

Terrestrial activity and conservation of adult California red-legged frogs *Rana aurora draytonii* in coastal forests and grasslands

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Abstract

The federally threatened California red-legged frog *Rana aurora draytonii* occupies both aquatic and terrestrial habitats in its adult life stage. The terrestrial activities of this species are not well known and require documentation to assist in the development of appropriate levels of protection under the US Endangered Species Act. We studied the terrestrial activities of radio-tagged red-legged frogs ($n=8-26$) inhabiting a coastal watershed in Santa Cruz County, California, during 1997–1998. In particular, we investigated (1) the use of terrestrial habitats by non-migrating adults in relation to season, breeding chronology, and precipitation, and (2) adult migration behavior, including seasonal timing, duration, distances traveled, and the use of corridors. Non-migrating red-legged frogs occupied terrestrial habitats briefly (median = 4–6 days) following infrequent summer rains, but resided nearly continuously on land (median = 20–30 days) from the onset of the winter wet-season until breeding activities commenced 1–2 months later. All of the non-migrating frogs remained within 130 m of their aquatic site of residence (median < 25 m). Intervals spent on land were again brief during mid/late winter (median = 1–4 days), despite frequent and copious rainfall. Adult migration to and from breeding sites occurred from late October through mid-May (wet season). We monitored 25 migration events between aquatic sites that were 200–2800 m apart. Short distance movements (< 300 m) were completed in 1–3 days, longer movements required up to 2 months. Most migrating frogs moved overland in approximately straight lines to target sites without apparent regard to vegetation type or topography. Riparian corridors were neither essential nor preferred as migration routes. Frogs traveling overland occurred in upland habitats as far as 500 m from water. Approximately 11–22% of the adult population was estimated to migrate to and from breeding sites annually, whereas the bulk of the adult population was resident at these sites. Adequate protection of red-legged frog populations inhabiting relatively undeveloped landscapes is liable to be achieved by retaining an array of suitable habitat elements within at least 100 m of occupied aquatic sites, and by imposing seasonal limitations on detrimental human activities occurring within this zone. Specific protections for migrating frogs are probably unwarranted in forest and rangeland environments because dispersal habitat is ubiquitous and migrating frogs are widely distributed across the landscape in space and time.

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1. Introduction

Applied conservation strategies for threatened and endangered species frequently rely on the use of buffer zones around critical habitat elements and on connecting corridors that allow for dispersal between suitable

habitat patches (Saunders and Hobbs, 1991, Hobbs, 1992, Beebe, 1996, Semlitsch, 1998). Many anurans would appear to be appropriate candidates for this type of approach. One such species, the California red-legged frog *Rana aurora draytonii*, was recently listed as federally threatened (USFWS, 1996), and is now a focal species in habitat protection and mitigation programs associated with land-use planning and the exploitation of natural resources.

California red-legged frogs occur from sea level to 1500 m elevation and occupy a variety of aquatic habitats in

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landscapes that are used predominately for agriculture, ranching, timber harvesting, or recreation. They are largely absent from urban and suburban residential settings. Important wetland sites for the species are rather easily identified and some form of protection or management of these wetlands theoretically preserves or enhances their habitat value to frogs. By contrast, little is known about the terrestrial activities of red-legged frogs in relation to any upland vegetation type or land use category. Stebbins' (1966) assessment that the species is "generally found in or near water but disperses after rains" adequately characterizes our current understanding of seasonal habitat use. In consequence, there is insufficient information on which to base decisions regarding land-use planning, land management, and the regulation of activities in terrestrial environments in a manner that achieves appropriate levels of protection of this species and its habitats under the US Endangered Species Act of 1973.

The purpose of the present study was to gather data on terrestrial activity by adult California red-legged frogs living in a coastal landscape dominated by forests and grasslands. Using radio transmitters, we investigated (1) the use of upland habitats in relation to season, breeding chronology, and precipitation, and (2) migration characteristics including timing, duration, distance traveled, and the use of corridors. Because we were not testing any specific hypotheses, the study is of a descriptive nature and is intended to provide a quantitative basis for the development of management and regulatory strategies that take into account both the aquatic and terrestrial habitat requirements of this species.

2. Study area

The study area is located in the lower Scott Creek watershed on the western slope of the Santa Cruz Mountains, northern Santa Cruz County, California (see Fig. 3). Elevations range from sea level to 300 m. Aquatic habitats include man-made stock ponds and agricultural reservoirs, permanent and seasonal streams, and a coastal lagoon at the mouth of Scott Creek. Several vegetation types are represented, but at larger scales the area is dominated by grassland and scrub on the coastal terrace to the west of Scott Creek, and by coniferous forest from Scott Creek eastward. Coast redwood *Sequoia sempervirens* predominates in drainage bottoms and on north-facing slopes, whereas various mixes of redwood, Douglas-fir *Pseudotsuga menziesii*, Monterey pine *Pinus radiata*, and hardwoods occur elsewhere. Permanent streams frequently support a narrow fringe of riparian woodland composed chiefly of red alder *Alnus rubra*.

The area has a moderate Mediterranean climate, with wet mild winters and relatively dry, temperate summers.

Winter temperatures rarely drop below 3 °C, and summer temperatures seldom exceed 32 °C. Morning and evening fog is common during the summer months. Annual rainfall is usually in the range 1.0–1.5 m, with 90% of it falling between November and May. In this study, El Niño weather patterns prevailed during the 1997–1998 wet season, during which 1.8 m of rainfall was recorded in our study area, including nearly 1.0 m during January and February.

3. Methods

3.1. Study species

California red-legged frogs are active the year-round in coastal areas. The species breeds in ponds, marshes, and lentic waters of streams between December and April (Jennings and Hayes, 1995). When not breeding, red-legged frogs occupy a broad spectrum of wetland habitats, including natural and artificial ponds and reservoirs, streams and other watercourses, freshwater lagoons, springs, and seeps. Males mature in 2 years, females in 3 years (Jennings and Hayes, 1985). Adult males (78–116 mm) are smaller than adult females (87–138 mm) (Hayes and Miyamoto, 1984).

3.2. Capture and radio transmitter attachment

We captured frogs at night and processed and released them onsite within 10–20 min after capture. Apart from trying to maintain equal sample sizes of both sexes, we selected individuals for radio-tagging haphazardly. Sites where frogs were radio-tagged (see Fig. 3) were chosen for their proximity to coniferous forests and included both ponds ($n=4$) and streams ($n=3$ sites). All study ponds were <0.1 ha in surface area.

Radio transmitters were attached to frogs using a bead-chain belt that was secured around the waist (Rathbun and Murphey, 1996). We used Holohil model BD-2G transmitters, designed with a 20 week battery life and weighing 1.65 g. The total weight of each unit, including the waist band, was less than 2.0 g. Only adult frogs (males with thumb pads, females >88 mm) were tagged. Adults weighed 48–214 g, with males smaller than females. Radio-tagged frogs also were injected with PIT tags (Camper and Dixon, 1988) for individual identification in the event of recapture after transmitter failure or loss.

3.3. Radio-tracking schedule

Data on radio-tagged frogs were gathered from 16 May 1997 through 22 May 1998. We attempted to maintain long-term records on 15–20 individual frogs,

but there was considerable attrition as individuals shed transmitters or transmitters failed, so new individuals were added as necessary. At any given time 8–26 adult frogs carried radio transmitters. In all, 56 radio-tagged individuals contributed to the data reported on here.

We present time series data in this paper by individual tracking sessions. Each tracking session comprised an interval of 1–3 days during which all tagged frogs were precisely located once. The average number of days taken to complete a tracking session was 1.4. Generally, three sessions were completed per week (mean = 2.8 sessions/week). In total we conducted 143 radio-tracking sessions. Because we did not track frogs every day, durations of individual bouts of terrestrial activity often were imprecisely known (± 1 or 2 days). Thus, median values reported here for various types of terrestrial activity are often stated as a minimum–maximum range. For most analyses, small sample sizes preclude any meaningful breakdown by sex.

3.4. Data records

All radio tracking was done during daylight hours, when adults are generally inactive (Hayes and Tennant, 1985). Frogs occupying terrestrial habitats were located by homing in on and then circling the tagged individual at a distance of a meter or less. Because frogs on land were nearly always hidden beneath concealing cover (see below), close-range tracking very seldom disturbed a focal animal.

Each time a frog was located its position was mapped (1:12,000 scale) with reference to a magnetic compass bearing and distance from a known landscape feature. Data were recorded on its behavior, proximity to water (pond, stream, or ravine), general vegetation type, and specific cover type. Distances relating to proximity to water were estimated visually or paced if they were < 50 m, and paced if they were in the range 50–200 m. These were rounded to the nearest 10 m over the range 30–100 m and to the nearest 25 m over the range 100–200 m. Longer distances were paced or measured from mapped locations and rounded to the nearest 50 m. In measuring distances traveled by migrating frogs, movement was considered to have been in a straight line between points of contact with the frog.

Daily rainfall and temperature records were obtained from a privately operated recording station located near the center of the study area.

4. Results

Adult red-legged frogs occupied terrestrial habitats in two distinct ways. Most individuals made short-range forays into upland habitats for periods of days to weeks in response to precipitation but returned to their aquatic

home site at the end of the upland interval. We refer to these as non-migrating frogs. Some individuals additionally made overland movements between two aquatic sites, typically before or after breeding. We refer to these as migrating individuals. This dichotomous characterization refers to the behavioral event itself and is not a permanent label assigned to the individual. Data on use of terrestrial habitats by migrating and non-migrating frogs are treated separately in the analyses below (Sections 4.1 and 4.2).

Frogs occupying terrestrial habitats were hidden from view in 96% of the tracking observations ($n=961$). Live plants (shrubs/herbs) provided concealing cover in 79% of the cases, followed in descending importance by woody debris and rootballs (14%), small recesses in vertical banks (4%), and forest floor litter (3%). The most commonly used cover species included California blackberry *Rubus ursinus*, poison oak *Toxicodendron diversilobum*, and coyote brush *Baccharis pilularis*, all of which were ubiquitous throughout the study area.

4.1. Part A: non-migrating frogs

4.1.1. Description of terrestrial habitat use

Use of terrestrial habitats by non-migrating frogs showed a clear response to rainfall during the summer and early winter months (Fig. 1). Frogs were virtually always < 5 m from their pond or stream of residence during dry intervals of the summer, but moved outward into upland habitats to distances of up to 130 m in response to summer rain ($n=8-18$ individuals). With the onset of the more frequent rains of winter, the median distance from water increased to a relatively constant 15–25 m through mid-December ($n=6-13$ individuals). Some frogs remained at distances of up to 100 m from water until late January. Ninety percent of the non-migrating frogs were always within 60 m of water (Fig. 1).

No similar response to rainfall was evident during mid- to late winter. Red-legged frogs ($n=8-24$) made little use of upland habitats during this season despite frequent and copious rainfall (Fig. 1). The reduced use of uplands appeared to be primarily related to breeding chronology. All radio-tagged males ($n=4$) entered breeding ponds and began calling from late November through mid-December. Six of seven radio-tagged females entered breeding ponds from early January through mid-February, and spawning in these ponds occurred from mid-January through late-March. The sharp drop in the median distance from water during mid-December and the correspondingly sharp drop in the maximum and 90th percentile distances from water late in January (Fig. 1) reflect the timing of these events. Individuals of both sexes remained closely tied to aquatic environments as the breeding season progressed. From February through May, 90% of the non-migrating frogs

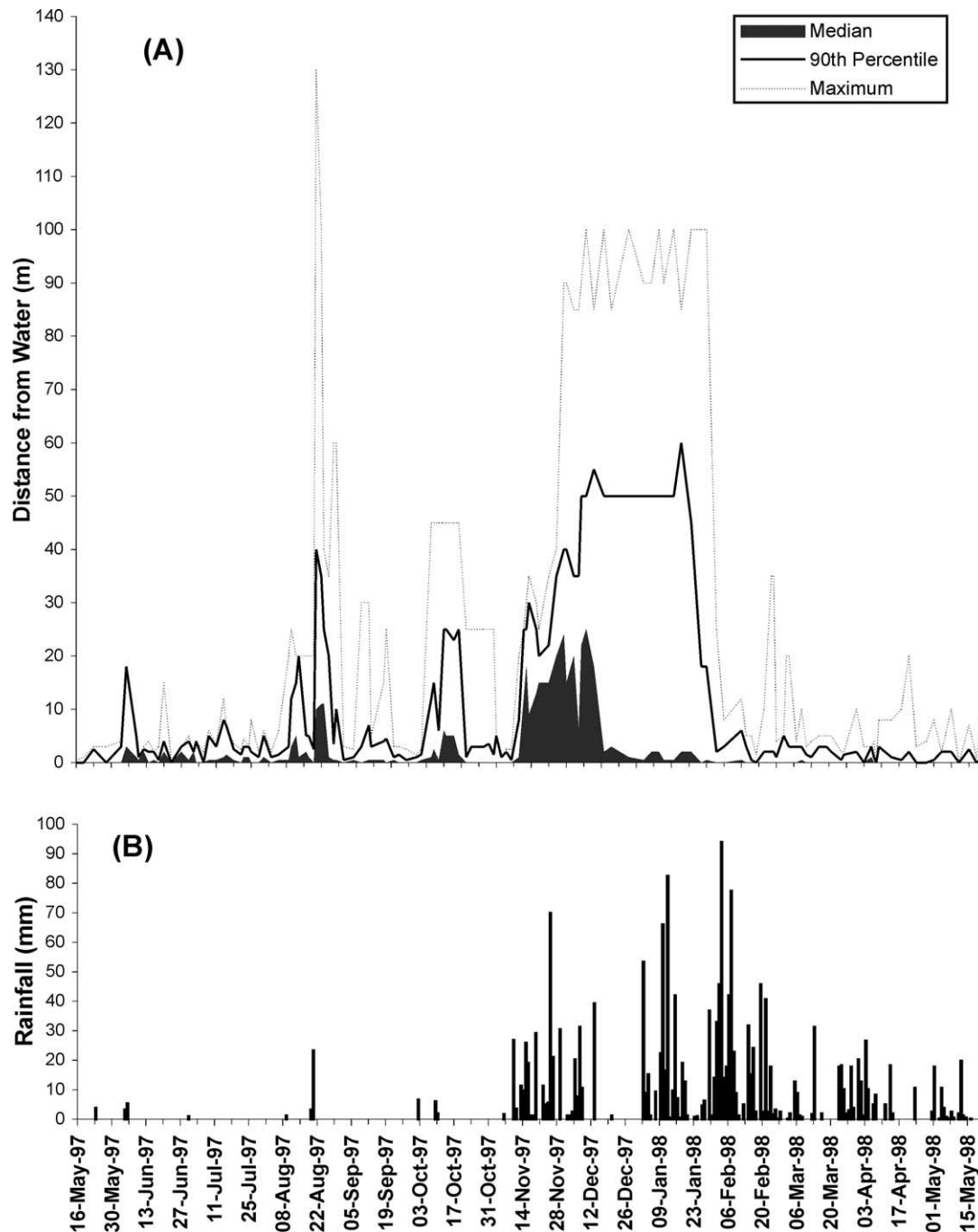


Fig. 1. Time series plots showing use of terrestrial habitats by non-migrating red-legged frogs in relation to rainfall, Santa Cruz County, California. Data are plotted by individual radio-tracking sessions for (A) median, 90th percentile, and maximum distances from water, and (B) daily rainfall totals. Sample sizes of tagged non-migrating frogs ranged from 8 to 24.

were always within 6 m of water. The sample of tagged frogs over this interval included up to 11 males and 13 females.

Variability in the ambient air temperature within the study area was so slight during the winter months that it was unlikely to have been a factor in frog use of uplands. The mean daily low temperature during the early winter season ($9.0\text{ }^{\circ}\text{C}$, range = $2.8\text{--}16.1\text{ }^{\circ}\text{C}$), when frogs made extensive use of uplands, was nearly identical to that of

the mid- to late winter season ($8.2\text{ }^{\circ}\text{C}$, range = $2.2\text{--}13.9\text{ }^{\circ}\text{C}$), when they did not.

4.1.2. Duration of bouts on land

Table 1 shows the duration of continuous intervals individuals spent in upland habitats at distances of > 10 m from water. Seasonal cutoffs were assigned based on obvious changes in rainfall/frog response (Fig. 1). The distance criterion of 10 m was chosen to eliminate the

Table 1
Duration of continuous intervals that non-migrating red-legged frogs spent in terrestrial habitats (> 10 m from water) by season, June 1997–May 1998, Santa Cruz County, California

Season	Month initiated	No. bouts	Median duration (days) ^a	Maximum duration (days)
Summer	June–October	31	4–6	22
Early Winter ^b	November–December	18	20–30	>63
Mid/Late Winter	January–May	9	1–4	7–10

^a Medians are given as ranges because frogs were not tracked every day. Thus, most bouts were recorded to ± 1 or 2 days.

^b Of the 18 bouts, seven were truncated because of predation, transmitter failure, lost contact with the frog, or having tagged the frog subsequent to its initiation of the interval on land. The broad median takes these into account.

influence of background levels of upland occurrence, as frogs routinely occupied a fringe of land immediately adjacent to water regardless of ambient conditions (see Fig. 1). During the summer season, when frogs moved into upland habitats in response to widely separated single rain events, the median duration of intervals spent in these habitats was 4–6 days (maximum = 22 days). By contrast, with the more regularly spaced rains of early winter, the median duration of bouts in uplands was in the range 20–30 days (maximum > 63 days). During mid/late winter, bouts on land were again brief (median = 1–4 days), despite the frequent occurrence of rain.

4.1.3. Use of ravines

Contiguous with the ponds at two of our radio tagging sites were ravines that had at least some surface flow during most of the year. Roughly one-third of all non-migrating frogs at these sites spent at least some time in ravines during each season (summer = 1 of 3 frogs; early winter = 3 of 9; mid/late winter = 7 of 23). Data on ravine bout-duration and distances moved away from the home pond (Table 2) were comparable to the corresponding data for movements into upland habitats (Fig. 1, Table 1). Non-migrating frogs inhabited ravines for as long as 38–42 days and moved up to

150 m from the home pond before returning to it. Small sample sizes and imprecise medians preclude a statistical comparison between the two data sets.

4.2. Part B: migrating frogs

We monitored 25 migration events, including 10 from sites of summer residence to breeding ponds (breeding migration) and six elective movements from breeding ponds to sites of summer residence (post-breeding migration). The remaining nine events were movements away from a pond that dried during June 1997 and again during May 1998.

4.2.1. Timing of breeding migration

We recorded the starting date for 9 of the 10 breeding migration events (Fig. 2). Eight of nine frogs migrating to breeding ponds initiated the movement between 31 October and 25 November. The ninth individual, a female, delayed its departure from its summer habitat until 10 January. The first frog to migrate did so prior to the onset of winter rains and traveled via a ravine that held running water over most of its length. Initiation of the remaining eight breeding migration events was in each case associated with a 1-day rainfall total in excess of 25 mm. Although rainfall clearly facilitates movements, it is possible that frogs migrating to breeding sites are not hormonally prepared to move until sometime late in October. No migration was associated with 8 mm of rain on two days early in October, nor with 28 mm late in August, despite the fact that frogs were able to reside in terrestrial habitats for up to 22 days in the wake of these rains (Table 1).

4.2.2. Timing of post-breeding migration

Post-breeding migration occurred between 29 January and 1 May, and in each of six cases was initiated in association with a one-day rainfall total of from 10 to 40 mm (Fig. 2). For females, there was some overlap in the timing of breeding and post-breeding migration. The first female to depart a pond after breeding (29 January) did so two weeks prior to the arrival of the last female (13 February) at the same pond. Our interpretation of these

Table 2
Use of ravines by non-migrating red-legged frogs at two sites where ravines with surface flow were connected to study ponds, June 1997–May 1998, Santa Cruz County, California

Season	Date initiated	No. bouts	Median duration (days)	Maximum duration (days)	Median distance (m) from Pond ^a	Maximum distance (m) from Pond
Summer	June–October	1	14–15	n/a	n/a	40
Early Winter	November–December	4	21–25	38–42	55	65
Mid/Late Winter	January–May	11	3–7	24–26	30	150

^a Median of the maximum distance each individual moved from the pond.

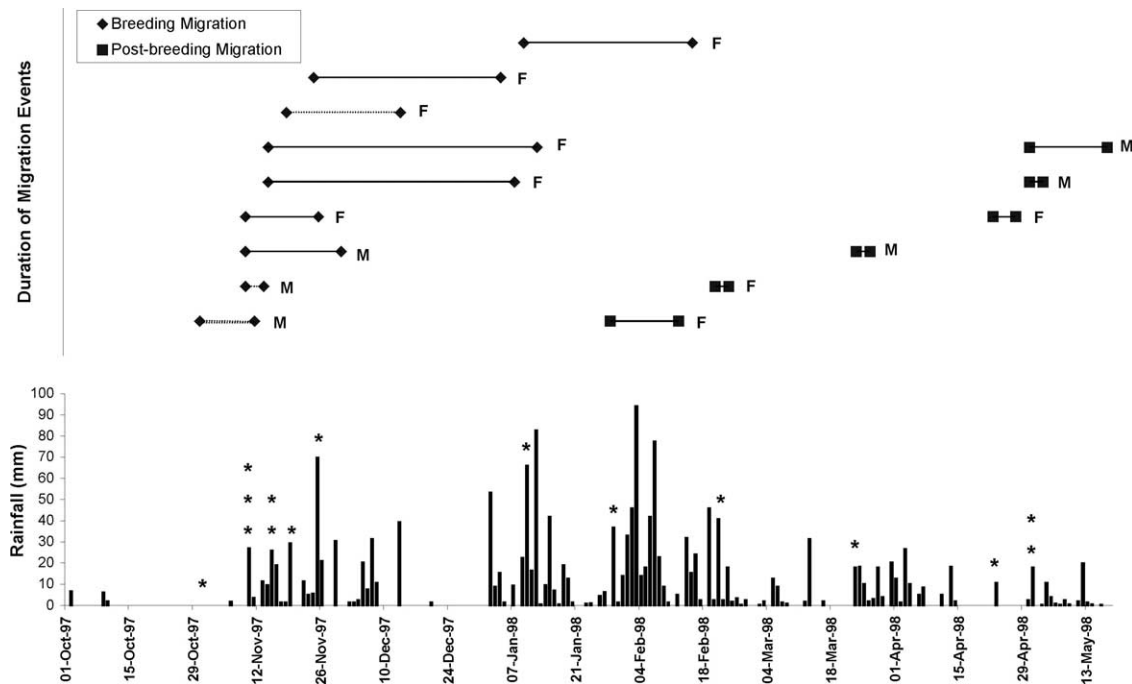


Fig. 2. Timing and duration of individual red-legged frog migration events in relation to daily rainfall totals, 1997–1998, Santa Cruz County, California. Dashed lines indicate that the event was truncated due to predation or loss of the radio transmitter. Abbreviations are M=male, F=female. One frog (female 15919) was excluded due to uncertainty regarding the onset of the event. She arrived at the breeding pond on 3 January. Asterisks show the initiation timing of each migration event.

movements as “post-breeding” is supported by the facts that (1) none of the three males that migrated from a breeding site did so until after the last known clutch of eggs was laid, and (2) all three females that migrated from breeding sites had lost 15–28% body mass during their tenure in the pond, suggesting that each had spawned.

4.2.3. Migration distance, duration, and use of uplands

Migrating frogs moved between sites that were separated by map distances of 200–2800 m. Each segment of a migratory route took the frog closer to its eventual target. Thus, movements were highly oriented toward target sites and usually tended to describe an approximately straight line between the source and target sites (Figs. 3 and 4). The minimum distance actually traveled was in most cases close to the shortest straight-line distance (Table 3). The longest route traveled was 3600 m by an individual moving between two sites 2800 m apart.

The tendency of most individuals to move in approximately straight lines to target sites suggests de facto that there was neither avoidance of nor preference for any particular landscape feature or vegetation type. Frogs traveled readily through the range of upland habitats represented in the study area. Maximum distances moved by individual frogs through various macro-habitat types were: coniferous forest (900 m), grass/scrub rangeland (1700 m), and agricultural land

(500 m), including both recently-tilled fields and maturing crops.

The duration of individual movements between aquatic sites ranged from 1–3 days at a minimum to 57–60 days at a maximum (Table 3). Although there was considerable variability in durations of longer movements (> 500 m), distance moved and movement duration were highly correlated ($r_s=0.901$, $n=16$, $P<0.0001$).

Thirteen of 16 migrating frogs traveled primarily or exclusively through terrestrial habitats between sites, covering total overland distances of 400–3200 m for completed movements. The longest single overland segment traversed without contacting a pond or stream was 1200 m. Migrating frogs temporarily occupied upland habitats as far as 500 m from any aquatic site (Table 3).

Most migrating individuals moved to the nearest pond to breed, and to the nearest pond or stream after breeding (Table 3). The three exceptions to this pattern all resided in the same pond (not used for breeding) during the summer and then migrated to breed in a pond 2800 m distant. In this case, the nearest known breeding pond was 600 m from the site of summer residence (Fig. 3).

Streams in the study area are not known to be used for breeding, presumably because scouring peak flows coincide with the red-legged frog breeding season. There are virtually no off-channel backwaters on these

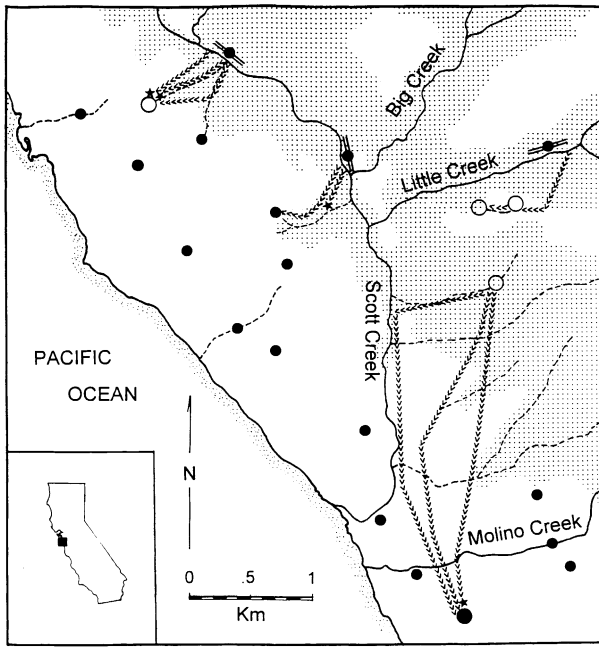


Fig. 3. Map of the study area, northern Santa Cruz County, California, and routes (arrows) taken by red-legged frogs migrating from sites of summer residence to breeding sites (breeding migration). A star indicates that the frog was preyed upon or shed its transmitter prior to reaching the target site. Circles represent ponds. Ponds used as radio-tagging sites appear as hollow circles ($n=4$). Permanent and seasonal streams are shown as solid and dashed lines. Locations of stream segments used as radio-tagging sites are indicated by two parallel lines running through a solid circle ($n=3$). The shaded area shows the extent of the coniferous forest. Unshaded areas are either grassland and scrub or agricultural fields.

streams. Six of seven frogs tagged in streams moved to ponds to breed (Table 3). The seventh was a female that had sustained a major abdominal wound, presumably during a predation attempt. She did not breed, and remained throughout the winter at the stream.

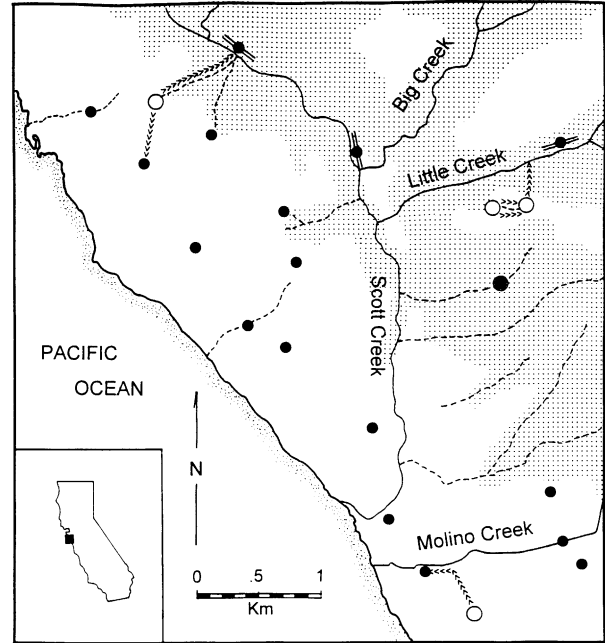


Fig. 4. Routes (arrows) taken by red-legged frogs migrating from breeding sites to sites of summer residence (post-breeding migration), northern Santa Cruz County, California.

Table 3

Summary data related to red-legged frog breeding and post-breeding migration events, 1997–1998, Santa Cruz County, California (Values in parentheses indicate truncated events.)

Frog	Map distance between sites (m)	Minimum distance moved (m)	Movement duration (days)	Total overland distance (m)	Longest overland segment (m) ^a	Maximum distance from water (m) ^b	End point habitats ^c	Nearest pond or stream?
<i>Breeding migration</i>								
15919	200	200	1–3	unk.	unk.	unk.	P to P	Yes
E755B	(300)	(350)	(2–4)	(350)	(350)	(250)	S to P	Yes
46118	(500)	(550)	(24–26)	550	550	150	S to P	Yes
C2302	(550)	(550)	(13)	0	0	< 10	S to P	Yes
81F54	650	800	17–19	800	800	300	S to P	Yes
02555	650	800	39–43	800	800	250	S to P	Yes
F5C45	700	750	20–23	400	400	150	S to P	Yes
1105C	(2600)	(2600)	57–60	(2600)	750	350	P to P	No
22E79	2800	3200	53–56	3200	1200	500	P to P	No
3432B	2800	3600	35–38	1150	600	300	P to P	No
<i>Post-breeding migration</i>								
15919	200	200	1–3	unk.	unk.	unk.	P to P	Yes
51C77	200	200	2–3	unk.	unk.	unk.	P to P	Yes
81F54	300	350	2–4	350	350	150	P to S	Yes
22E79	450	500	14–16	500	500	225	P to P	Yes
B0B45	500	500	2–4	500	500	250	P to P	Yes
F5C45	700	700	16–20	0	0	< 10	P to S	Yes

^a Longest distance traveled between two points of contact with water. Value is 0 if frog moved via a ravine.

^b Maximum distance from a pond, stream, or ravine with surface flow.

^c P = Pond; S = Stream.

4.2.4. Topographic component of migration

The study area is comprised of low mountainous terrain that is bisected at regular intervals by steep-sided drainages. The average percent slope for paired aquatic sites between which frogs migrated ranged from 12 to 33%. Ignoring the averages, canyon side-slopes frequently exceeded 50% slope over distances of 100 m or more. One such slope, which was scaled by two tagged frogs, included a 77% elevation gain over 180 m. Except for vertical rock faces, we did not observe any topographic constraints to frog migration.

The three frogs that made the longest movements each traveled via a different route to reach the same destination (Fig. 3). The longest of these followed drainage contours to the maximum extent possible, traveling 3600 m in the horizontal plane and 190 m in elevation (minimum possible). The shortest of the trio made a nearly straight-line movement of 2800 m in the horizontal plane, but traveled approximately 610 m upward and downward in elevation by crossing topographic contours over five drainage divides.

4.2.5. Rates of travel during migration

Migrating frogs tended to move in spurts of a day or two and then remain quiescent for intervals of several days. Because we did not locate individual frogs daily, we do not have tightly bounded data on numbers of days spent moving versus resting. Known distances moved (> 30 m) in 24 hours ($n=8$) ranged from 150–500 m.

4.2.6. Use of corridors for migration

In the study area, watercourses (streams and ravines) and their associated vegetation are the only obvious features of the landscape that might function as migration corridors for migrating red-legged frogs. The migration routes of 14 individuals were documented in sufficient detail to evaluate the role of watercourse corridors in facilitating migration. Of these 14 individuals, six inhabited sites with no obvious connecting corridor to the target site, and thus could only (and did) travel via overland routes. By contrast, eight frogs (at three sets of paired sites) had the immediate option to migrate to the target site via a connecting watercourse route. Of the eight, three principally followed watercourses and five traveled via overland routes. Thus, obvious migration corridors in the form of watercourses or riparian vegetation strips were neither essential to facilitating red-legged frog migration nor were they used in preference to overland routes.

4.2.7. Movements away from drying ponds

We monitored nine individuals that abandoned a pond that dried during early June 1997 and early May 1998. Seven of the nine moved to the nearest permanent pond 200 m away, one lingered in a wet ravine for 51–52

days (early June–late July) before entering the nearest pond, and one moved overland 300 m to the nearest stream over the course of 9–11 days.

4.2.8. Estimate of adult migration rate

Based on prior observations, we did not expect red-legged frogs to breed at stream sites or at one of our study ponds. In consequence, frogs tagged at these sites during the summer of 1997 had been selected, in part, with an intentional bias toward a high likelihood of migration, in order to gather data pertinent to that life-history characteristic. Of the original batch of 10 frogs that migrated to breeding sites, we were able to maintain contact with four through May 1998. We also attached a radio transmitter to a male captured on land while in the process of moving 500 m to a breeding pond. We followed this individual through May 1998 as well. All five of these individuals also migrated post-breeding, three to their previous summer site and one to a new site; the origin of the fifth frog was unknown. All five had migrated by 1 May. By contrast, three other individuals that were followed from the summer of 1997 through May 1998 did not migrate either pre- or post-breeding. Thus, breeding and post-breeding migrations may involve predominantly the same individuals.

To obtain an unbiased estimate of the proportion of adults that migrate to and from breeding ponds, we attached radios to 20 haphazardly selected individuals at two breeding sites (Site 1 = 5 males and 4 females; Site 2 = 5 males and 6 females). At each site the first 4–6 frogs of each sex encountered during capture sessions were fitted with radios. The experimental group was tracked from early February through early May, which encompassed the range of post-breeding migration dates in the control group.

Of the 20 selected frogs, two migrated to new sites, one was preyed upon early in April, and two shed their radios during April and could possibly have migrated subsequently. Excluding the individual lost to predation, the proportion of migrating individuals represented in this sample ($n=19$) falls in the range 10.5–21.1%. (Data for each site are 1–3 of 9, and 1 of 10). These data suggest that there is a relatively small segment of the adult population that is liable to migrate in any given year, and that most adults are resident the year around at favorable breeding sites. Morphological characteristics of frogs that migrated were indistinguishable from those that did not. The mean snout-urostyle length of males that migrated was 88.2 mm ($n=5$, range = 81–96 mm) compared with a mean of 87.9 mm ($n=8$, range = 79–95 mm) for those that did not (two-tailed $t=0.102$, $df=11$, $P=0.921$). For females, the corresponding data were mean length of 106.0 mm ($n=7$, range = 88–117 mm) for those that migrated, versus 104.9 mm ($n=10$, range = 88–123 mm) for those that did not (two-tailed $t=0.191$, $df=15$, $P=0.851$).

5. Discussion

This study provides the first quantitative description of terrestrial habitat use by California red-legged frogs and, as such, has important conservation implications pertaining to the development of appropriate land management strategies and regulatory guidelines for this species. In particular, we are able to make biologically-based recommendations for the application and design of terrestrial buffer zones at occupied aquatic sites, and to evaluate the role corridors play in adult red-legged frog migration.

5.1. Conservation of non-migrating frogs: buffer zones

Data on migration rates from this study indicate that more than 75% of the adult population is resident at permanent aquatic sites over the course of a year. Moreover, 90% of the radio-tagged frogs that were not migrating between aquatic sites remained within 60 m of water at all times and the farthest any non-migrating frog moved from water was 130 m. Although a larger sample size might enhance the precision of these distance thresholds, our results are liable to be quite robust given that there was little variability in observed behavior among individuals. Non-migrating frogs uniformly showed no proclivity to wander far from the home site, even during the early winter season ($n=238$ tracking records; 17 frogs) when they spent continuous intervals of up to 2 months on land (Table 1). This is particularly noteworthy in view of our finding that red-legged frogs are capable of moving 150–500 m in a single night.

These data indicate that the judicious application of terrestrial buffer zones adjacent to small ponds and streams may often be an effective means of protecting and maintaining populations of California red-legged frogs in coastal forests and grasslands (see also Rudolph and Dickson, 1990; Burke and Gibbons 1995; Dodd, 1996; Dodd and Cade, 1998; Semlitsch, 1998). Conservation and resource management planning for activities that alter the local environment should strive to retain a well-distributed array of natural habitat elements that provide protective cover for red-legged frogs to a distance of at least 100 m from occupied aquatic sites. Dense patches of shrubs and herbaceous vegetation are particularly important habitat elements in this regard. Within designated buffer zones, incidental mortality of red-legged frogs resulting from human activities occurring adjacent to occupied wetlands can likely be minimized or avoided through seasonal restrictions. Our data indicate that the potential for detrimental impacts to red-legged frog populations is highest during the early winter months.

5.2. Conservation measures relating to migrating frogs

Due to overlap in the timing of breeding and post-breeding migration events (Fig. 2), individual frogs may

be moving overland between aquatic sites at any time during the winter months (tentatively mid-October through mid-May). However, given (1) the comparatively low numbers of individuals involved in migration (<25% of the adult population), (2) that individuals move to a particular site over a broad spatial scale, and (3) that migration is spread out over time and does not occur as a synchronous en masse event, the density of red-legged frogs migrating through uplands is usually so low that protective considerations may often be unwarranted.

This conclusion, however, may pertain only to relatively undisturbed environments, such as forests and rangeland, where artificial barriers to migration and persistent human-related sources of mortality are largely absent. High-quality dispersal habitat is nearly ubiquitous in these types of landscapes. In degraded environments, this general conclusion may not apply. As landscapes become increasingly developed with buildings, abnormally high predator densities, roads, and related infrastructure, connectivity between aquatic sites decreases and migration between aquatic habitat patches may become more perilous (Simberloff et al., 1992; Rosenberg et al., 1997). Low recruitment of dispersing individuals is likely to play an insidious and primary role in the extirpation of frog populations from suitable aquatic sites in developing landscapes (sensu Sjögren, 1991; Sinsch, 1992b; Sjögren Gulve, 1994; Stacey et al., 1997; Vos and Chardon, 1998).

5.3. The role of corridors in red-legged frog migration

Where an obvious, direct corridor exists between two occupied aquatic sites, it undoubtedly will receive regular use by migrating frogs. However, there is no evidence from this study that natural corridors are either essential to migrating frogs or that they will be used preferentially over alternative upland routes. This finding in no way diminishes the value of ravines and small watercourses as frog habitat per se, and they constitute important landscape features for red-legged frogs the year around (Table 2), regardless of their relative role in facilitating migration.

Attempts to mitigate adverse impacts to red-legged frog habitat through the designation or creation of movement corridors in areas scheduled for development are problematical. The tendency of frogs to move in more or less straight lines to target sites indicates that it would be difficult to attempt to channel movements through provisional corridors (see also Rathbun et al., 1997). Moreover, local topography, vegetation, and drainage contours cannot necessarily be used to predict likely migration routes to or from occupied sites. In our study, three frogs that moved between two aquatic sites that were 2800 m apart did so over a swath through the landscape that was 600–700 m wide

(Fig. 3); one individual followed drainages to the maximum extent possible, whereas two moved overland across the topography. Additionally, although many individuals move between adjacent aquatic sites, not all do. Thus, proximity to another suitable site cannot always be used to predict directional dispersal probabilities. Our prediction for the three individuals mentioned above would have been that they would migrate 600 m northward to the nearest breeding pond, rather than 2800 m southward to an alternative site.

Recent reviews of the literature on wildlife corridors have concluded that there is yet little evidence in support of their effectiveness in achieving desired goals, despite their widespread use in conservation strategies (Simberloff et al., 1992; Rosenberg et al., 1997; see Beier and Noss 1998 for dissenting view). While we suggest caution in the application of corridors as a mitigation tactic for red-legged frogs, our results may not be wholly applicable to developed landscapes. It is possible that, as habitat connectivity decreases, red-legged frogs will become more reliant upon topographic or vegetative corridors or that they may exhibit other compensatory behavioral responses that favor successful migration (e.g. Rosenberg et al., 1998).

5.4. Anuran migration: comparative data

Aspects of adult migration have been investigated in a small number of anuran species and in general the data compare favorably with those presented here on California red-legged frogs. In our study, adult red-legged frogs traveled map distances of up to 2.8 km in a single season. Among the more vagile anuran species, adult *Bufo calamita* and *B. bufo* are known to make seasonal migrations of up to 3 km (Sinsch, 1989), *Hoplobatrachus occipitalis* of up to 6 km (Spieler and Linsenmair, 1998), and *Rana lessonae* of typically 1 km or less (Sjögren Gulve, 1994). In a review of data for 16 species of North American anurans, Dodd (1996) reported movement distances of 1–2 km in *Bufo americanus*, *B. cognatus*, *Rana capito*, and *R. pipiens*. The straight-line movements and spatial orientation toward target sites that we recorded for red-legged frogs have also been documented in other species of frogs and toads (van Gelder et al., 1986; Sinsch, 1989, 1990, 1992a; Kusano et al., 1995; Sjögren Gulve, 1998; Matthews and Pope, 1999). Rates of travel, too, are similar among species studied. Our radio-tagged red-legged frogs moved 150–500 m overnight, compared with 89–440 m for *B. bufo* (Gittens et al., 1980; van Gelder et al., 1986), 120–1400 m for *H. occipitalis* (Spieler and Linsenmair, 1998), and up to 160 m for *Rana pipiens* (Dole, 1965). During migration, brief bouts of movement separated by longer intervals of inactivity typify both red-legged frogs (this study) and common toads (van Gelder et al., 1986).

5.5. Limitations of the data

Our estimate of adult red-legged frog migration rates is derived from frogs that inhabit permanent, small ponds (<0.1 ha) that support breeding and year-round use and where nearby alternative aquatic sites are available. Whereas these conditions are not uncommon elsewhere within the species' range, the migration rate at any particular site is liable to be a function of many variables, including rainfall patterns, fluctuations in water levels, degree of isolation from other sites (Sjögren, 1991; Sjögren Gulve, 1994), regional metapopulation density, and carrying capacity of the site. Similarly, we note that patterns of terrestrial habitat use by non-migrating frogs that inhabit large, complex wetland sites may be substantially different from those reported here. The extent to which our results can be generalized awaits data from other study sites.

This study describes behavior and habitat use of adult frogs only. Subadult red-legged frogs occupy a range of aquatic habitats and also are found dispersing during rains, but are not obliged to reside at breeding sites during the winter. From routine capture efforts, we know that subadults are under-represented at breeding ponds during the winter season (personal observation). Presumably they are primarily terrestrial at this time, but we lack data on use of terrestrial habitats for this age class. This includes an appreciable proportion of the population, including males <2 years and females <3 years of age (Jennings and Hayes, 1985). Post-metamorphic anurans may often disperse radially from their natal sites (Dole, 1971; Schroeder, 1976; Sinsch, 1997), and are known to move up to 5 km over the 2–3 years between metamorphosis and first-breeding (Schroeder, 1968, 1976; Dole, 1971; Berven and Grudzien, 1990; Sinsch, 1997). There is convincing empirical evidence that post-metamorphic dispersal contributes significantly more to regional metapopulation persistence than does adult dispersal (Sinsch, 1992b; Sinsch and Seidel, 1995; Sinsch, 1997; also see Breden 1987). Thus, allowance for juvenile dispersal may in some cases be a critical consideration in long-term conservation planning. Application of our results to real conservation situations should beware this limitation.

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