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A Telemetric Study of the Movement Patterns and Habitat Use of *Rana muscosa*, the Mountain Yellow-legged Frog, in a High-elevation Basin in Kings Canyon National Park, California

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ABSTRACTS.–In a high-elevation (3470 m) lake basin (upper Dusy Basin) in Kings Canyon National Park, California, we used radio transmitters on 24 mountain yellow-legged frogs (*Rana muscosa*) to gather basic information on their movement patterns. *Rana muscosa* have declined throughout their range in the Sierra Nevada and restoration plans require information on their movement ecology. Our study indicates that *R. muscosa* had different movement patterns and habitat associations during the 1997 summer period (August and September) compared to October when winter dormancy began. In August, visual surveys found frogs in 10 of the 11 lakes in upper Dusy Basin. During August most tagged frogs moved little (mean movement 77 to over five day periods) and all were found in the lake or adjacent stream where they were originally tagged. During September, movement increased compared to August Frogs moved from the original capture lake mean distances of 145 m,and moved cumulative distances of 315-466 m. By October, frogs were again sedentary (mean distance moved 43 mt and frogs were found in three of the 11 lakes in the basin. Moreover, mean home ranges (adaptive kernel 90% contours) also were different throughout the summer and were highest for frogs tracked during September (5336.2 m^2) compared to August (385 m^2, and October (52.8 m^2. Before this study it was assumed that R. muscosa over-wintered in the deepest portion of the lake, However, most lakes were frozen when our study ended, and tagged frogs were found nearshore under ledges and in deep underwater crevices suggesting that at least some *R. muscosa* over-winter in these nearshore areas. In this study, we found *R. muscosa* in different aquatic habitats over the course of their activity period and that they readily moved between these habitats using both aquatic and overland pathways. The movements appear to be associated with seasonal migrations between summer and over-wintering sites.

The mountain yellow-legged frog, *Rana muscosa*, was once one of the most common amphibians in high elevation aquatic ecosystems of the Sierra Nevada (Grinnell and Storer, 1924; Zweifel, 1955), but has become increasingly rare (Bradford et al., 1993; Jennings, 1996). The primary reason for the decline has been attributed to the introduction of trout into the originally fishless habitats where *R. muscosa* occur (Mullally and Cunningham, 1956; Cory, 1963; Bradford, 1989; Bradford et al, 1994; Jennings, 1996; Knapp, 1996). In recent surveys of over 1100 high elevation (>2500 m) lakes and ponds in the Sierra Nevada's John Muir Wilderness where fish stocking still occurs, mountain yellow-legged frogs were found in only 5% of the lakes (Matthews and Knapp, 1999). In contrast, Kings Canyon National Park, where fish stocking was terminated in the late 1970s, had frogs in 35% (379 of 1083) of the sampled lakes. Presumably, predation on tadpoles and young frogs has caused the elimination of *R. muscosa* from the majority of lakes inhabited by introduced fish (Bradford, 1989; Hayes and Jennings, 1986; Knapp and Matthews, in press). Remaining populations have become increasingly isolated and, therefore, are more susceptible to local extinctions without the opportunity for recolonization from neighboring populations (Bradford et a]., 1993), especially if movement is minimal.

Rana muscosa inhabits high-elevation (1370 to 3660 m) lakes and streams in the Sierra Nevada (Zweifel, 1955; Mullally and Cunningham, 1956). Due to the extreme environment encountered at high elevations (e.g., long winters, sustained freezing, and low temperatures), frogs may only be active for a few months during the summer after snowmelt and before the winter freeze. Tadpoles over-winter for at least two to three years (Zweifel, 1955; Cory, 1963, Bradford et al., 1993) and adults, like other anurans, presumably perform migrations to locate suitable areas for reproduction, feeding, and over-wintering (Baker, 1978; Sinsch, 1990). During the summer, tadpoles and adults seek the warmest thermal regimes (Bradford, 1982) and presumably feed to store fat reserves for winter dormancy that can last up to nine months (Bradford, 1983). Despite the information describing population declines, habitat use information on *R. muscosa* is lacking or speculative. *Rana muscosa* is highly aquatic and reportedly is never found more than two or three jumps from water (Mullally and Cunningham, 1956; Stebbins, 1985) suggesting that movement is restricted to aquatic pathways. And although never directly observed, *R. muscosa* is believed to over-winter in the deepest portions of lakes below the ice,thus requiring lakes >4 m deep for survival (Bradford, 1983).

Our study was designed to gather quantitative information on *R. muscosa* movements and habitat use during summer and fall. With this information, we should be able to more effectively restore some of their habitat in the Sierra Nevada. Movement distances and ranges will also be important for predicting recolonization. patterns and for metapopulation analysis (Hanski and Gilpin, 1997). During August-October 1997, we used telemetry to determine *R. muscosa* home ranges, their movement between lakes, and typical habitat associations during the summer and fall as lakes began to freeze.

MATERIALS AND METHODS

Study Area.–The study was conducted in upper Dusy Basin, Kings Canyon National Park, California (Latitude 37°5’40”, Longitude 118°33’45’) at an elevation of 3470 m (Fig. 1). The site supports a large population of *R. muscosa* of varying age classes. The glacially formed granite basin supports alpine fell field vegetation with low-growing herbaceous plants, dwarf shrubs, and few krummholzed white-bark pines (Holland and Keil, 1995). There are a series of streams, lakes, and ponds in the basin that are fed by snowmelt. The study area covers approximately 0.75 km^2. Our study focused on 11 lakes and ponds in Dusy Basin. All lakes and streams within the study area have been numbered and mapped using a Trimble Pro XL GPS system accurate to 1 m. Only lakes 1 and 3 (all water bodies being considered lakes) support self-sustaining populations of trout. Fish were also found in some of the connected creeks. This scenario will likely be typical of future refuges in National Forest Wilderness areas where, after re-introductions of mountain yellow-legged frogs, self-sustaining fish populations will likely persist in large lakes despite fish stocking changes. Lakes ranged in size from 114 m^2 to 5.3 ha and were 0.25 to 10 m deep.

Field Techniques.–We attached radio transmitters (Holohil Systems Ltd.; BD-2 transmitters; 15 mm x 7 mm x 4 mm thick) to 24 *R. muscosa* (snout-vent length > 55 mm) and documented movement from August 2-October 28,1997 (Table 1). We tagged frogs larger than 55 mm to minimize possible effects of transmitter weight.

To attach radio transmitters, a waist-belt made of aluminum ball or beaded chain was used, similar to that used on the California redlegged frog, *Rana aurora draytonii* (Rathbun and Murphey, 1996). The total weight of the attached transmitter and belt was approximately 1.5 g, which is below the 10% rule that attached objects not exceed 10% of body mass (Heyer et al., 1994). Frogs were hand-captured, weighed, measured, tagged,and then released at the capture site. Sex was determined by the enlarged nuptial pad at the base of the inner-most finger found in adult males (Stebbins, 1985). The transmitter batteries lasted about one month. To monitor movements over August, September, and October, we tagged frogs in three different groups: Group one consisted of 12 frogs monitored from 2 August-25 August, group two consisted of nine frogs monitored from 3 September-30 September, and group three consisted of three frogs monitored from 3 October through 28 October. We attempted to remove transmitters and belts just before the battery expired. After frogs were tagged they were relocated on

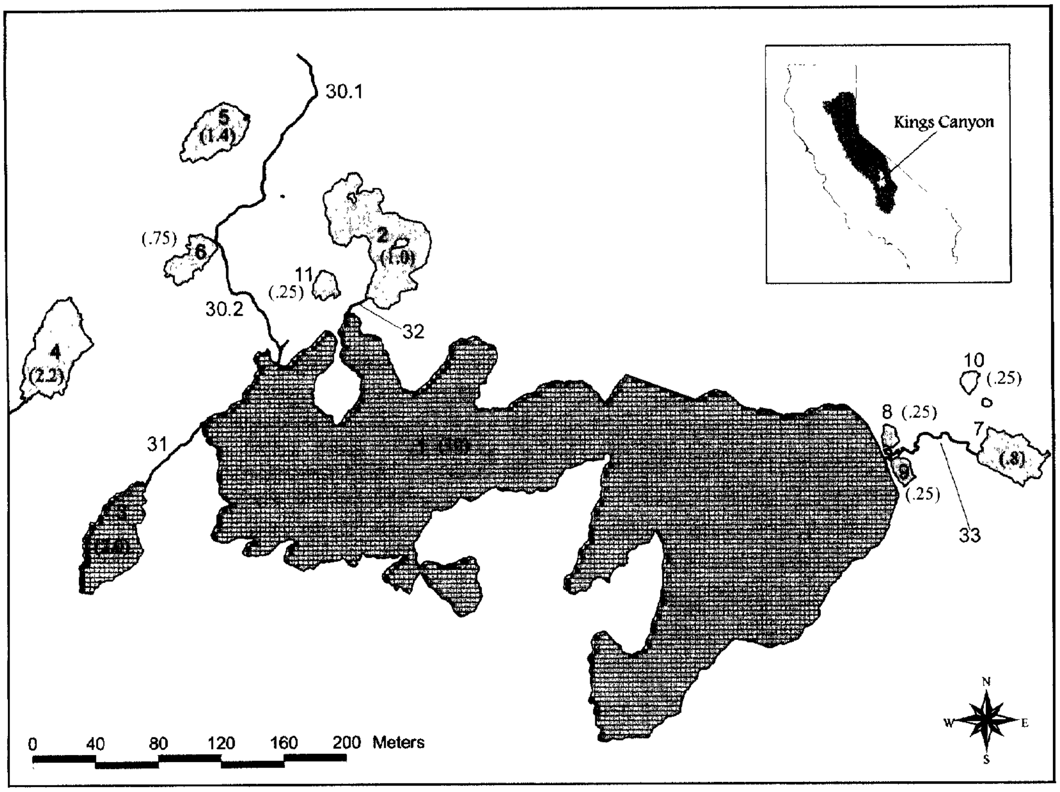

FiG. 1. Map of upper Dusy Basin, Kings Canyon National Park, showing takes 1-11 and associated creeks 30.1, 30.2, 31, 32, and 33. Numbers in parentheses represent maximum depth measured in meters. Grid indicates lakes with trout.

an almost daily basis and usually three times per day using an Advanced Telemetry Systems (ATS, Islanti, Minnesota) Challenger 4000 receiver and a hand-held three-element Yagi antenna. When frogs were relocated, we recorded their position (using GPS), their habitat association (rocks, bedrock, undercut bank, willow, silt), whether they were in water or on land, exposure (covered or exposed), and air temperature. If frogs were moving over land when trackers were present, trackers remained about 10 m from the frog and recorded movements, behavior, and distance traveled overland. GPS locational data were post-processed using a base station about 160 km away in Mammoth Lakes, and corrected positions were accurate to about 1m. We characterized the total available habitat by mapping each body of water in the study area and quantified the availability of nearshore habitats. Water temperature data were collected every five minutes for the duration of the study using Onset Optic Stowaway and Tidbit water temperature loggers. We also accessed air temperature data collected one km from the study site at the Bishop Pass California Department of Water Resources site at an elevation of 3415 m (http://cdec.water.ca.gov).

To determine the gross habitat shifts of the different *R. muscosa* life history stages in the study basin, we counted juvenile, subadult, and adult frogs at each water body about every seven days. In these counts, we walked the take perimeter during the warmest portion of the day (1000-1400) and recorded the number of individuals of each life stage. Throughout the study, we looked in the deeper portions of lakes, and searched under ledges and in crevices. To search under ledges and in crevices along the shoreline, we used a waterproof infrared video camera with a burrow probe (Burrow Probe 3, Fuhrman Diversified).

Data Analysis.–Maps drawn for each tagged frog documented their positions during the tracking period. Month-long home ranges were computed using the adaptive kernel method (Worton, 1989) in the CALHOME Home Range Analysis Program (Kie et al., 1996). We used the x-y la

TABLE 1. Summary of weights, lengths, days tagged, number of locations and home ranges for radio telemetered mountain yellow-legged frogs for August, September and October, 1997 + SE (ranges and number of frogs in parentheses) in Dusy Basin, Kings Canyon National Park, California.

	Starting weight (g)	Length (mm)	Days tagged	# locations	Home range (m^2)	Recovery weight (g)
August females	34.0 + 1.6 (23–43)(12)	70.0 + 1.9 (60–83)(12)	15.5 + 1.7 (8–23)(12)	29.8 + 3.8 (7–43)(12)	385.5 + 113.4 (19.4–1028)(10)	39.2 + 2.6 (23–49)(10)
September females	37.1 + 3.2 (19–46)(8)	71.9 + 2.2 (60–79)(8)	21.6 + 3.0 (10–31)(8)	37.7 + 4.4 (21–51)(8)	5099.0 + 1506.2 (53–9807)(7)	38.1 + 3.1 (34–47)(5)
September male (1)	19	60	26	41	6990	19
October female (1)	43	76	22	22	3.2	—
October males	22.3 + 3.8 (18.5–26)(2)	63.5 + 5.5 (58–69)(2)	17.5 + 5.5 (12–23)(2)	22.5 + 0.5 (22–23)(2)	77.5 + 4.5 (73–82)(2)	—

to determine if movement habits changed over the tracking period, mean distance traveled per month was compared (Kruskal-Wallis ANOVA on ranks) for August, September, and October. To equalize comparisons, we computed average daily movement over three 5-d periods for each month. This allowed us to compare time periods in which equal point locations were recorded for the frogs. Individual frogs in each 5-d time period were used for the unit of replication. In addition, we computed the cumulative distance moved for each frog each month.

We used t-tests (one-sided, ($\alpha \leq 0.05$) to test whether mountain yellow-legged frogs used habitat features in different proportions to what was available (Zar, 1996). We summarized the proportion of observations for individual frogs that occurred within each habitat feature then computed the mean proportion using the individual frogs as the unit of replication. These means of habitat feature associations were compared with the known proportion (constant) of the available habitat features for each lake where the frogs were found. The proportion of habitat features was calculated separately for August, September, and October and only included the lakes where tracked frogs were found during those time periods.

To determine if there were differences in the proportion of observations in exposed versus covered or protected habitats, we first compared the means for August, September, and October with ANOVA and then used the Student-Newman-Keuls multiple range test. We summarized the proportion of exposed and covered observations for individual frogs, and then compared the mean values using individual frogs as the unit of replication. A frog was considered exposed if it was visible to the observer even if it was under a willow or undercut bank and was considered covered when it was invisible to the observer by being under a rock or in a deep hole.

RESULTS

Twelve frogs were tagged and followed during August (Table 1) and they remained in the original lake or creek where captured (Fig. 2). Home ranges were computed for 10 frogs (two frogs shed their tags and there were not enough points to compute home ranges) and their movements were confined to areas ranging from 19.4 to 1028 m^2.

In contrast, home ranges were larger in September (ranging from 53 to 9807 m^2) and six of the nine individual frogs tagged in September moved from their original capture lake by the end of the month. For example, frog #415 (Fig. 2A) was tagged in lake 4 where it stayed for five

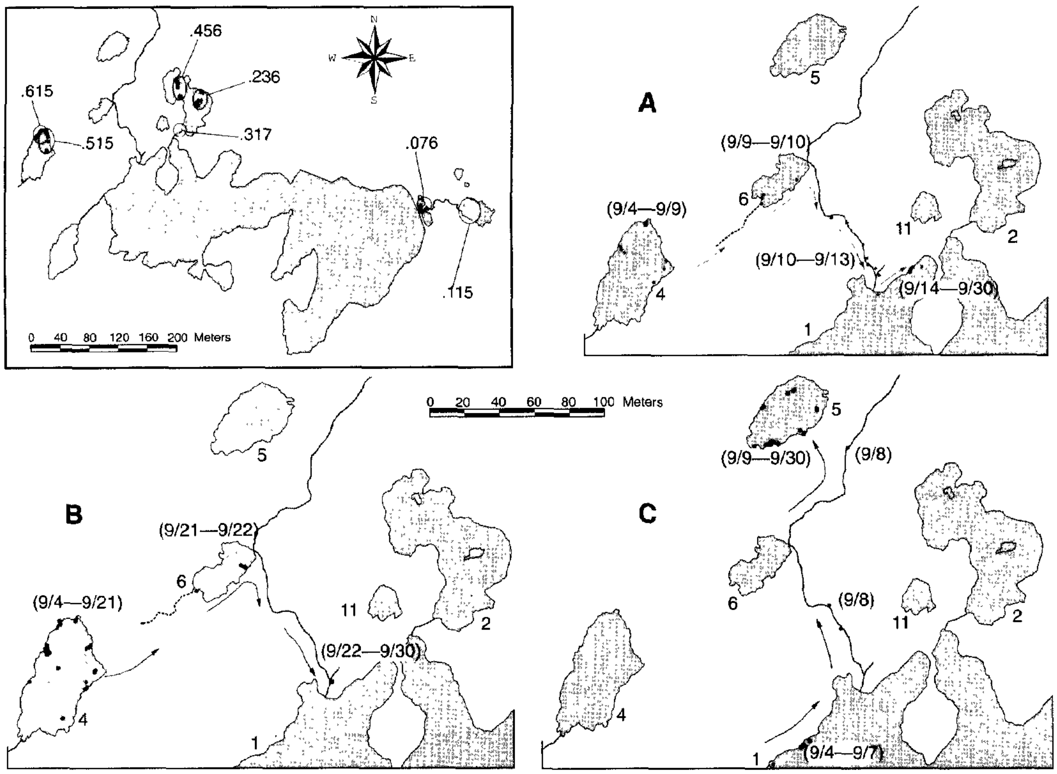

FIG. 2. Map of tagged frog locations during August 1997 for seven transmitters (076, 115, 236, 317, 456, 515, and 615) and magnifications displaying movement in September for transmittered frogs 415 (A), 477 (B), and 575 (C). Arrows show estimated movement route based on tracking frogs three times per day. The overland movements in both A and B were observed by researchers from the approximate middle point between lakes 4 and 6. GPS was used to track the exact paths represented by the dashed lines.

days until it moved overland into small lake 6. it then moved into the larger lake where it stayed until its transmitter was removed on 30 September. Frog 477 (Fig. 2B) moved in a similar path, and both 415 and 477 were observed at mid-day when air temperatures ranged from 5.5 to 12.5 C as they moved overland from lake 4 to lake 6. In about 40 min they moved 66 m over dry rocky terrain to reach lake 6. Once these frogs reached lake 6 they remained stationary for two days and then followed a stream into the 5.3 ha. lake 1. Frog #575 was tagged on 4 September in a creek adjacent to lake 1 where it stayed for three days (Fig. 2C). By 9 September it moved into lake 5. The three frogs that did not move out of their original capture lake in September were not tracked for the duration of the month because their transmitters fell off.

The three transmittered frogs tagged in October stayed in the same lake where they were tagged and limited movement was recorded (mean home ranges 3.2 to 82m^2). By the end of October, the transmittered frogs were never out in the open and were found up to 2 m under ledges and in rock crevices along the shoreline. In addition to the transmittered frogs, we also found several other mountain yellow-legged frogs in shoreline crevices using the burrow probe. Many of these frogs had previously been captured and individually tagged using passive-integrated transponder (PIT) tags, so we were able to observe a consistent behavior throughout the population. Many of the PIT tagged individuals had also moved from other lakes within the basin to these similar over-wintering habitats (Pope, 1999). Lakes and ponds were frozen in the nearshore area by the end of October and minimum air temps ranged between 0 and - 14 C. No movement away from banks and nearshore ledges was observed in October.

The majority of the crevices where frogs were found were in fractured bedrock that sloped steeply into the water along the shoreline. Water depth was between 0.4 m and 1.2 m and the entrance to the crevices ranged from 0.2 m to 1 m below the surface of the water. Frogs were always in water when they were observed in the crevices although in some crevices there was an obvious connection with air. The entrances were usually very narrow (~5 cm diameter) but some then opened to larger areas deeper into the crevice. We were restricted by the diameter and maneuverability of the probe, but in a couple instances were able to get about 2 m into the crevices. At that point there was at least 1.5 m thickness of granite above the crevice.

Mean home ranges were highest for frogs tracked during September (5336.2m^2 ± 1325 SE, N = 6) compared to August (385m^2 1 ± 113 SE, N = 10) and October (52.8m^2 , ± 25 SE, N = 3; ANOVA, P < 0.05). The mean distance traveled over five day periods was significantly higher in September compared to August and October (Kruskal-Wallis ANOVA on ranks, P < 0.001). Frogs moved about 145 m per five-day period in September, 77 m in August, and 43 m in October. The cumulative distance moved over the tracking month was also highest in September and ranged from 72 to 443 m in August, 315 to 666 m in September, and from 65 to 102 m in October.

In general,frogs used habitat features in different proportions to what was available (onesided t-test, α < 0.05; Fig. 3). For example, in August frogs used undercut bank and willow habitats in higher proportions to what was available and used bedrock less than what was available (Fig. 3). In September and October frogs were associated with rocky habitats significantly more than was available. In addition, habitat associations changed from month-to-month. Frogs were associated with rocky habitats more often in September and October than August (75% and 79% of observations compared to 31%). In contrast, frogs were never found associated with willow or silt in October but were found in these habitats in 37% of the observations in August (Fig. 3).

There was a greater mean proportion of observations of tagged frogs in exposed habitats in August (mean proportion = 0.34, N = 12 frogs) and September (mean proportion = 0.41,N = 8 frogs) compared to October (mean proportion = 0, N = 3 frogs) (normality and variance tests passed, ANOVA, P < 0.001; SNK multiple comparison, P < 0.001). In August and September, frogs were typically found in exposed habitats during the day and in covered habitats at night, early morning, and during stormy or cold periods, whereas in October frogs were only found in covered habitats (100% of observations under rock ledges or in bedrock crevices).

Frog counts also indicated a change in distribution from August through October. Frogs were found in 10 of the 11 lakes (all except lake 3) surveyed in Dusy Basin during August. In contrast, frogs were found in three of 11 lakes (lakes 1, 4, and 5) surveyed during October. Counts then declined to almost 0 in all lakes coincident with declines in air temperature (Fig. 4). In lake 4, frog counts ranged from 45-80 per count in early August and by early October two adult frogs were found. Counts declined in all of the lakes including lakes 1 and 5, which appeared to serve as the main over-wintering lakes, because frogs were less likely to be out in the open as the season progressed and temperatures decreased.

Air and water temperatures declined from August through October and minimum temperatures were especially low after several snowstorms in September and October (2, 11, 18 September and 9 October). While snowstorms are normal in the Sierra Nevada in the summer, the takes may not freeze some years until November. However, the lakes in Dusy Basin began freezing earlier in 1997 compared to previous years (G. Durkee, pers. comm.).

Frogs were checked periodically to evaluate whether the transmitters were causing any adverse effects (e.g., abrasions or behavioral problems). There appeared to be little or no adverse reaction to the transmitter belts and 10 of 14 frogs gained weight from the time they were tagged until the transmitter was removed. Similar weight changes were also observed in our PIT tagging study of 582 mountain yellow-legged frogs (Pope, 1999). Three frogs had small skin abrasions (~ 1 mm diameter) on the ventral side of their waists when the transmitters were removed but it is not believed that they caused behavioral modifications. Monitoring of these individuals revealed rapid healing (within two days). None of the frogs were ever found entangled in vegetation or wedged between rocks.

DISCUSSION

Our study indicates that *R. muscosa*'s movement patterns and habitat associations shifted in August, September, and October. Because of the stormy or cold periods, whereas in October shortened active season in high-elevation lakes in the Sierra Nevada, August presumably represents an important feeding time. In Dusy Basin during August, mountain yellow-legged frogs were distributed in 10 of 11 lakes and in all creeks, were fairly sedentary, and were

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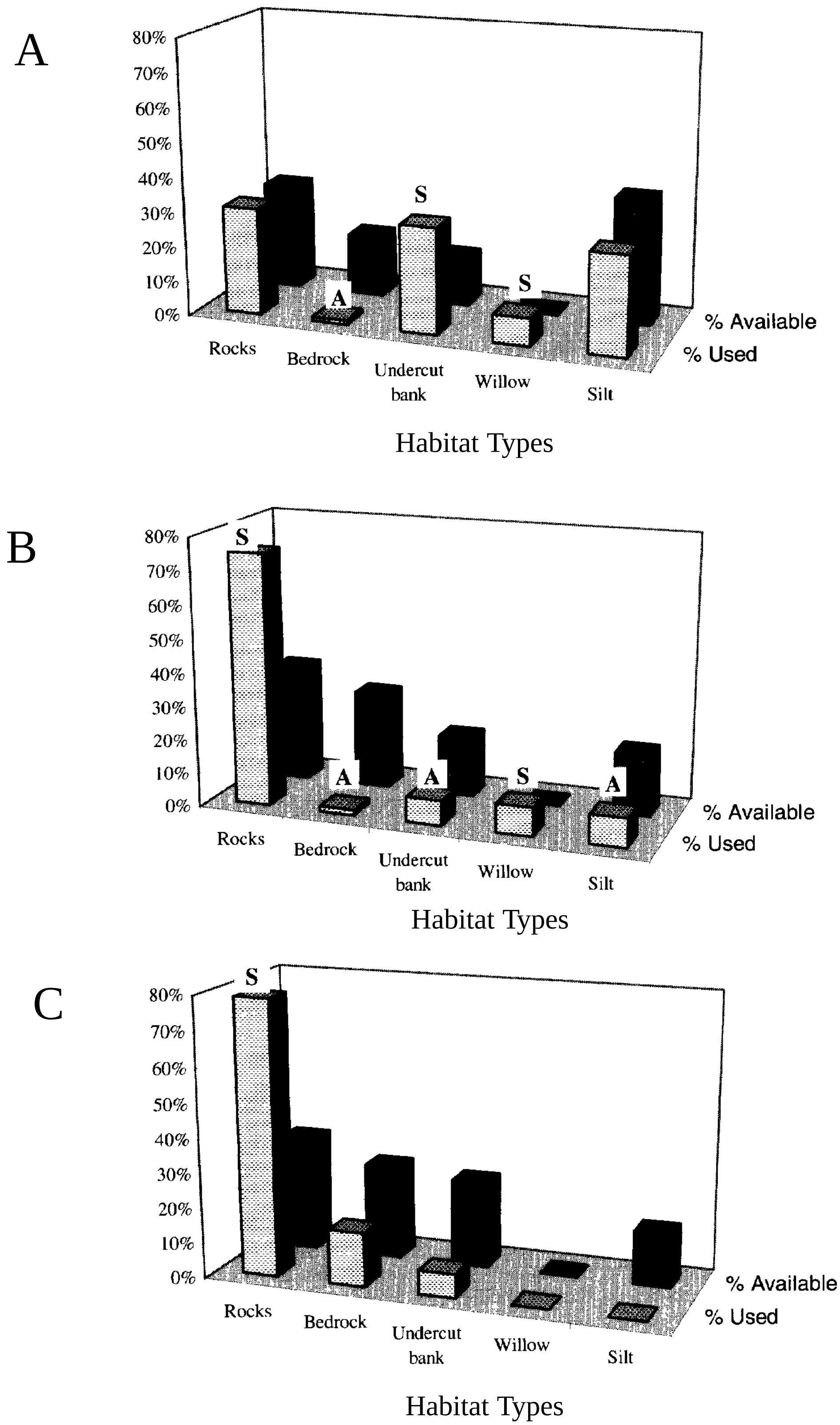
Fig. 3. Habitat use information for tagged frogs in August (A), September (B), and October (C), showing percentage of observations associated with rocks,bedrock,undercut bank, willow, and silt as compared to availability of those habitats in the lakes where they were found. Significant differences between the % available and % used (one-sided t test, a ≤ 0.005) are represented by an A (avoided) or S (selected).


A
80%
70%
60%
50%
40%
30%
20%
10%
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S
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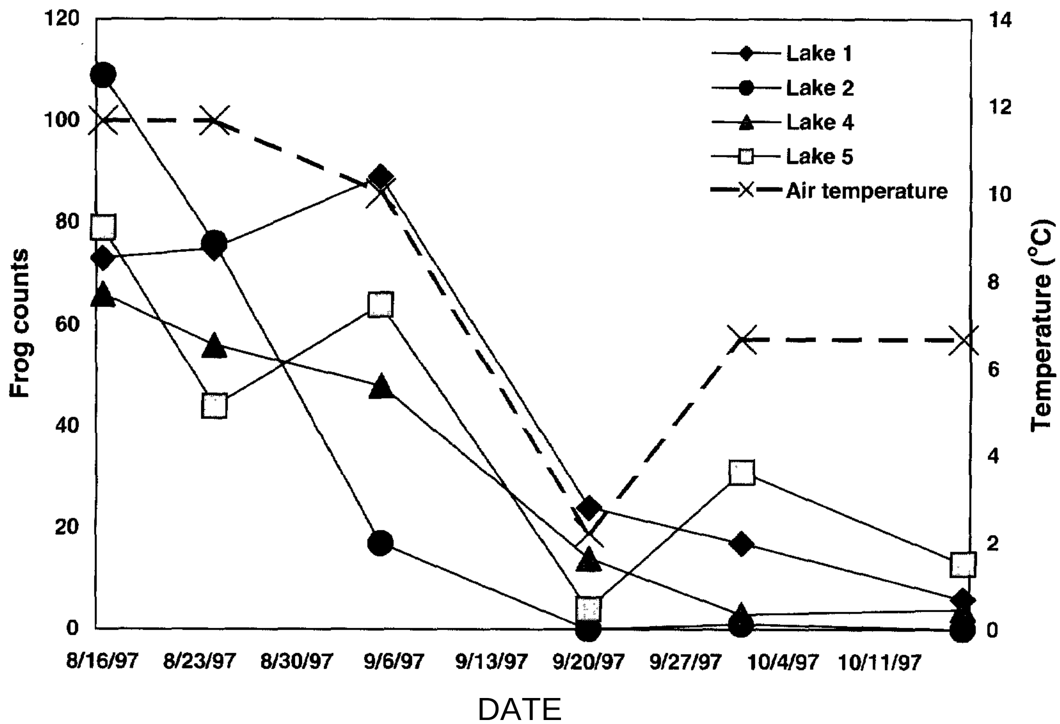

FiG. 4. Visual frog counts for lakes 1, 2,4, and 5 from August 16 through October 11, 1997 and air tern-peratures at the time of the counts (measured at the California Department of Water Resources station in Dusy Basin about I km from study lakes).

often out in the open. Frogs were most abundant in the smaller shallow ponds where water temper-atures were warmer and Pacific tree frog (*Hyla regilla*) tadpoles were most abundant. Indeed, mountain yellow-legged frogs were observed on three occasions eating Pacific tree frog tadpoles (Pope, in press). By mid-September, most mountain yellow-legged frogs moved several hundred meters and by October were found only in one large (5.3 ha), deep (10 m) lake with fish and two small (1028-1747 m^2), shallow (1.2-2.2 m) lakes without fish. By the end of October movement was uncommon and frogs were found close to shore either under rock ledges or in crevices. We suspect that frog habitat require-ments changed from being food driven during August and early September to winter shelter driven in late September and October. We be-lieve that the trans-mitters had little or no effect on frog behavior because we observed similar movements and habitat use in an associated study using small (2 mm diameter) PIT tags on 582 frogs (Pope, 1999).

Before this study, it was assumed that mountain yel-low-legged frogs over-wintered in the deepest portions of lakes under ice similar to some other ranids (Emery et al., 1972), and that survival was highest when the lakes did not freeze to the bottom (Bradford, 1983). Because more frogs survived in deeper lakes (> 4 m) after a severe winter,it was believed that mountain yel-low-legged frogs would have higher survival rates if they accessed the more oxygen rich, deep lakes (Bradford, 1983). We concluded that frogs in Dusy Basin over-winter in near-shore crevices and thus, shal-low lakes and the shallow portions of deep lakes serve as important winter habitat. In our study,radio transmit-ters and the burrow probe allowed us to locate frogs as lakes began to freeze for the winter and when there was about a two-inch layer of ice along the nearshore lake surface. At this time, frogs were always associated with deep rock crevices under banks and no observations of frogs moving to the deeper sections of lakes were recorded. Even when *R. muscosa* moved to the deeper 10 m lake (lake 1),the transmittered frogs did not move to the deepest section and instead stayed close to shore where water depths ranged from 0.2 m to 1.5 m. Frogs were also observed (using the burrow probe) in groups of more than eight individuals under ledges in lake 1 suggesting they may aggregate while over-wintering. The granite surrounding the over-wintering sites likely serves to insulate the frogs from the extreme winter temperatures much like underground burrows and caves insulate hibernating mammals. Even so, *R. muscosa* like other ranid frogs may withstand temperatures below freezing (Schmid, 1982; Storey and Storey, 1986; Storey, 1990). Indeed,it is believed the limiting factor in winter is low dissolved oxygen and not low temperature (Bradford, 1982, 1983). Thus, *R. muscosa* may be able to survive over winter in nearshore holes, crevices, and ledges if there is an adequate supply of oxygen either in the water or air.

Although past reports have not documented mountain yellow-legged frogs more than a few jumps from water (Mullally and Cunningham, 1956; Storer and Usinger, 1963), we saw two transmittered frogs and one additional frog move over dry land at least 66 in. Thus, to migrate to their presumed over-wintering habitat, overland movements may occur. The frogs traveled in short bursts of two to five hops,and appeared to rest between bursts. Movement was in a fairly direct, straight- line path (except when avoiding obstacles) and the routes used involved the shortest distance traveled over dry land.

In light of this study, restoration basins should include lakes with variable shorelines and depths to allow for their changing habitat needs. Their movement and wider distribution in the summer suggests that mountain yellow-legged frogs could recolonize future restoration basins if located near existing populations. Their more restricted distribution in the late fall suggests they may have unique over-wintering habitat requirements and further study of particular lake features and microhabitats serving as overwintering sites is necessary.

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