new upland habitat. She eventually returned to pool 6, Round Valley Creek, Contra Costa County, California, USA.

As temperatures decreased during the first winter, several individuals hid under an underwater rock on the bottom of Pool 3. Of the two large rocks located at the southern end of this pool, one contained a cavity underneath the rock that was easily accessed by the frogs. Frog inactivity was significantly correlated with water temperature ($r = 0.80$, $F = 37.2$, $P < 0.0002$). On 1 December (water T = 8°C), 22% (2/9) of frogs with transmitters occurred beneath the same rock. On 6 December (water T = 6° C), 56% (5/9) frogs used this rock. These five frogs aggregated under this rock over the following eight days (three survey periods), and two frogs remained under the rocks for another six days (two survey periods).

TABLE 5. Season of movements and number of *Rana draytonii* by habitat and the percentage (%) of frogs with transmitters of both sexes combined.

			Moving Frogs			
Season	Habitat	Year	Females	Males	Total	%
Fall	Terrestrial	1	4	3	7	24
		2	3	2	5	25
	Aquatic	1	-	1	1	3
		2	2	-	2	10
Winter	Terrestrial	1	-	2	2	7
		2	2	1	3	15
	Aquatic	1	-	2	2	7
		2	5	-	5	25
Spring	Terrestrial	1	-	1	1	3
		2	2	-	2	10
	Aquatic	1	-	1	1	3
		2	2	-	2	10

Site fidelity within Pool 3, the pool with the most radio-tagged frogs, was high. Twenty-four of 49 frogs were not only site-faithful to the pool, but they were position faithful within the pool. During the first year, nine individuals stayed at a specific location for an average of eight survey periods (an average of 47% of the total time surveyed for each frog). One individual stayed at two locations for 5-6 survey periods. During the second year, eight frogs stayed at the exact location for eight survey periods (an average of 34% of the total time surveyed for each frog). Four individuals moved to different location. Three of these individuals moved terrestrially and came back to a different location within the pool. One individual relocated to a new pool after being found in a different location within the source pool. Three other frogs moved among many locations within a given pool (19, 15 and 3 different sites, respectively) after either aquatic or terrestrial movements. Individuals within pools 2, 3, 4 and 7, repeatedly remained within specific areas of the pools, even outside of the breeding season. These areas were primarily along the undercut banks and overhanging vegetation. One nocturnal observation at Pool 3 revealed 27 frogs following the same path while moving up onto the western hillside above the pool.

Quantitative analysis of terrestrial habitat.— Comparison of plots where frogs occurred and random plots provided information on whether or not the frogs chose a particular feature of the terrestrial environment. There were no significan differences between occupied plots (n = 16) and random plots (n = 19) in slope (t = 1.40, *P* = 0.171), aspect (t = 0.22, *P* = 0.827), or elevation above the creek (t = 0.87, *P* = 0.387). Occupied plots were significantly closer to the creek (mean = 39.6 ± 33.4 m) than random plots ($\bar{x}$ = 56.2 ± 19.8 m; *z* = -2.0367, *P* = 0.0417). Occupied plots were closer to the nearest pool, ($\bar{x}$ = 14.03 ± 2.09 m) than were random plots ($\bar{x}$ = 21.3 ± 2.1 m; *z* = -2.08, *P* = 0.036). These results suggest that in a broad sense, frogs use habitats in the vicinity of aquatic areas.

Frogs moved onto cooler slopes. Evaluation of the slope of the hillsides to which the frogs moved revealed that 31% (5/16) occupied plots were onto northern-facing slopes, 19% (3/16) plots were on eastern-facing slopes, 12.5% (2/16) plots were on southern-facing slopes, and 37.5% (6/16) plots were on western-facing slopes. The average aspect was 0.37 ± 1.02 for occupied plots and 0.11 ± 1.19 for random plots. Frogs preferred somewhat cooler plots. Evaluated in terms of frog locations (more than one frog used some plots) the data are as follows: northwest-facing slopes had eight frogs, north-facing slopes had three frogs, southeast-facing slopes had six frogs, west-facing slopes had three frogs, and east-facing slopes had one frog.

There were no significant differences between the plots used by frogs and the random plots for any one habitat component (e.g., "branch", 'rocks" and "root"). Vegetative cover ("canopy", "duff" and "herb") was similar among the plot types. However, after grouping variables together into various categories (Fig. 7), I found that occupied plots had more total object cover (mean = 0.708 m^2) than random plots (mean = 0.307 m^2; *t* = 2.509, df = 33, *P* = 0.015). Total shelter cover was significantly higher in occupied plots (mean = 0.21 m^2) than in random plots (mean = 0.059 m^2; *t* = 2.033, df = 33, *P* = 0.0502), but total subterranean cover was not significantly different between occupied plots (mean = 0.018 m^2) and random plots (mean = 0.008 m^2; *t* = 1.47, df = 33, *P* = 0.15).

DISCUSSION

This research provides a clearer understanding of terrestrial movements of *Rana draytonii* in an inland environment. This research may help determine patterns of recolonization and metapopulation dynamics that are important for making better management decisions. My study revealed no sex-specific differences of SVL or BM between moving and non-moving frogs. This was similar to previous reports of *R. draytonii* in Marin County (Fellers and Kleeman 2007), in Santa Cruz County (Bulger et al. 2003), and for other ranids (Spieler and Linsenmair 1998).

During this study I observed no migration of *R. draytonii*. Movements to and from breeding habitats were aquatic and took place in the same stream corridor. However, this population used upland habitats during the non-breeding season. Individuals made terrestrial forays and returned to source pools, which were often the

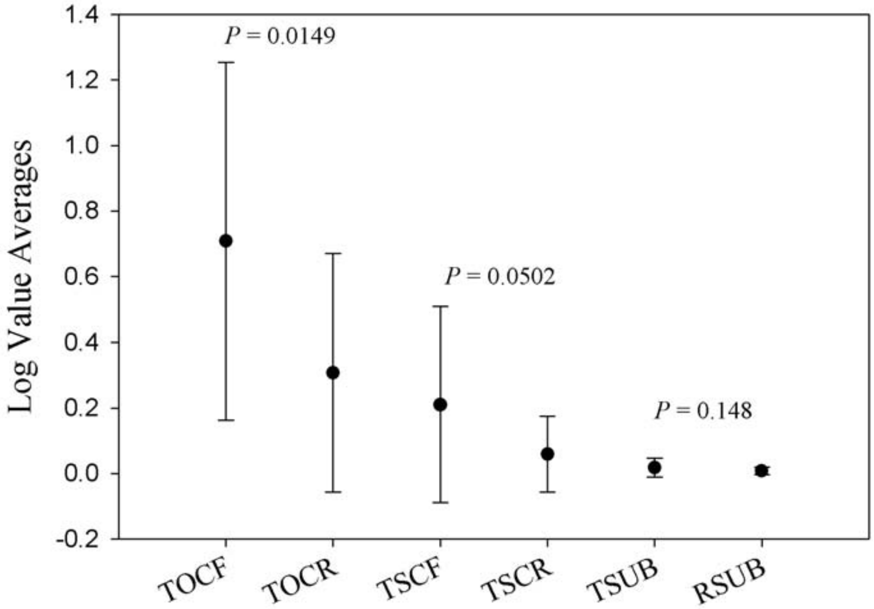

FIGURE 7. Habitat comparison between plots that housed California Red-legged Frogs (*Rana draytonii*) and random plots at Round Valley Creek, Contra Costa County, California, USA. Significant differences occurred between plots containing frogs and random plots based on total object cover and total shelter cover, but not on total subterranean cover. The cover values were natural log transformations and compared with a t-test. Lines represent one standard error. TOCF = Total object cover where frogs were present, TOCR = Total object cover in random plots, TSCF = Total shelter cover where frogs occurred, TSCR = Total shelter cover in random plots, TSUB = Total subterranean cover where frogs occurred, and RSUB = Total subterranean cover in random plots.

nearest available pools. Males dispersed aquatically to a new breeding pool and stayed there until the end of the breeding season. Some individuals may move away from the source pool during a tracking period; whereas, others remain in the same location for extended periods. At Pool 3, 57% of nonmoving individuals occurred in specific areas within the pool 47% of the time during the first year and 34% of the time during the second year.

The majority of females in my study that made terrestrial forays went back to the source pool for breeding, which was often the pool closest to their terrestrial site. However, it was unclear whether females relocated to their source pool in response to male choruses or based on site fidelity to their breeding habitat. Six females made multiple terrestrial forays and moved back to their source pools. One female moved terrestrially for 50 days, then moved to a downstream pool, after which she moved to a new terrestrial site and then returned to her source pool. Breeding site fidelity is known in other amphibians (Forester 1977; Juterbock 1987; Trauth et al. 2006).

Of the frogs that left their breeding pool, either terrestrially or aquatically, movements typically began after the first 0.5 cm of rain of the season. A similar pattern occurred in the *R. draytonii* population in Santa Cruz (Bulger et al. 2003), where fall and winter rains stimulated the initial terrestrial movements of a small percentage (~ 25%) of the sampled population, with the highest percentage of movements (56%) occurring in the fall. This observation is consistent with other reported movements of amphibians. For example, in Marin County, *R. draytonii* movement > 30 m generally coincided with winter rains, although some frogs only moved when the pond began to dry (Fellers and Kleeman 2007).

Two possible hypotheses may explain the movements of frogs away from their source pools. The first suggests that frogs move out of the streams to avoid initial flood-waters and the instream scouring effects of winter storms. The second hypothesis suggests that frogs move onto land to feed.

If frogs avoid flooding, then perennial pools in streams may not be used for breeding. In the Santa Cruz County study area, *R. draytonii* did not use perennial stream habitat for breeding and the scouring flows that occur during the breeding season reduces the habitat suitability for breeding (Bulger et al. 2003). In Marin County, although *R. draytonii* used the riparian zone along the creek for post-breeding habitat, the primary breeding areas were stock ponds (Fellers and Kleeman 2007). Although I found several individuals moving onto land after a rain period, not all of the radio-tagged frogs moved from the creek during rains. In addition, the frogs in my study did breed in the perennial pools in this seasonal creek, despite the potential for scour. Therefore, my study appears to refute this hypothesis.

If this species is moving to upland habitat to forage, then individuals would be observed to move relatively short distances. Waterfall Frogs (*Litoria nannotis*) have been reported moving into upland habitat to forage during rain events (Hodgkison and Hero 2001). I found frogs to be highly aggregated in their source pools, a condition that could limit food abundance. Furthermore, females made more forays than males and most of these occurred in fall, prior to the breeding season. These movements could be related to their greater energetic need for egg production, as has been shown in female Small-mouthed Salamanders (*Ambystoma texanum*) (Finkler and Cullum 2002).

Frogs moved greater terrestrial distances (41.8 m) to non-aquatic habitats in the fall, and smaller distances during the winter and spring. My findings are similar to those of Rathbun et al. (1993) who reported movements up to 26 m away from the stream in early November, and sustained terrestrial foraging activity until early December. Bulger et al. (2003) found non-migrating individuals moved the greatest distances (130 m) during summer and fall rains, and terrestrial distances were smaller during the breeding season, with 90% of radio-tracked frogs found within 6 m of water. Fellers and Kleeman (2007) tracked one female for 16 months, during which she made a single 110 m excursion, but not to a breeding pond.

Some site fidelity exists in other species. Fidelity to seasonal pools by Oregon Spotted Frogs (*Rana pretiosa*) was 40% during the breeding season, 57% in dry season, and 57% in the wet season (Watson et al. 2003). This could result from habitat preference or reflect that some microhabitats had more amenable physical dimensions to shelter the frogs (Spieler and Linsenmair 1998). Research on the Crowned Bullfrog (*Hoplobatrachus occipitalis*) revealed that if retreats with suitable properties were limited, then they would be used continuously by the same individuals or simultaneously by more than one frog (Spieler and Linsenmair 1998). Site fidelity shown in my study may be a reflection of the limited retreat sites in Pool 3.

The inactivity of frogs in my study during December of the first year was correlated with water temperature. As water temperatures decreased during the winter months, frogs aggregated together underneath the same rock under water, despite the availability of other rocks providing similar aquatic habitat. A similar finding in Mountain Yellow-legged Frogs (*Rana sierrae*) found groups of more than eight individuals under a single ledge (Mathews and Pope 2001). This behavior may somehow protect them from freezing temperatures (Mathews and Pope 1999). Oregon Spotted Frogs occurred deeper when surface temperatures were 0-3°C colder than subsurface temperatures. Water surface temperatures at my study site were near freezing during the coldest periods, and it is possible that the frogs were escaping extreme nighttime cold temperatures.

Frog-occupied plots contained more "total object cover" and "total shelter cover" than randomly-located plots in surrounding areas. Atypical objects (e.g., log jams, barn doors) and natural objects (e.g., large logs, boulders, roots) provided cover. Daytime shelters in harsh environments are important because they provide anurans and other amphibians with opportunities for thermal regulation, and protection from desiccation and predators (Spieler and Linsenmair 1998). Frogs that select terrestrial shelters may ameliorate water loss. .

Most frogs (31%) in plots with no cover objects were on north-facing slopes. In the northern hemisphere, these areas are more mesic than south-facing slopes, thus shelter from the drying effects of the sun is less critical. Consequently, frogs on north-facing slopes may not require shelter to avoid desiccation. Some frogs that moved to xeric south-facing slopes found refuge in ground squirrel burrows. Although some ground squirrel burrows occurred nearer to pools than other types of cover, frogs did not use these burrows as often as more distant cover types. In Marin County, *R. draytonii* found shelter in small mammal burrows, Coyote Brush (*Baccharis pilularis*), and small clumps of grass (Fellers and Kleeman 2007); whereas, in Santa Cruz County, *R. draytonii* used plants (79%) and woody debris (14%) to conceal themselves (Bulger et al. 2003). Both Marin County and Santa Cruz counties are more xeric than at my study site and may reflect more vegetated habitats in which the frogs may seek refuge.

Conservation Recommendations.—I recommend inclusion of several key components for aquatic and terrestrial buffer zones protecting *Rana draytonii*. First, breeding and non-breeding habitat must be connected to provide migration and dispersal corridors (Rittenhouse and Semlitsch 2007). A viable buffer zone in this study site would encompass the known breeding pools and the aquatic habitat in between at a width to ensure the quality of the riparian habitat. Second, a minimum of 92 m of upland habitat must surround aquatic habitats to maintain the upland habitat quality for populations in this area and should extend the length of the creek. Finally, object cover, such as downed trees, logs, and boulders must exist to provide protection from predators and desiccation. Based on my data, ground squirrel burrows should not be considered as wholly suitable cover.

Acknowledgements.—I thank my committee members: Phil Northen for his guidance and support of this project, Dan Crocker and Nathan Rank for their assistance with the analysis, and Derek Girman for his recommendations throughout the project. I also thank Phillip Leitner for equipment loans, East Bay Regional Parks for access to Round Valley Regional Preserve, Swaim Consulting for making figures, and Sycamore Associates for equipment. I also thank the U.S. Fish and Wildlife Service and California Department of Fish and Game for authorizing this study through issuance of a 10(a)(1)(A) permit (PRT-TE802089-2) and Scientific Collectors Permit (801103-02). The handling of individuals complied with the Society for the Study of Amphibians and Reptiles (SSAR) Guidelines for Use of Live Amphibians and Reptiles in Field Research (www.iacuc.ucsd.edu/PDF_References/ASIH-HL-SSAR).

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APPENDIX 1. Identity of frogs and their terrestrial sites used in establishing frog plots. "Pool" is the source pool from which the frogs moved. A "-" denotes a plot-to-plot movement.

Plots	Frog I.D.	Pool	Year
1	F36	6	2
2	F48	2	2
3	F7	3	1
4	F14	3	1
5	F7	3	1
6	F6	3	1
7	M18	3	1
8	M23, M32, M13	3	2
9	F35	3	2
10	M26, M39	3	2
11	F17	5	1
12	F36	6	2
13	F36		2
14	F36	6	2
15	F37	6	2
16	F37	6	2

TRISH TATARIAN is a wildlife biologist out of the San Francisco Bay Area, California, USA. She has degrees from Sonoma State University (M.S.) and San Francisco State University (B.S.). As a general ecologist, Trish started in biology studying Peregrine Falcons (*Falco peregrinus*) and raptor movements. She has since focused on the enigmatic amphibians of California and is currently conducting research on the ecology of California Red-Legged Frog in the Sierra Nevada.

APPENDIX 2. Distance and direction frogs moved into terrestrial habitat.

Plot #	Sex/ID	Pool	Distance Moved (m)	Direction Frog Moved	Slope	Survey Periods
1	F36	6	9	E	NW	7
2	F48	2	31.6	SE	N	1
2	F48	2	31.6	SE	N	1
3	F7	3	58.8	SE	NW	1
4	F14	3	102	NE	N	1
5	F7	3	33.1	SE	NW	2
6	F6	3	30	SE	NW	1
7	M18	3	11.55	NW	SE	1
8	M13	3	19	E	NW	1
8	M23	3	19	E	NW	1
8	M32	3	19	E	NW	1
9	F35	3	44.5	E	NW	2
10	M26	3	1	NW	SE	1
10	M39	3	1	NW	SE	1
11	F17	5	11.6	NW	SE	1
11	F17	5	11.6	NW	SE	1
12	F36	6	85.95	NE	W	3
13	F36	6	76.9	N	W	3
14	F36	6	91.4	NE	W	5
15	F37	6	22.6	W	E	1
16	F37	6	4	W	SE	1

Appendix 3. Individual movement distances of frogs and number of survey periods associated with each movement. A "*" denotes a continuous foray. Terrestrial movements are pool-to- land (PL), land-to-land (LL) and land-to-pool (LP).

Frog I.D.	Terrestrial (m)	Aquatic (m)	# of Survey Periods	Notes
Year 1				
F6	30.3 (PL)	-	1	
F7	58.7 (PL), 33.93 (PL)	-	1, 2	
M11	-	33.4	4, off frog	Found off frog after 4 survey periods
M13	19 (PL)	20.1	1, off frog 1	
M16	-	200	relocated	Moved to new pool
F17	11.6 (PL), 11.6 (PL)	-	1, 1	
M18	11.6 (PL)		1	
M23	19 (PL)	661.4	1, relocated	Moved to new pool
M24	-	11.8	1	
M26	4.6 (PL)	-	1	
Year 2				
F30	-	36.5	1	
M32	19 (PL)	-	1	
F33	-	43.9	4	
F34		70.4, 269.8	4, 16	Frog stationary after initial movements in each case
F35	44.5 (PL)	-	2	
F36	85.9 (PL), 91.4 (LL), 9 (PL), 2.4 (LL)	15.8, 7.9	3*, 5*, 7*, 1*	
F37	22.6 (PL), 3 (LL), 5.4 (PL)	36.5	1,* 1*, 1	
M39	1 (PL)	-	1	
F40	-	43.89, 43.89	1, 1	
F44	-	48.1	16	
F48	31.6 (PL), 31.6 (PL)	-	1, 1	Separate movements

Appendix 4. Year 1 use of a specific rock in Pool 3.

Date	Frog ID	# of Frogs	# Frogs With Transmitters in Pool 3	Air °C	Water °C
12/1/99	18M, 23M	2	9	8	8
12/6/99	2F, 18M, 19M, 23M, 27M	5	9	13	6
12/10/99	19M, 22F	2	7	6	7
12/13/99	2F, 18M, 19M, 23M	4	6	7	8
12/20/99	18M, 23M, 27M	3	6	12	7
12/27/99	2F, 17F, 18M, 19M, 23M, 27M	6	6	4	3
12/30/99	2F, 17F, 18M, 19M, 23M, 27M	6	6	12	4
1/3/00	2F, 17F, 18M, 19M, 23M, 27M	6	6	4	4
1/5/00		0	6	11	9
1/12/00		0	6	11	8
1/14/00	19M	1	6	9	8