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California Red-Legged Frog (*Rana draytonii*) Movement and Habitat Use: Implications for Conservation

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Abstract.—Nonbreeding habitats are critically important for *Rana draytonii*, especially for individuals that breed in temporary bodies of water. We radiotracked 123 frogs to evaluate seasonal habitat use. Individual frogs were continuously tracked for up to 16 months. Some individuals remained at breeding ponds all year, but 66% of female and 25% of male frogs moved to nonbreeding areas, even when the breeding site retained water. Frogs at our main study site moved 150 m (median), roughly the distance to the nearest suitable nonbreeding area. The greatest straight-line distance traveled was 1.4 km, although the presumed distance traveled was 2.8 km. Females were more likely than males to move from permanent ponds (38% of females, 16% of males), but among dispersing frogs, males and females did not differ in distance moved. Some frogs left breeding sites shortly after oviposition (median = 12 days for females, 42.5 days for males), but many individuals remained until the site was nearly dry. Fog provided moisture for dispersal or migration throughout the summer. Our data demonstrate that maintaining populations of pond-breeding amphibians requires that all essential habitat components be protected; these include (1) breeding habitat, (2) nonbreeding habitat, and (3) migration corridors. In addition, a buffer is needed around all three areas to ensure that outside activities do not degrade any of the three habitat components.

Rana draytonii (California Red-Legged Frog) was once an abundant frog throughout much of central and southern California and is believed to have inspired Mark Twain's fabled story ''The Celebrated Jumping Frog of Calaveras County.'' Now this frog is rare in both the Sierra Nevada foothills and the southern portion of its range (Jennings and Hayes, 1994). In parts of the central Coast Range, there are still large, vigorous populations, some of which probably rival those present 200 years ago (Fellers, 2005). *Rana draytonii* was federally listed as a Threatened species on 24 June 1996, and the recovery plan states that it ''. . . has been extirpated from 70 percent of its former range . . . Potential threats to the species include elimination or degradation of habitat from land development and land use activities and habitat invasion by non-native aquatic species'' (U.S. Fish and Wildlife Service, 2002:iv).

Rana draytonii use ponds or pools for breeding during the wet season (December through March) and ponds, riparian areas, or other aquatic habitats during the rest of the year. In Marin County, stock ponds are the most commonly used breeding sites. There is only one published report on migration or nonbreeding habitat requirements for this frog. Bulger et al. (2003) described movements of 56 *R. draytonii* in a coastal area about 100 km south of San Francisco. They found that 80–90% of the frogs remained at one breeding site all year. Frogs radiotagged at nonbreeding sites often moved in a straight-line between breeding and upland habitats without apparent regard to intervening vegetation or topography. Frogs traveled overland up to 2,800 m, and Bulger et al. (2003) recommended a 100 m buffer zone around breeding sites.

The California Red-Legged Frog recovery plan outlines the necessary actions for recovery. One task is to ''conduct research to better understand the ecology of the California Red-Legged Frog including the use of uplands, dispersal habits, and overland movements'' (U.S. Fish and Wildlife Service, 2002:84). This is a concern not only for *R. draytonii*, but also for many endangered and nonendangered vertebrates that migrate between breeding and nonbreeding areas. This includes salamanders (*Ambystoma*; Madison, 1997; *Triturus*; Joly et al., 2001), frogs (*Rana*; Richtor et al., 2001; Pope et al., 2000), snakes (*Farancia*; Gibbons et al., 1977), turtles (Burke and Gibbons, 1995; Bodie, 2001), and many species of passerine birds (Keast and Morton, 1980). Lamoureux and Madison (1999) made the point that studies need to examine amphibian habitat requirements at all times of the year not just during the breeding season. We designed our study to address this concern for *R. draytonii*.

Materials and Methods

Study area.—Our study was conducted in Marin County, California, 45 km northwest of

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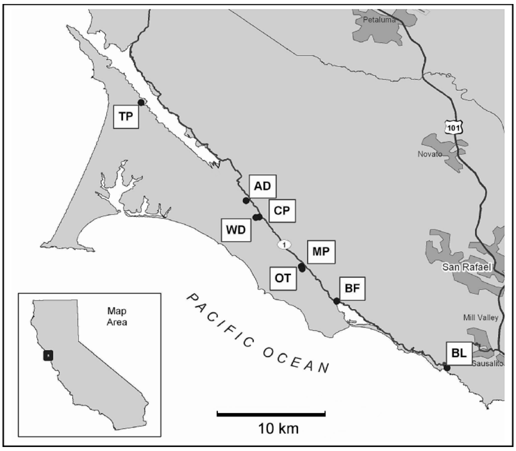

FIG. 1. Sites where California Red-Legged Frogs (*Rana draytonii*) were radiotagged at Point Reyes National Seashore and Golden Gate National Recreation Area, Marin County, California. Site descriptions are listed in Table 1.

San Francisco. All sites were within 6 km of the ocean and located at either Point Reyes National Seashore or Golden Gate National Recreation Area (Fig. 1). The local climate is Mediterranean, with an average annual rainfall of 100 cm that largely occurs between November and March. Mean monthly temperatures range from 8.6°C (December) to 16.6°C (August/September) at the headquarters of Point Reyes National Seashore in Olema Valley (National Park Service weather records). Most frogs ($N = 112$) were tagged in the Greater Olema Valley (Olema Valley and Pine Gulch Valley; 38°01′41″N, 122°46′50″E). To evaluate movement and habitat use in areas with contrasting habitats, nine frogs were tagged at Big Lagoon (37°51′36″N, 122°34′29″E), and two were tagged at Tomales Point (38°09′19″N, 122°54′43″E; Fig. 1).

Most of the Greater Olema Valley was characterized by a mixture of grazed and ungrazed grasslands interspersed with seasonal drainages with California bay (*Umbellularia californica*) and coast live oak (*Quercus agrifolia*). The west side of the valley was predominantly a Douglas fir forest (*Pseudotsuga menziesii*). Olema and Pine Gulch Creeks had well-defined riparian zones composed of California bay, red alder (*Alnus rubra*), willow (*Salix* spp.), big-leaf maple (*Acer macrophyllum*), and Douglas fir, with an understory dominated by blackberry (*Rubus discolor*), poison oak (*Toxicodendron diversilobum*), stinging nettles (*Urtica dioica*), and western sword fern (*Polystichum munitum*). Within the valley, there were 24 *R. draytonii* breeding sites. Fourteen of these were artificial stock ponds, and the others were naturally occurring ponds or marshes. Aquatic vegetation was predominantly cattails (*Typha* spp.), pennywort (*Hydrocotyle verticillata*), and rushes (*Juncus* spp.). About half of the ponds were seasonal, whereas the others usually held water all year. Study sites within the Olema Valley were selected to represent a range of habitats and because there was a sufficiently large *R. draytonii* population at each of the study sites.

The Big Lagoon study site consisted of a cattail marsh with a seasonal creek (Green Gulch Creek) that flowed into it. The marsh had several small areas where water depth was 1.0–1.5 m during the winter, but most of the marsh was covered by < 0.25 m of water, even during the wet season. A levee on the north side separated the marsh from a permanent creek (Redwood Creek), but a set of culverts allowed water to enter the marsh during higher winter flows. Water retention in the marsh varied with rainfall but was also influenced by how much water the National Park Service allowed to pass through flood gates on the culverts. The Tomales Point study site was a nonbreeding site at a seasonal seep. The dominant vegetation was coyote brush (*Baccharis pilularis*), with a few wax myrtle (*Myrica californica*). The nearest breeding pond was 650 m away.

Field methods.—Frogs were caught at night either with a dip net or by hand. We marked each frog with a passive integrated transponder (PIT) tag (TX1400L, Biomark, Meridian, ID; www.biomark.com) for individual identification and recorded sex, snout–vent length (SVL), and mass. Each frog was radiotagged by attaching a transmitter (model BD-2G, Holohil Systems Ltd., Carp, Ontario, Canada; www.holohil.com) to a belt of aluminum beaded chain that was slipped over the frog's extended rear legs and up onto the waist (Rathbun and Murphey, 1996). The transmitters were either a dull green or light brown color. The aluminum belt was painted flat black to eliminate reflections. The smallest frog we radiotagged was 32 g, and the mass of the transmitter and belt was approximately 2.1 g (6% of the frog's mass). When possible, we recaptured frogs before the battery died (20-week life) and fitted a new transmitter. We tagged frogs during all months of the year except August, with most being tagged just prior to, or during, the December to March breeding season.

A total of 123 individual frogs was radiotagged (47 females, 76 males) between 5 November 1997 and 1 May 2003 at eight sites (Table 1). Twenty-three frogs were consecutively fitted with two transmitters, six frogs with three transmitters, and one frog wore six

TABLE 1. Sites where California Red-Legged Frogs (*Rana draytonii*) were fitted with radiotransmitters in Marin County, California. Figure 1 shows the geographic distribution of the sites.

		Number of frogs tagged		Days tracked	
Site name	Habitat	M	F	Median $\bar{x} \pm$ SD	Range
Greater Olema Valley					
CP	Permanent pond	44	31	86 89.6 ± 56.0	2–229
MP	Seasonal pond	19	9	76 80.5 ± 47.3	12–191
AD	Seasonal pond	2	4	127 139.0 ± 75.0	63–253
BF	Seasonal pond	2	2	112 109 ± 74.9	28–184
WD	Permanent pond	0	1	134	134
OT	Permanent pond	1	0	121	121
All sites	–	68	47	83 91.3 ± 56.1	5–253
Big Lagoon					
BL	Permanent marsh	9	0	68 66.8 ± 36.8	16–130
Tomales Point					
TP	Seasonal seep and ditch	0	2	283	68–498

consecutive transmitters. Seventy-eight percent of all transmitters ($N = 166$) were recovered. Three frogs (two females, one male) lost their transmitters but were subsequently recaptured and outfitted with new transmitters 54, 244, and 493 days later. This yielded 126 telemetry histories. We generally located radiotagged frogs twice weekly; more often when the frogs were making regular movements. We recaptured frogs every 3–4 weeks to check for injuries and ensure proper fit of the transmitter belt. Frogs were radiotagged for 91 days (median) at the Olema Valley study sites and for 67 and 283 days at the Big Lagoon and Tomales Point sites, respectively.

Frogs were located using a TR-2 receiver (Telonics, Mesa, AZ; www.telonics.com) or an R-1000 receiver (Communication Specialists, Inc., Orange, CA; www.com-spec.com) with a directional ''H'' or three-element yagi antenna. Fine scale location of transmitters was accomplished with a partially stripped coaxial cable inserted into a length of PVC pipe that was used as a probe (Fellers and Kleeman, 2003). Radio locations were only determined during the day.

Frog locations were plotted on a 7.5′ USGS topographic map by noting proximity to a mapped feature or permanent local landmark (e.g., dead snag, fence corner). On a few occasions, locations were initially determined using a Garmin 12XL GPS unit (Garmin International Inc., Olathe, Kansas, www.garmin.com), but these locations were later visited and mapped on a topographic map using local landmarks. Telemetry data were analyzed by plotting coordinates on digitized USGS topographic maps (1:24,000 scale) using Topo! software (National Geographic TOPO! Maps, San Francisco, California; maps.nationalgeographic.com/topo). Unless otherwise noted, movements represent straight-line distances between successive locations. For some frogs, we also calculated a longer distance moved based on locations between breeding and nonbreeding sites. For example, frogs found at several successively further distances along a riparian corridor were presumed to have followed the creek between sites. This typically resulted in a longer distance moved than would be obtained using a straight-line distance and is referred to as presumed distance. Statistical analysis was conducted using Statistix (Version 7, Analytical Software, Tallahassee, Florida; www.statistix.com/home.html). We used $\alpha = 0.05$ to evaluate statistical significance.

Olema Creek passed within 110 m of our main study site (CP) in Olema Valley (Fig. 1). To evaluate use of nonbreeding habitat, we conducted nocturnal surveys along all or part of a 4.8-km segment of Olema Creek where it flowed past our study area. One or two observers walked the creek while carefully searching both pools and stream banks for frogs. Observers used a combination of spotlights and binoculars to locate animals (Corben and Fellers, 2001). Radiotelemetry was not used as part of these nocturnal surveys. We believe that most of the frogs we located used the adjacent pond (CP) for breeding because (1) it

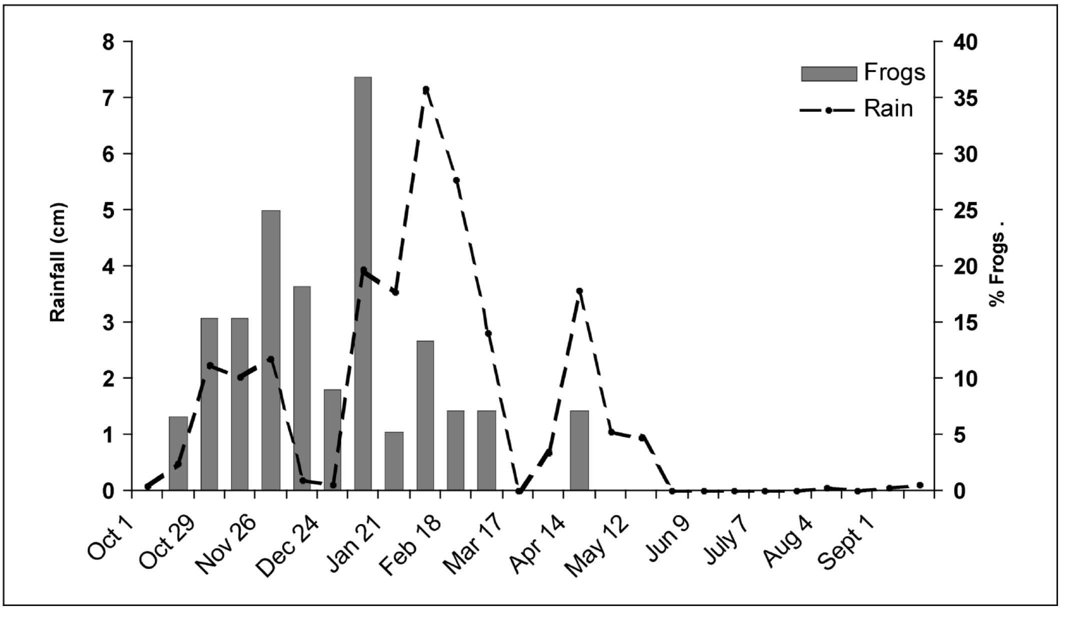

FIG. 2. Biweekly rainfall and the percent of radiotagged *Rana draytonii* that moved ≥30 m between October 1999 and September 2000.

was the closest breeding site and (2) some of the frogs found along the creek had been fitted with radiotransmitters at the pond.

RESULTS

Frogs made small-scale movements (<30 m) throughout the year. Movements of <30 m could be made without leaving the breeding sites; hence, they were considered local, non-dispersal. Movements ≥30 m generally coincided with winter rains, although some frogs did not move until their seasonal habitat was on the verge of completely drying. In general, frogs moved toward breeding ponds with the onset of heavy winter rains. Frogs departed from breeding ponds at varying times throughout the rainy season, with some frogs remaining at permanent ponds all year. Some frogs made large-scale movements during the dry season (May through October), as seasonal breeding sites dried. A regression of the percent of frogs that moved ≥30 m versus rain showed that more frogs moved with higher amounts of rain (P = 0.006). We show rainfall and movements for the 1999–2000 season (Fig. 2), the year we had the most frogs simultaneously radiotagged.

Frog movements in the greater Olema Valley.— One hundred fifteen frogs were tracked for a mean of 91 days each (range = 5–253, Table 1). Median distance moved from the breeding site was 0 m, but for the 36 frogs that moved ≥30 m, the median was 150 m (range = 30–1400 m, Table 2, Fig. 3). In many cases, frogs almost certainly moved more than the straight-line distance between sites. This was confirmed with individuals that were located in transit. Presumed distance moved for those frogs that moved ≥30 m was 185 m (median, range = 30–1400 m).

A higher proportion of radiotagged females moved ≥30 m than males (13 of 68 males, 23 of 47 females, χ^2 = 11.49, df = 1, P < 0.01). For frogs that moved ≥30 m, distance traveled was not significantly different for males (N = 13) and females (N = 23; median = 210 vs. 140 m, respectively; Wilcoxon rank sum T = 1.22, P = 0.22). Because some frogs lost their transmitters or were killed by predators (see below), the median distance moved might be greater than what we measured. Of the 36 frogs that moved ≥30 m, 22 (11 males, 11 females) reached a destination where they remained for at least two weeks. For these frogs, median distance traveled was 175 m. The median for these males and females was not significantly different (210 vs. 120 m; Wilcoxon rank sum T = 0.56, P = 0.58), in part because of the large variability in distance traveled.

A higher proportion of females left breeding sites than males. At our main study site (CP), nine of 21 (43%) females left the breeding site, whereas only four of 25 (16%) males departed. Females left the breeding site sooner than males (1, 5, 5, 5, 12, 55, 60, 76, 92 days for females [median = 12]; 31, 38, 47, 69 days for males

TABLE 2. Distance moved for 110 California Red-Legged Frogs (*Rana draytonii*) with radiotransmitters at three study sites in Marin County, California. Sixteen frogs radiotagged at nonbreeding sites are not included in this tabulation.

		Distance moved for frogs that moved ≥30 m						Frogs that moved <30 m
	Sex	Minimum	Median	Maximum	Mean	SD	*N*	*N*
Olema Valley								
CP	Males	200	240	490	293	135	4	31
CP	Females	100	320	1400	421	416	10	14
MP	Males	270	270	270	270	–	1	18
MP	Females	150	150	150	150	0	2	7
AD	Males	–	–	–	–	–	0	2
AD	Females	30	80	90	70	28	4	0
BF	Males	80	80	80	80	–	1	1
BF	Females	40	95	150	95	78	2	0
WD	Males	–	–	–	–	–	0	0
WD	Females	–	–	–	–	–	0	1
OT	Males	560	560	560	560	–	1	0
OT	Females	–	–	–	–	–	0	0
Big Lagoon								
BL	Males	30	105	390	158	136	6	3
	Females	–	–	–	–	–	0	0
Tomales Point								
TP	Males	–	–	–	–	–	0	0
TP	Females	30	40	50	40	14	2	0

[median = 42.5]), but the sample size was small, and the difference was not significant ($T = 0.61$, df = 11, $P = 0.55$).

Some of the dispersing frogs moved well away from the breeding site. One female (10.7 cm SVL) left the pond at our main study area (CP), crossed Olema Creek (the primary nonbreeding area) and stopped at a pond 320 m from the breeding pond. Two females (10.9 and 10.1 cm SVL) moved from CP, across Olema Creek and eventually resided in marshes, 0.88 and 1.02 km from the breeding site. Another female (10.6 cm SVL) moved down Olema Creek and up a small tributary for a total distance of 2.8 km (see individual case histories below).

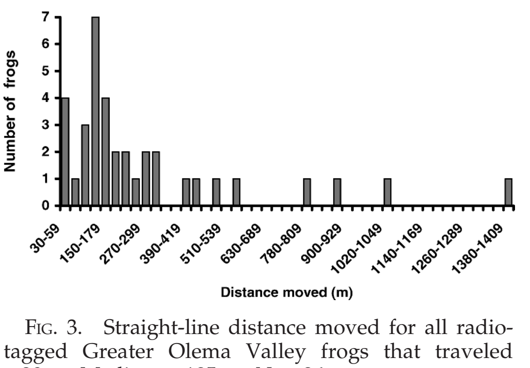

FIG. 3. Straight-line distance moved for all radiotagged Greater Olema Valley frogs that traveled ≥30 m. Median = 185 m, $N = 36$.

Fourteen of the breeding sites in the Greater Olema Valley were stock ponds surrounded by pastures. At these sites, all frogs that left the breeding site had to cross heavily grazed grassland to reach another pond or the riparian area. Frogs moved directly across these fields, typically traveling the most direct route to their destination. Movements of 100–200 m across open grasslands were common. With one exception, movements taking more than one night were along riparian corridors. One frog, however, spent five days sitting in a small clump of rushes in an open grassland (45 m from the breeding pond) before moving another 100 m to a small riparian area where it spent the next 50 days.

In two instances, we radiotagged females that appeared to have recently laid eggs (i.e., gaunt sides, conspicuously loose skin). Both frogs left the breeding pond within two days and moved to a seasonal marsh 800 m away. One frog took 32 days (5 December 1997 to 5 January 1998), whereas the other took five days (14–19 January 2000). A gravid female was fitted with a transmitter at a seasonal pond on 29 January 2001. By 8 February 2001, she had moved to an adjoining swale dominated by rushes. When captured on 28 February 2001, she had laid her eggs, as indicated by a sudden drop in mass. By 3 April 2001, she had moved 150 m to a riparian area where she remained until the transmitter was removed on 1 August 2001.

Frog movements at Big Lagoon.—The nine male frogs at this site moved a median distance of 70 m (0–390 m, Table 2). Frogs made small-scale movements (<30 m) throughout the time they were radiotagged (26 December 2002 through 3 June 2003). Most movements were between three of the deeper parts of the marsh, but one frog moved 390 m up Green Gulch Creek (when part of the marsh dried), to a seasonal creek that flowed into the marsh system. The other frogs moved to the only remaining pool at the west edge of the marsh, 50–75 m away. Most frogs did not use the riparian zone along the adjacent Redwood Creek. One individual spent four weeks there, and another frog moved to the riparian zone just before it lost its transmitter. We found frogs in the riparian area during only one nocturnal survey, although we regularly found them in the marsh or adjacent cattails.

Frog movements at Tomales Point.—The two female frogs radiotagged at this site (6.7 and 10.6 cm SVL) were relatively sedentary and apparently did not move to a breeding site. They had transmitters for an average of 283 days (68 and 498 days). Both frogs moved >30 m, with a mean of 65 m (Table 2). Although it might have been possible for the female that we tracked for 498 days to have moved to a breeding pond, laid eggs, and returned to her nonbreeding site without our noticing her absence, the gradual increase in mass throughout the time we tracked her indicated that this did not happen, and she apparently did not breed during the time we radiotracked her.

Use of riparian habitat.—On six of the 21 nocturnal stream surveys, there were ≥4 frogs per 100 m of stream, and one survey located seven frogs per 100 m (2 September 1999). Because radiotagged frogs known to be present (i.e., located during the same day by telemetry and also found along the creek on subsequent days) were frequently not seen during nocturnal surveys, the number of frogs along the creek was greater than what we observed, but it is not possible to determine by how much. For example, during a nocturnal survey on 5 July 2000, we observed one of the radiotagged frogs known to be along the creek, but we did not find two other radiotagged frogs whose presence had been confirmed earlier that day. Similarly, a nocturnal survey on 3 August 2000 did not detect either of two radiotagged frogs known to be present earlier that day; however, two untagged adults and nine subadults (<5.5 cm SVL) were observed. Nocturnal surveys also suggested that frogs tended to concentrate along portions of the creek nearest the breeding sites (Fig. 4).

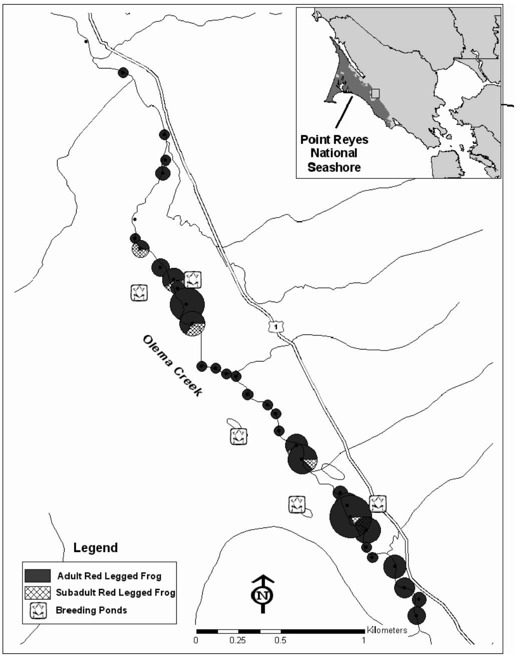

FIG. 4. Distribution of *Rana draytonii* along Olema Creek as detected during nocturnal surveys 4–6 October 1999. The distribution of frogs was similar during other surveys. Circles represent frogs, and size of each circle indicates relative number of frogs.

Diurnal behavior.—We conducted our radiotracking during the day and were frequently able to confirm visually the exact location of frogs with transmitters. This allowed us to evaluate diurnal microhabitat use. It was not unusual to find California Red-Legged Frogs basking in full sun, immediately adjacent to the water. Although we observed this behavior primarily at breeding ponds, occasionally frogs were found in similar situations in nonbreeding riparian areas.

Frogs that were not basking used a variety of cover. In permanent ponds, they sat entirely underwater in the deeper portions of the pond (>0.75 m), usually in association with the emergent vegetation. At sites with deeper water, *R. draytonii* sat on the bank in close proximity to the water. In shallow, seasonal ponds (<0.4 m deep), frogs were usually under vegetation (e.g., rushes, blackberries, hedge nettles [*Stachys ajugoides*]) at the edge of the pond. In seeps or seasonal streams, frogs were found under blackberry thickets interspersed with poison oak, coyote brush, hedge nettles, stinging nettles, and mats of rushes. Along permanent streams, frogs were found in or near pools with a depth of >0.5 m and associated with structurally complex cover (e.g., root mass, logjam, or overhanging bank). When on stream banks, frogs sat under dense vegetation as far as 2 m from the water's edge. Vegetation was predominantly western swordfern, blackberry, hedge nettle, and giant horsetail (*Equisetum telmateia*).

Predation.—We documented two predation events and had circumstantial evidence for three others. A Great Blue Heron (*Ardea herodia*) ate two radiotagged frogs sometime between 4 and 18 January 2000 (Fellers and Wood, 2004). Three other frogs appeared to have been killed by predators. The skin, bones, and transmitter of one frog were found at the base of a guano-stained fence post, along with a number of raptor pellets. Two frogs appeared to have been killed by mammalian predators, although we have no definitive proof. We found the skin, internal organs, PIT tag, and transmitter of a frog in a riparian corridor, and we found pieces of skin, internal organs, and the transmitter of another frog. One frog appeared to have been stepped on by a large, hoofed animal, probably one of the cows that grazed in the pasture. We found the anterior two-thirds of the frog in a pasture; the posterior portion of the frog had been crushed into the ground. Although we did not observe any predation during our nocturnal surveys along Olema Creek, we regularly observed raccoons (*Procyon lotor*), Black-Crowned Night Herons (*Nycticorax nycticorax*), river otters (*Lutra canadensis*), and nonnative rats (*Rattus* spp.). At breeding sites, we observed Great Blue Herons, but other potential predators probably visited the ponds and marshes at times.

Injuries from transmitters.—Twenty frogs had injuries from transmitter belts (17% of radiotagged frogs). The most common injury consisted of small abrasions on the dorsum or, less frequently, a midventral abrasion. The wounds generally healed within two weeks if frogs were fitted with transmitter belts with one additional bead. Eleven of the injured frogs were reweighed at the time the wound was noticed, and all frogs had gained mass since their initial capture. We reweighed 23 uninjured frogs with transmitters; 18 (78%) gained mass after initial capture, two (9%) had no change, and three (13%) lost mass. The mean mass gain for these frogs was 21%, and mean mass loss was 8.5%. Overall, we do not believe that the minor injuries caused by the transmitter belt interfered with frog behavior.

Individual case histories.—The frog that was radiotagged for the longest time had a transmitter for 16 months. When first caught on 12 May 1999, the female frog weighed 42.5 g and was 7.3 cm SVL. It grew steadily and was 77.7 g and 8.9 cm when last captured on 14 June 2000.

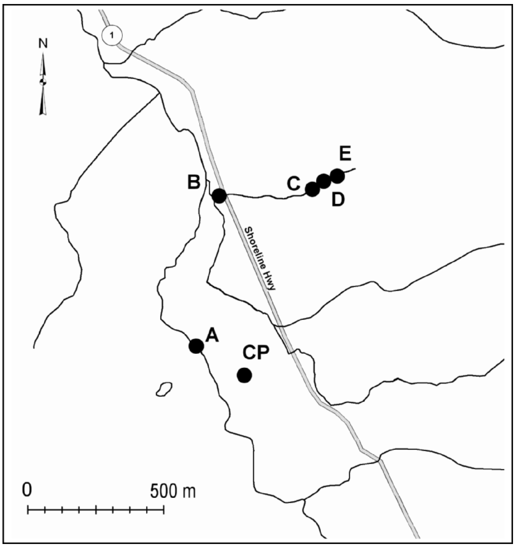

FIG. 5. Movements of a female radiotagged *Rana draytonii* that was captured at a breeding pond (CP) and subsequently moved to sites A–E. The frog was 10.5 cm (SVL) and was tagged during the breeding season (19 January 1999). The straight-line distance from CP to E was 1.4 km, but the presumed distance moved was 2.8 km.

The frog was caught in a puddle (1.0 $\times$ 0.3 m, 15 cm deep) that had formed in a rut created by a roadside seep along an abandoned dirt road on Tomales Point (site TP, Fig. 1). For 16 months, this frog made frequent, small (2–10 m) movements, within a 200-m^2 area surrounding the seep. The furthest the frog moved was 110 m. It used a variety of microhabitats: underwater in the puddle, underground in small mammal burrows, partially buried in duff beneath wax myrtle and coyote brush, and sitting in small clumps of grass. Although this frog was an adult female, it did not move to the nearest known breeding pond (650 m away) during the winter of 1999–2000. On 1 September 2000, the transmitter was found in the grass beneath a coyote brush, 6 m from where the frog had last been found. We could not determine whether the transmitter had fallen off or whether the frog had met a predator.

One frog moved at least 1.4 km. This was a female (10.5 cm SVL) tagged at a breeding pond (CP) during the breeding season (19 January 1999). On 23 January 1999, she was located under a fallen tree, 240 m away in Olema Creek. On 30 January 1999, she had moved a minimum of 650 m to a pool in a small tributary of Olema Creek (Fig. 5). It is quite likely that the frog followed Olema Creek to the tributary, which would have required a movement of 1.0 km to reach that point. By 14 February 1999, the frog had moved either across a two-lane, paved country road or under the road through a culvert. She then moved up a small, seasonal drainage, 430 m from her previous location. The presumed distance traveled by this frog was 2.8 km. The frog stayed in this drainage and was often found under blackberry brambles and thickets of poison oak along the stream. The transmitter and remains of the frog were found on 14 June 1999, apparently the victim of avian predation (see Predation above).

Discussion

The California Red-Legged Frog recovery plan emphasizes protection and recovery of breeding habitat (U.S. Fish and Wildlife Service, 2002), and most protection efforts have focused on breeding sites. One challenge in managing *R. draytonii* has been the paucity of data on habitat use beyond the breeding site, thus making it difficult to evaluate requirements for nonbreeding habitat and connecting migration corridors. Our study provides insights into *R. draytonii* movement and habitat use in a coastal environment and establishes a basis for making decisions about habitat protection.

Migration of *R. draytonii* from the breeding sites we studied was highly variable. Some frogs remained at breeding ponds all year, whereas others spent only a few days. Two-thirds of female frogs and 25% of male frogs moved from breeding areas. Bulger et al. (2003) found that 80–90% of *R. draytonii* remained at one breeding site all year. In our study, frogs at sites that held water only seasonally often lingered until the site was on the verge of drying completely. Because all our study sites were in an area where summer fog is the norm (E. J. Null, NOAA Technical Memorandum, NWS WR-126, 1995; Lundquist and Bourcy, 2000), frogs could move throughout much of the summer with little risk of desiccation. Once along the riparian corridor, frogs used a range of microhabitats that provided both cover and moisture, especially blackberry thickets, logjams, and root tangles at the base of standing or fallen trees. Regular summer dispersal across open grassland is in contrast to what Rothermel and Semlitsch (2002) reported for juvenile *Ambystoma* and *Bufo* in Missouri where desiccation appeared to be a significant factor affecting amphibian dispersal across fields adjacent to their artificial pools.

There was a wide range of migration distances (30–1400 m, straight-line). Our main study pond was 110 m from a riparian zone that provided suitable nonbreeding habitat (CP, Fig. 1). For frogs that moved at least 30 m from the pond, the median movement was 150 m. Relatively short movements from breeding sites was also suggested by the nocturnal surveys of riparian vegetation along Olema Creek (Fig. 4) where we found more frogs in areas adjacent to breeding sites. At Big Lagoon, where nonbreeding habitat was immediately adjacent to breeding sites in the marsh, the median distance moved was 68 m, and none of the frogs went more than 390 m. These short movements were similar to Columbia Spotted Frogs (*Rana luteiventris*); Pilliod et al. (2002) found no significant difference between males ($\bar{x}$ = 367 m moved) and females ($\bar{x}$ = 354 m). Bartelt et al. (2004) reported that male Western Toads (*Bufo boreas*) traveled shorter distances from breeding ponds than females (581 m ± 98 and 1105 m ± 272, respectively). Because there is relatively little data on these species, it is not possible to determine whether the differences are species-specific or dependent on the local landscape.

When frogs moved beyond the minimum distance to reach a suitable nonbreeding area, some followed riparian corridors, whereas others moved directly toward sites where they stayed through the nonbreeding season. Because most frogs moved from a breeding pond, across a grazed pasture, to a riparian area, they did not have the option of following a waterway during their initial movement. This is similar to Bulger et al. (2003), where frogs mostly moved in a straight line without apparent regard to intervening vegetation or topography. However, there were a few individuals in each study that moved primarily along a creek.

During our nocturnal surveys of Olema Creek, some frogs were well hidden by cover, whereas others sat fully exposed on top of logs or even on the sandy edge of the creek, places where California Red-Legged Frogs were rarely seen during the day. It is unclear why some individuals spent hours exposed to predation when good cover was only 1–2 m away. A frog in the open would have a wider field of view to detect and capture prey, perhaps partially mitigating the risk of predation. We documented predation by a Great Blue Heron, had evidence of predation by a raptor, and suspect that two other frogs succumbed to mammal predators. Additionally, we occasionally observed predators along Olema Creek including raccoons, Black-Crowned Night Herons, river otters, and nonnative rats (*Rattus* spp.). At a marsh that was not part of this study, we regularly observed night herons, and *R. draytonii* were so skittish that we have never been able to capture a single individual.

Based on their findings that 60% of the radiotagged frogs stayed within 30 m of their breeding sites, Bulger et al. (2003) recommend a 100-m buffer with an array of suitable habitat elements around breeding sites. Although that might work well at their study area, we do not believe that a simple, symmetrical buffer is typically adequate. At our main study site, a 100-m buffer would not include any suitable nonbreeding habitat. Because the pond completely dries every 4–5 years, such a buffer would result in the elimination of the local population. By contrast, the Big Lagoon site has suitable nonbreeding habitat immediately adjacent to the marsh. At that site, maintaining the marsh habitat and the natural water levels would likely be adequate for long-term survival.

Three important conclusions from our study are that (1) most frogs move away from breeding sites, but only a few move farther than the nearest suitable nonbreeding habitat; (2) the distance moved is highly site-dependent, as influenced by the local landscape; and (3) land managers should not use average dispersal or migration distances (from our study, or any other) to make decisions about habitat requirements. A herpetologist familiar with *R. draytonii* ecology needs to assess the local habitat requirements.

Recommendations.—Maintaining populations of pond-breeding amphibians, such as *R. draytonii*, requires that all essential habitat components be protected. These include (1) breeding habitat, (2) nonbreeding habitat, and (3) migration corridors. In addition, a buffer is needed around all three areas to ensure that outside activities do not degrade any of the three habitat components.

For *R. draytonii*, nonbreeding habitats must have several characteristics: (1) sufficient moisture to allow amphibians to survive throughout the nonbreeding season (up to 11 months), (2) sufficient cover to moderate temperatures during the warmest and coldest times of the year, and (3) protection (e.g., deep pools in a stream or complex cover such as root masses or thick vegetation) from predators such as raptors (hawks and owls), herons, and small carnivores.

Breeding habitat has been well described (U.S. Fish and Wildlife Service, 2002; Stebbins 2003) and receives most of the management attention (US Fish and Wildlife Service, 2002). However, nonbreeding areas are equally important because some *R. draytonii* spend only a week or two at breeding sites, yet nonbreeding habitat is frequently ignored and is generally not well understood. Aside from our study, Bulger et al. (2003) are the only ones to publish details on the use of nonbreeding habitat by *R. draytonii*. Additional research on nonbreeding habitat is needed, especially in other parts of range where *R. draytonii* occupy a diversity of ecotypes.

Migration corridors are frequently not considered in management planning for California Red-Legged Frogs. Our work and that of Bulger et al. (2003) indicate that *R. draytonii* migration corridors can be less ''pristine'' (e.g., closely grazed fields, plowed agricultural land) than the other two habitat components. Bulger et al. (2003) observed that *R. draytonii* did not avoid or prefer any landscape feature or vegetation type. They tracked frogs that crossed agricultural land, including recently tilled fields and areas with maturing crops. Our study site did not encompass such a diversity of habitats, but frogs readily traversed pastureland that surrounded the breeding sites. While conducting other research, we observed five frogs crossing a recently burned field as they moved toward a breeding pond during the first rain of the season (25 October 2004). Both our study and that of Bulger et al. were conducted at study sites near the Pacific Ocean where summer fog and high relatively humidity reduce the risk of desiccation for dispersing amphibians (E. J. Null, NOAA Technical Memorandum, NSW, WR-126, 1995; Lundquist and Bourcy, 2000). Though desiccation was probably not a problem for frogs in our study, amphibians are often faced with a variety of hazards including roads (Gibbs, 1998; Vos and Chardon, 1998), degradation of habitat (Vos and Stumpel, 1995; Findlay and Houlahan, 1997; Gibbs, 1998), and predation (Gibbs, 1998), as well as desiccation (Rothermel and Semlitsch, 2002; Mazerolle and Desrochers, 2005).

Buffers are often described as the area that frogs use near breeding sites. Such usage combines migration corridors and nonbreeding habitat, as well as the adjacent area necessary to protect these areas. We believe that it is important to identify each habitat component separately and then include a buffer that is sufficiently large to maintain the integrity of each habitat type. Such a buffer cannot be defined as a standard distance but rather as an area sufficient to maintain the essential features of the amphibian habitat. Hence, a riparian area adjacent to a forest undergoing clear-cut logging would need a relatively large buffer to protect it from increased sedimentation and the increased temperature fluctuations that occur after logging. Less severe habitat modifications adjacent to amphibian habitat could be accommodated with a narrower buffer (deMaynadier and Hunter, 1995, 1999; Gibbs, 1998).

Buffers are typically described as a fixed-width boundary around breeding sites (Semlitsch and Bodie, 2003). However, the distribution of habitat components is rarely symmetrical

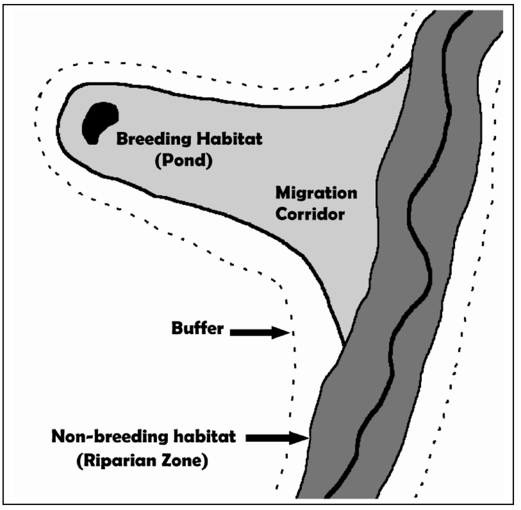

FIG. 6. Stylized diagram of typical *Rana draytonii* habitat showing the critical habitat components and the required asymmetrical buffer.

(e.g., a pond with frogs dispersing in all directions to surrounding nonbreeding area). At all of our study sites, frogs moved primarily in one direction, often toward the nearest riparian area, similar to what Rothermel and Semlitsch (2002) reported. As suggested by Regosin et al. (2005), protecting frog habitat in these situations requires an asymmetrical conservation area (Fig. 6). Because it is often not obvious from casual inspection what areas frogs are relying upon, delineating each habitat component and determining the size of a suitable buffer requires either an expert opinion from a field biologist with extensive experience with the species of interest or a field study to monitor radiotagged frogs.

The design of protected areas is often developed with the unstated assumption that only the most sedentary frogs can or need to be protected. The resulting systematic loss of individuals that move the farthest can have unexpected and unwanted effects (Gill, 1978; Berven and Grundzien, 1990). Long-distance dispersers are the individuals most likely to reach distant breeding sites and, hence, provide the genetic diversity that is important for survival of small populations. Additionally, those same dispersers are the individuals that would colonize sites where frogs have been lost because of random events that periodically extirpate local populations. By consistently selecting against frogs that disperse the greatest distances, the effective size of a metapopulation is reduced and the size of the effective breeding population is smaller; smaller breeding populations have a greater likelihood of extirpation (Gill, 1978; Sjogren, 1991).

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