# Movement Ecology and Seasonal Distribution of Mountain Yellow-Legged Frogs, *Rana muscosa,* in a High-Elevation Sierra Nevada Basin

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Movement ecology and seasonal distribution of mountain yellow-legged frogs (*Rana muscosa*) in Dusy Basin (3470 m), Kings Canyon National Park, California, were characterized using passive integrated transponder (PIT) surveys and visual encounter surveys. We individually PIT-tagged 500 frogs during the summers of 1997 and 1998 and monitored these individuals during seven recapture surveys in 1997 and 15 recapture surveys in 1998 from the time they emerged from overwintering in July until the lakes froze for the winter in October. Probability of movement between lakes was associated with abundance of *Hyla regilla* larvae in the different lakes of origin, activity of the frogs (overwintering, breeding, feeding), and time of year. Overland movements exceeding 66 m were observed in 17% of the tagged frogs. Movement between lakes 1 km apart was detected. Site fidelity from 1997 to 1998 was high, and 97% of the tagged frogs recaptured in October of both years were found in the same overwintering lakes. Frogs were more narrowly distributed in spring and fall than in summer. Summer frog densities (number per meter of shoreline) were positively related to water temperature, air temperature, maximum lake depth, and presence of *H. regilla* larvae and negatively related to presence of trout. Mountain yellow-legged frogs use a range of aquatic sites throughout their activity period, and basins with a variety of deep lakes and shallow ponds may be the most appropriate reserves for this declining species.

M OUNTAIN yellow-legged frogs (*Rana muscosa*) have become increasingly rare in their high-elevation aquatic habitats in the Sierra Nevada, and they have recently been petitioned for listing under the Endangered Species Act. Although population declines are well documented (Bradford et al., 1994; Drost and Fellers, 1996; Matthews and Knapp 1999), basic quantitative data on the ecology and ethology of natural populations of *R. muscosa* is poorly known. A recent study used radio telemetry to assess movement and microhabitat use of *R. muscosa* during one summer (Matthews and Pope 1999), but no attempt has been made to interpret the movements of *R. muscosa* populations in relation to their entire annual period of activity.

Many anurans move among different sites during their annual activity period to avail themselves of specific resources required for hibernation, reproduction, and nutrition (Sinsch, 1990; Stebbins and Cohen, 1995). For species such as *Eleutherodactylus johnstonei* (Ovaska 1992), hibernation, reproduction, and foraging all take place in the same locality, whereas species such as *Hyla arborea* (Stumpel 1987) inhabit areas where resources for these activities are spatially separated. Whether populations of *R. muscosa* make periodic movements among different sites or remain in one locality that provides all necessary resources is unknown.

The objectives of this study were to investigate the movement ecology of a population of adult *R. muscosa* from the time the frogs emerge from overwintering until the lakes freeze for the winter. Specifically, we used passive integrated transponder tagging (PIT-tagging), recapture surveys, and visual count surveys to quantify seasonal frog distributions in Dusy Basin lakes and streams and to determine factors that influence the probability of movement among the different lakes and ponds. Site fidelity was also evaluated by comparing the 1997 distribution and movement data to that gathered in 1998.

## Materials and Methods

*Study area.*—The study area is upper Dusy Basin at an elevation of about 3470 m in Kings Canyon National Park (KCNP), California (37°5′40″N, 118°33′45″W; Fig. 1). The basin supports alpine vegetation with low-growing herbaceous plants, dwarf shrubs, and occasional white-bark pines (Holland and Keil, 1995). The general study area covers approximately 1.0 km² and includes five stream segments and 11 lakes and ponds. All bodies of water within the study area were numbered and mapped (Fig. 1) using a Trimble (no endorsement by the USFS is implied) Pro
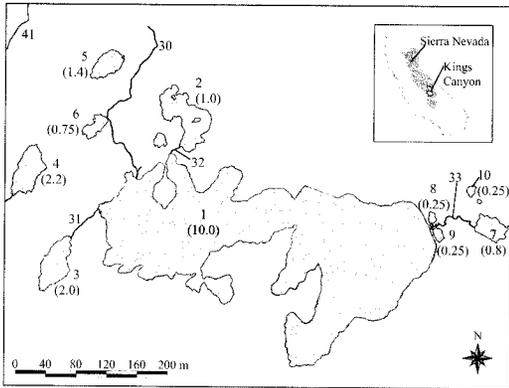
Fig. 1. Map of upper Dusy Basin, Kings Canyon National Park, showing lakes 1–11 and associated creeks 30, 31, 32, 33, and 41. Numbers in parentheses represent maximum depth measured in meters. Lakes 1 and 3 contain self-sustaining populations of introduced trout.

TABLE 1. SURVEY DATES AND PERCENT OF PIT-TAGGED FROGS RECAPTURED WITHIN EACH SURVEY PERIOD FOR THE DUSY BASIN 1998 FIELD SEASON.

| Survey # | Start date | End date | % recaptured |
|---|---|---|---|
| 1 | 12 Jul | 18 Jul | 2.1 |
| 2 | 20 Jul | 24 Jul | 9.7 |
| 3 | 25 Jul | 29 Jul | 12.5 |
| 4 | 30 Jul | 5 Aug | 37.8 |
| 5 | 6 Aug | 12 Aug | 37.8 |
| 6 | 13 Aug | 19 Aug | 41.9 |
| 7 | 20 Aug | 27 Aug | 43.7 |
| 8 | 28 Aug | 3 Sep | 36.6 |
| 9 | 6 Sep | 13 Sep | 38.5 |
| 10 | 14 Sep | 18 Sep | 28.4 |
| 11 | 19 Sep | 25 Sep | 30.2 |
| 12 | 27 Sep | 2 Oct | 14.3 |
| 13 | 3 Oct | 5 Oct | 11.6 |
| 14 | 6 Oct | 8 Oct | 0.6 |
| 15 | 14 Oct | 15 Oct | 5.2 |

XL GPS system accurate to one meter. The main lake in the basin (10 m deep, 5.3 ha) supports a self-sustaining population of hybrid rainbow-golden trout (*Oncorhynchus mykiss* × *O. aquabonita*), but most of the smaller neighboring ponds (< 2.5 m deep, area < 3000 m²) have no fish (Fig. 1).

*Data collection.*—The 1997 field season began 27 July and ended 28 October when lakes were freezing over. The 1998 season started on 11 July when snow and ice still covered about 95% of the surface area of the lakes and streams and ended 15 October when lakes were again freezing over. The winter between the two field seasons had a snowpack that was 177% of the average recorded at the Bishop Pass Station, approximately 1 km from the study area (California Dept. of Water Resources, http://cdec.water.ca.gov). The 1998 field season encompassed the entire annual activity cycle of mountain yellow-legged frogs in Dusy Basin, and fieldworkers were on site in Dusy Basin daily from 11 July to 15 October.

Adult mountain yellow-legged frogs greater than 40 mm snout–vent length (SVL) were individually marked using PIT tags. The tags have a lifespan of 50–100 years and so allow for subsequent reidentification of the tagged animals throughout their life. Tags were inserted under the skin of each frog by hand through a V-shaped nick made at the sacral hump with a pair of sharp scissors.

Recapture surveys were conducted throughout the summer by consecutively revisiting all water bodies in the study area and capturing by hand or dip net all frogs possible (Table 1). The PIT-tag number, location of capture, weight, length, and sex were recorded for each frog. If the frog did not already have a PIT tag and was greater than 40 mm SVL, a tag was inserted. After 20 August 1998 when 500 frogs had been tagged (390 frogs in 1997 and 110 frogs in 1998), no additional frogs were given PIT tags. Seven recapture surveys were conducted in each body of water in the study area in 1997 and 15 recapture surveys were conducted in 1998 (Table 1). Onset Optic stowaway and tidbit water temperature loggers (± 0.2 C) were set to record temperatures every 30 min and were placed approximately 20 cm deep in the nearshore habitat of the lakes and streams in the basin (excluding lakes 8 and 10) during both summer seasons.

Eighty-one additional frogs were PIT tagged in a lake (3398 m elevation) approximately 1 km southeast of the study area in 1997 to determine whether any longer range movement occurred between the populations. This lake is separated from the study area by steep terrain, and the only aquatic pathway that approaches the lake from the study area (within 420 m) supports high densities of trout.

Visual count surveys were conducted once per week at each water body in the study area. The surveys involved one person walking the perimeter of a lake or stream and counting all adult and juvenile frogs and all larvae seen of both *R. muscosa* and *Hyla regilla*. Air and nearshore water temperatures (about 20 cm deep) were recorded at the time of the survey using a

thermocouple thermometer (± 0.1% C). To understand frog distribution in relation to timing and location of reproductive activity, all lakes and streams were surveyed for egg masses starting on 15 July 1998. We walked the shoreline and in the ponds searching for egg masses. When an egg mass was found, it was given a unique number, marked with a pin flag and mapped using GPS.

*Data analysis.*—To assess the temporal change in distribution of frogs over the course of an activity season, we separated the count survey data into four periods (11 July through 25 July when lakes were thawing, 28 July through 8 August when breeding occurred, 11 August through 30 September when frogs were primarily feeding and sunning, and 4 October through 14 October when lakes were beginning to freeze) and compared the proportion and mean number of frogs observed in the water bodies during these periods. The 1998 weekly count survey data were also used to develop a semiparametric generalized additive model (Cleveland and Devlin, 1988; Hastie and Tibshirani, 1991) to determine estimated frog densities (number per meter of shoreline) as a function of water temperature at the time of the survey, air temperature, maximum water depth, number of *H. regilla* tadpoles and presence/absence of trout. The independent variables were selected because other researchers have suggested these factors may influence frog distribution (Mullaly and Cunningham, 1956; Bradford, 1982; Knapp and Matthews, 2000) or were variables we had observed in association with mountain yellow-legged frogs in the field. For example, we observed that adult *R. muscosa* prey on *H. regilla* larvae (Pope, 1999). We used the likelihood ratio test to determine the significance of each covariate in the presence of all other covariates. All regression-related calculations were made using S-Plus version 4.5.

To determine the possible factors leading to frog movement and to relate movements with frog activity, we used a general additive model to estimate the probability of a frog leaving a particular lake based on explanatory covariates including sex, weight, date, lake of origin, time lapsed between captures, type of lake (overwintering, summer), number of *H. regilla* larvae in lake of origin, and water temperature. Logit semiparametric regression with a loess smoothing function was used to estimate the effects of covariates on the probability of movement using the following equation:

$$\Pr[\text{Frog left lake } x \text{ in time interval } t, t + \Delta]$$

$$= \frac{e^{\theta}}{1 + e^{\theta}}$$

where the linear predictor $\theta = \alpha + f_1(\text{number of } H. regilla \text{ larvae in lake } x) + f_2(\text{date}) + \text{type of lake} + f_3(\Delta)$, $\Delta =$ time elapsed between initial capture ($t$) and recapture, and $f =$ nonparametric smooth curve to be estimated from the data.

The best combination of independent variables was determined using the likelihood ratio test. Because water temperature, frog sex, and frog weight were found to have no significant influence on movement probability when the other variables were included, they were not used in the final equation. Time elapsed between recaptures was included as a variable to account for the difference in recapture intervals for the different frogs. We grouped the lakes in the study area into two categories based on whether they were used as overwintering lakes. The lakes used as overwintering lakes (1 and 5) were compared to the rest of the lakes in the study area that were used primarily during the middle of the summer (see Results).

Because overland movement greater than two or three hops (< 2 m) from water has only recently been documented (Matthews and Pope, 1999), we calculated the number of frog movements between lakes that were not connected by aquatic pathways. Only PIT-tagged frogs that moved between lakes 4 and 5, 4 and 6, and between lake 5 and stream 41 were included because these frogs had to travel a minimum of 66 m overland (straight line distance between lake 4 and lake 6) to change water bodies (Fig. 1). The proportion of PIT-tagged frogs that moved overland at least 66 m was calculated. Although exact dates of movement could not be determined, the dates when frogs were last seen in a water body before overland movement and first seen in a new water body after overland movement were compared to determine whether the movements coincided with shifts in activity of the frogs (i.e., movement to feeding lakes and movement back to overwintering lakes).

Spatial location records gathered from the tagged frogs in 1998 were compared to 1997 location data to assess whether frogs returned to the same or different lakes in different years. We compared locational information on individual frogs that were captured within 10 calendar days of each other in both years. The data were subdivided by month (August, September, and October), and the proportion of frogs cap-

tured in the same water body in both 1997 and 1998 was calculated for each month.

## RESULTS

*Seasonal distribution.*—The heavy snowpack from the 1997/1998 winter delayed the start of the 1998 field season. We arrived at Dusy Basin on 11 July 1998 when the lakes and streams were beginning to thaw, and thus we were able to observe initial emergence of mountain yellow-legged frogs. Frogs emerging through the melting ice were only seen at lakes 1 and 5 and 88% of all frogs observed during the first two count surveys in the study area were found in these two lakes (Fig. 2A). Twelve frogs were observed traveling over ice and snow during this period. Eleven were observed moving between lakes; however, one frog was found wandering over the snow near base camp about 60 m upslope from the basin water bodies. At the end of July and beginning of August, when lakes were between 60% and 100% thawed and 154 egg masses were found in the basin, the highest numbers of frogs were found in lakes 2 and 5 (Fig. 2B) where the most egg masses were also found (91 and 48, respectively). By mid-August and September, frogs were found in every water body in the basin (Fig. 2C). In the final count surveys in October, distributions narrowed, and 73% of all frogs were again found in lakes 1 and 5 (Fig. 2D). Lake 1 is the largest and deepest lake in the basin (area = 53,187 m², max depth = 10 m) and contains fish, whereas lake 5 is a small, relatively shallow fishless lake (area = 1028.3 m², max depth = 1.4 m).

The numbers of frogs observed per m of shoreline in a given water body throughout the 1998 season were positively correlated with water temperature (likelihood ratio test, $P < 0.01$), air temperature ($P < 0.01$), maximum lake depth ($P < 0.01$), and presence of *H. regilla* tadpoles ($P < 0.01$) but were negatively correlated with presence of trout ($P < 0.01$, general additive model multiple $R^2 = 0.63$).

*Movement.*—By assessing the effects of covariates (number of *H. regilla* tadpoles, date, time between recaptures, and type of lake) on the probability of a PIT-tagged frog leaving a lake, we determined that a frog was least likely to leave a lake used primarily during midsummer when *H. regilla* tadpoles were common in the lake ($P < 0.01$, Fig. 3). In contrast, the probability of a frog leaving an overwintering lake (1 or 5) was not influenced by the relative abundance of *H. regilla* tadpoles ($P = 0.35$). The probability of a frog leaving a summer lake increased as the sea-
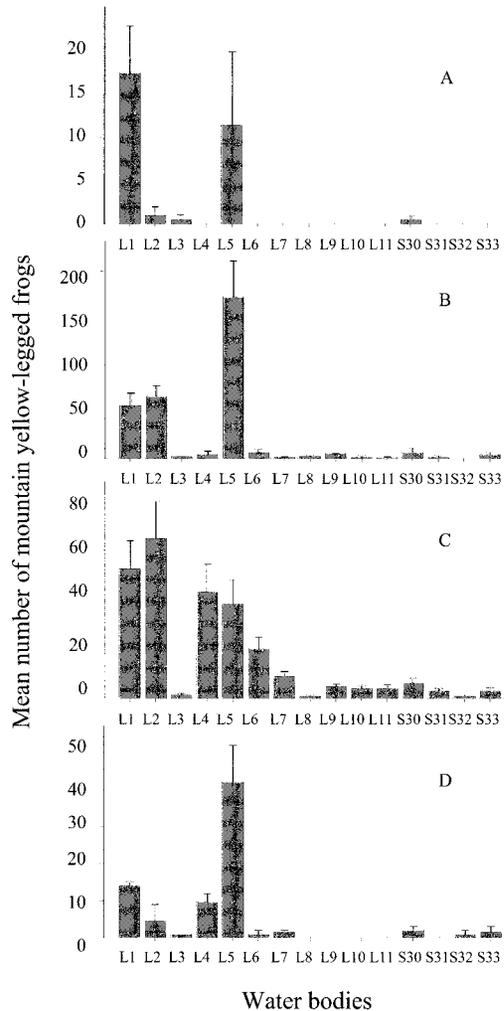


Fig. 2. Mean number of mountain yellow-legged frogs ($\pm$ 1 SE) observed in each water body (L = lake, S = stream) during 1998 count surveys separated into four time periods. (A) 11 July through 25 July when lakes were thawing; (B) 28 July through 8 August when breeding occurred (new egg masses found); (C) 11 August through 30 September when frogs were primarily feeding and sunning; (D) 4 October through 14 October when lakes were beginning to freeze. Note difference in scale among graphs.

son progressed ($P < 0.01$) with the highest likelihood of movement occurring between mid-September and October (Fig. 3). The probability of a frog leaving an overwintering lake decreased as the season progressed ($P = 0.09$), with the lowest likelihood of movement occurring between mid-September and October (Fig. 3). Factors such as air temperature, water temperature, sex of frog, and weight of frog did not appear to influence the probability of leaving a
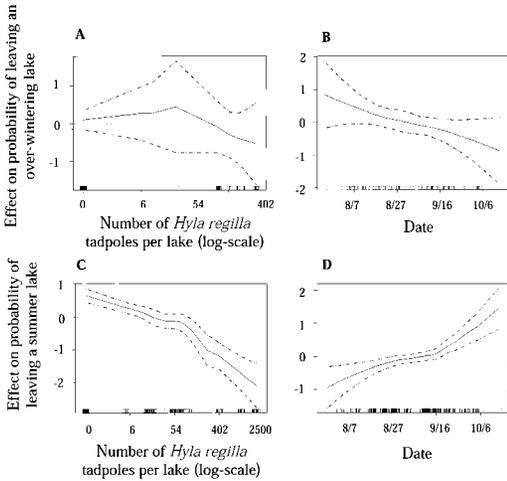
Fig. 3. Estimated effects of covariates (number of *Hyla regilla* tadpoles and date) on the probability of a frog leaving an overwintering lake (A and B) or a summer lake (C and D) using a general additive model with a loess smoother. Dotted lines represent approximate 95% confidence intervals and horizontal line indicates average effect level where 95% bounds completely above or below the line indicate significance. Hatch marks at the bottom of each graph represent data points.

lake (i.e., there were no significant relationships observed).

We calculated the number of movements of frogs between water bodies that were not connected by aquatic pathways (lakes 4 and 5, 4 and 6, 5 and stream 41) and, therefore, required overland movement. A total of 81 frogs (17% of the PIT-tagged frogs) made 178 overland movements that were a minimum of 66 m (straight line distance between lakes 4 and 6). Of the 81 frogs, nine moved overland between lake 5 and stream 41, a minimum distance of 142 m. In 1998, the mean date frogs were last seen in lake 5 before overland movement was 3 August ($\pm$ 1.9 days), and the mean date frogs were first seen in a different water body was 22 August ($\pm$ 1.8 days). In contrast, the mean date frogs were last seen in lake 4 or stream 41 before moving to lake 5 was 4 September ($\pm$ 1.9 days), and the mean date frogs were seen again in lake 5 was 28 September ($\pm$ 2.2 days).

Eighty-nine percent of the 390 frogs tagged in 1997 were recaptured within the study area in 1998. Of the frogs captured within 10 calendar days of each other in August 1997 and August 1998 ($n = 131$), 76% were found in the same water body both years. During August, site fidelity was highest in lake 2 (90%, $n = 70$) and lowest in the smaller ponds and streams including lakes 6, 8, 9, and 11 and streams 30 and 41

(39%, $n = 19$). In September, 59% ($n = 170$) were found in the same water body both years and in October, 97% ($n = 28$) were found in the same water body (21 of 21 in lake 5 and 6 of 7 in lake 1).

One adult female of the 81 frogs tagged in a lake 1 km southeast of the study area was recaptured in lake 5 on 23 September 1997. The same frog was recaptured back in the lake where it was originally tagged in the summer of 1998. A one-way trip requires a minimum of 420 m of overland travel and approximately 600 m of travel in a fast-flowing stream containing introduced trout.

## DISCUSSION

This study is the first to provide ecological and behavioral data over the entire activity cycle of mountain yellow-legged frogs from the time they emerged from overwintering until the lakes froze for the winter. Like some studies of other anurans (Breckenridge and Tester, 1961; Crump, 1986; Stumpel, 1987), our results suggest a pattern in which adult *R. muscosa* move among overwintering, breeding, and feeding sites. Apparently, mountain yellow-legged frogs are more narrowly distributed early in the season and late fall because of restricted overwintering habitat. As the lakes are thawing, adults move to breeding sites (based on the number and location of egg masses) then spread throughout available aquatic habitats in midsummer. Highest summer densities and total numbers of frogs were found in fish-free lakes that have many *H. regilla* tadpoles, are deeper than 1 m, and have warm near-shore water temperatures.

Although no well-defined pulses of movement were observed in the population, we did observe patterns that coincide with changes in activity from overwintering to breeding and feeding and back again to overwintering. During midsummer feeding months, the probability of a frog leaving a lake was low when relatively large numbers of *H. regilla* larvae occurred in the lake. Because we observed adult *R. muscosa* feeding on *H. regilla* larvae on several occasions (Pope, 1999; unpubl. data), we believe the correlation is the result of a predator/prey relationship between the two species.

Overland movements exceeding 66 m were observed in 17% of the tagged frogs, demonstrating that mountain yellow-legged frogs use terrestrial pathways as well as aquatic pathways. On average, overland movement away from overwintering lakes occurred in the beginning of August and movement to overwintering lakes

occurred in mid-September. Prior to a recent telemetry study conducted in Dusy Basin (Matthews and Pope, 1999), terrestrial movements of more than two or three hops (< 2 m) from water had not been documented. We also discovered one frog that moved approximately 1 km from a lake outside the study area to lake 5 and then was found back in the lake where it was originally tagged the following summer. This is the longest movement distance recorded for this species and includes a 72-m elevation gain and a minimum of 420 m of overland travel to enter the study area.

A high percentage (89%) of the frogs tagged in 1997 were recaptured in 1998, suggesting that overall adult survival was high even over the long winter. During this study, mountain yellow-legged frogs displayed high site fidelity between years and returned to the same overwintering and summer habitats in 1997 and 1998. Although typical spring conditions occurred much earlier in 1997 than 1998, perhaps making seasonal periods different for the frogs, we still saw a high percentage of frogs recaptured in the same water body, especially in October when they were preparing to overwinter. During August, site fidelity was lowest in smaller ponds and streams, suggesting that frogs may use these sites opportunistically when conditions are appropriate. Site fidelity and homing probably contribute to the relatively high survival of adult frogs in the basin because they enable relocation and occupation of specific habitats appropriate for winter survival.

At least some of the study population overwintered in a shallow lake (< 1.5 m) that likely froze to the bottom in the winter of 1997–1998 (a temperature probe placed at the bottom of the deeper lake 4 revealed freezing temperatures for over five months), yet numerous healthy frogs emerged from the same lake the following July. Most anuran species are susceptible to hypoxic and anoxic conditions (Penney, 1987; Storey, 1990) that are found in shallow high-elevation ponds of the high Sierra Nevada during the winter (Bradford, 1983). Although some frogs have developed physiological freeze tolerance (e.g., *Rana sylvatica*; Schmid, 1982; Storey and Storey, 1986; Layne and Lee, 1987), mountain yellow-legged frogs have not (Bradford, 1983). Mountain yellow-legged frogs should require lake depths greater than 4 m to overwinter because shallow lakes would become oxygen depleted and cause frogs to die of anoxia (Bradford, 1983). The frogs overwintering in lake 5 may avoid the freezing temperatures and low dissolved oxygen by spending the winter in underwater crevices. Matthews and Pope

(1999) used a burrow probe and radio telemetry during late fall when ice coated the surface of the lakes and located frogs over 1.5 m deep in granite cracks and crevices along the shoreline of the lakes in Dusy Basin. Frogs were under water when they were observed in the crevices although there were usually air pockets in the crevices (Matthews and Pope, 1999).

The behavioral characteristics reported here may facilitate selection of sites for mountain yellow-legged frog reintroductions or reserves. The Dusy Basin population is probably quite typical of remnant mountain yellow-legged frog populations in USFS Wilderness basins where trout are stocked in the larger lakes. Basins with a variety of deep lakes and shallow ponds, similar to Dusy Basin, may be the most promising reserve areas to maximize the chances of survival for mountain yellow-legged frog populations.

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