SPATIAL ECOLOGY OF AN INLAND POPULATION OF THE FOOTHILL YELLOW-LEGGED FROG (*RANA BOYLII*) IN TEHAMA COUNTY, CALIFORNIA

HUMBOLDT STATE UNIVERSITY

By

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A Thesis

Presented to

The Faculty of Humboldt State University

In Partial Fulfillment

Of the Requirements for the Degree

Master of Arts

In Biology

(December 2008)

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ABSTRACT

SPATIAL ECOLOGY OF AN INLAND POPULATION OF THE FOOTHILL YELLOW-LEGGED FROG (*RANA BOYLII*) IN TEHAMA COUNTY, CALIFORNIA

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Understanding the movements of anurans is important for developing successful conservation plans because breeding, foraging, and overwintering resources are often separated by time and space. I used radio-telemetry to study the movements and habitat use of the Foothill Yellow-legged Frog (Rana boylii), a stream-dwelling species experiencing significant population declines. Seventy-nine frogs (11 males and 68 females) inhabiting an inland watershed were opportunistically captured, fitted with radio-transmitters, and monitored during three two-month study periods. Females were tracked during one spring (2004) and two fall/winter seasons (2004 and 2005), while males were tracked during one spring season (2004). Site-specific weather conditions were monitored to evaluate associations with frog movement and habitat use. Movements and habitat use were highly variable among individuals during all study seasons. Frogs either centered activities at their initial capture locations or moved hundreds to thousands of meters among different stream habitats. The greatest distances traveled by male and female frogs were 0.65 km and 7.04 km, respectively. Frog size and age were independent of seasonal distances traveled. Mobile males and females moved 65.7 and 70.7 m/day (median), respectively, in spring and mobile females moved 37.1 m/day (median) in fall/winter. The maximum travel rate was 1386 m/day. Frogs used watercourses as movement corridors and rarely moved > 12 m from the stream channel. Spring movements were not associated with weather, but fall/winter movements were associated with increasing rain and humid conditions. Females showed an upstream directional bias during spring movements and a downstream bias for fall/winter movements. The results from this study highlight the need to manage *R. boylii* populations at the watershed scale to ensure protection of spatially separated resources commonly used by individuals throughout the year.

DEDICATION

I dedicate this thesis to my family, Ronald J. Bourque, Vicki M. Bourque, and Jason R. Bourque, who inspired and encouraged my interest in wildlife and passion for herpetology.

ACKNOWLEDGMENTS

I thank my advisor Dr. Sharyn Marks for her editorial comments, encouragement, and support. I also thank my committee members Dr. Jim Howard, Dr. Matt Johnson, and Dr. Steve Sillett for their thoughtful comments and criticisms during the design and review of this project. Their inputs greatly influenced and improved the quality of this study. I am indebted to the members of the Sunflower Coordinated Resource Management Plan for granting me permission to conduct this study on their lands. Bill Burrows deserves special recognition for his perpetual support and inspiration. I thank my good friend and colleague Justin Garwood. His passion and tenacity for researching the movement ecology of ranid frogs greatly influenced the development of this project and his continuous input and encouragement throughout the years contributed greatly to its completion and success. I thank Dr. William Bigg, Dr. Megan Donahue, Karen Pope, and Garth Hodgson for assistance and advice with data analyses. I am also sincerely grateful to many others who contributed to the completion of this thesis. These people include: Anthony Baker, Melissa Dean, Clara Wheeler, Monty Larson, Jamie Bettaso, Rebecca Degagne, Casey Justice, Matt Thomas, Rebecca Studebaker, Steve Norman, Andrew Suppinger, and members of the Humboldt State University Herpetology Group.

Financial support for this study was received from the Bureau of Land Management (awarded to S. Marks), Humboldt State University Department of Biological Sciences Master's Student Grants (2004 and 2005), Woolford-Hegy Scholarship, and Tehama County Resource Conservation District.

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INTRODUCTION

The Foothill Yellow-legged Frog (*Rana boylii*) is a highly aquatic ranid that ranges from southwestern Oregon to northern Baja California, Mexico (Loomis, 1965) at low to mid-elevations (0-2,040 m) west of the Sierra Nevada and Cascade Mountains (Fitch, 1938; Marr, 1943; Stebbins, 2003; Storer, 1925; Zweifel, 1955). This species is the smallest ranid in the Pacific Northwest (snout-urostyle lengths < 82 mm and weight \leq 42 g; Hayes et al., 2005), and unlike congeners that occupy ponds and marshes, it resides exclusively in rivers and streams (Duellman and Trueb, 1986). Rana boylii was once ubiquitous in low-gradient drainages but populations have since declined, and in 1994 this frog became a candidate for federal listing (USDI, 1994) and was listed as a California Species of Special Concern (Jennings and Hayes, 1994). The severity of population declines varies within its range, but the most alarming declines have occurred throughout inland regions where many populations are considered either threatened or extinct (Jennings and Hayes, 1994). Factors implicated as causes for these declines include habitat alteration and destruction (Lind et al., 1996), the introduction of bullfrogs (Lind et al., 2003; Moyle, 1973), and pesticides (Davidson, 2004; Davidson et al., 2002). In recent years populations have declined further (Lind, 2005), but conservation efforts have been hindered because the ecology of this species is poorly understood (Jennings and Hayes, 1994; USDI, 1994). Several qualitative and quantitative descriptions of R. boylii ecology exist (Fitch, 1938; Hayes and Jennings, 1988; Kupferberg, 1996; Lind et al., 1996; Storer, 1925; Van Wagner, 1996; Zweifel, 1955), but much of what is known is restricted to its breeding requirements. *Rana boylii* breed in shallow, slow flowing stream habitats with cobble and boulder substrates (Ashton et al., 1997; Stebbins, 2003). However, habitats critical to the survival of this species must also provide post-metamorphic life history stages with resources for nutrient acquisition (i.e., food and water) and shelter (e.g., protection from predators and harmful environmental conditions). Among anurans, habitats that provide breeding, foraging, and overwintering resources are often distributed in discrete patches and often require individuals to migrate annually, sometimes traveling greater than 1 km between habitats (Sinsch, 1990).

Until recently, information on *R. boylii* movements and habitat use outside of the breeding season was limited to only one study (Van Wagner, 1996) and anecdotal observations (Kupferberg, 1996; Twitty et al., 1967), which demonstrated that individuals at least occasionally make modest movements (≤ 600 m) between breeding and non-breeding habitats. However, no detailed studies have effectively monitored the movements of individual frogs to accurately quantify the extent, frequency, directionality, timing, and routes of travel within and among habitats distributed across the landscape. Detailed information on the spatial ecology of this species is urgently needed to develop conservation strategies that will ensure protection of critical non-breeding resources (i.e., foraging and overwintering sites) and migration corridors at the appropriate spatial scale. This information is also essential for assessing the impacts of management activities (e.g., cattle grazing, gravel mining, water diversions, and impoundments) on extant populations, stream restoration, and the potential for future recolonization where populations have been extirpated.

This study describes *R. boylii* spatial ecology using radio-telemetry to monitor the movements and habitat use of adults in an undammed inland watershed. The specific objectives of this study were to: 1) quantify the distances traveled, directionality, rates, and routes of movements for male and post-reproductive female *R. boylii* during the breeding and non-breeding seasons, 2) determine if *R. boylii* move among breeding, summer foraging and overwintering habitats and describe what habitat characteristics differ between habitat types, 3) examine if frog movements differ by frog size or age, and 4) determine if the timing of frog movements are associated with seasonal changes in site-specific weather conditions. The results of this study provide insights into the postbreeding resource needs of *R. boylii* and can be used as a foundation for future decisions on species conservation.

MATERIALS AND METHODS

Study Area

This study was conducted in the Red Bank Creek watershed, within the boundaries of an area managed by the Sunflower Coordinated Resource Management Plan (SCRMP), located in Red Bluff, Tehama County, California (40° 3' 48.1" N, 122°36' 25.5" W; Figure 1). This watershed originates in the foothills of the Yolla Bolly Mountains and is a tributary to the North Sacramento River Basin. The landscape has moderate topographic relief (elevations ranging between 300-550 m) and is generally composed of loose erosive soils (schist) carved into a series of low rolling ridges. The dominant terrestrial plant community is comprised of mixed chaparral (e.g., *Manzanita* sp. and *Ceanothus* spp.) and gray pine (*Pinus sabiniana*) with a transition to oak woodlands (*Quercus* sp.) and grasslands along the eastern edge of the study site.

The region has a Mediterranean climate. It is hot and dry most of the year (April-October) with a distinct rainy season (average annual precipitation = 58 cm) that occurs from November-March (Western Regional Climate Center 2003). During spring (April-June) the average daily air temperature is 16.4° C (range = 7-24°C), and temperatures rise throughout the summer with daily highs often reaching 35° C. During the fall and winter months (October-March), average daily air temperature is 10.3° C (range = 0-20°C) and rarely drops below freezing. These mild winter conditions allow *R. boylii* to be active year-round (personal observation).

Data for this study were collected from a population of *R. boylii* in the upper Red Bank Creek watershed (drainage area $\approx 47.7 \text{ km}^2$). Habitats available to *R. boylii* in the study area included an ~ 8 km segment of the main channel and adjoining tributaries (Figure 1). Red Bank Creek is the dominant aquatic resource. This perennial low gradient creek is 4-10 m wide and contains a full range of meso-habitats (e.g., riffles, runs, glides, and pools). Average water depth is 0.25 m and the deepest pools did not exceed 0.75 m. Average base flows recorded in 2004 and 2005 were 2.5 cubic meters per second (m³/s) in spring and 0.08 m³/s in late fall. Average daily spring water temperature was 16.8°C (ranges = 10-22°C) and average fall/winter temperature was 9.9°C (range = 1-18°C).

Tributaries feeding Red Bank Creek are numerous and include intermittent and ephemeral creeks. There are three intermittent creeks (Keystone Creek, Abernathy Canyon Creek, and an unnamed creek) within the study area. These low gradient (< 5%) drainages are 2-3 m wide and have flowing surface waters during the wet season, but dry almost completely by early-mid summer. Remnant pools do occur in these waterways and can provide habitat for frogs year-round. Ephemeral creeks are the most abundant type of watercourse with respect to length of stream channel, but these steep (> 5% gradient) and narrow (< 1 m) drainages have flowing surface waters only during substantial rains and dry completely within weeks following. Therefore, these habitats are unsuitable for frogs during most of the year.



Figure 1. Map of the study site showing ephemeral (dashed gray lines), intermittent (solid gray lines), and perennial creeks (solid black lines) in the Red Bank Creek watershed.

Riparian and aquatic vegetation is sparse throughout the study area and is restricted to perennial and intermittent drainages. When present, riparian vegetation occurs in narrow bands (< 3 m) and is dominated by willows (*Salix* spp.) and alders (*Alnus* spp.) but occasionally includes cottonwoods (*Popular* spp.) and mulefat (*Baccharis* spp.). Aquatic vegetation generally occurs in deeper slow-flowing habitats (e.g., pools and glides) and consists of rushes (*Juncus* spp.) and cattail (*Typha latifolia*).

Despite the occurrence of livestock grazing and reservoirs within the surrounding landscape, this watershed apparently has a natural hydrological regime and supports a healthy population of *R. boylii*. There is also a diverse assemblage of native aquatic vertebrates including Sacramento pikeminnow (*Ptychocheilus grandis*), resident rainbow trout (*Onchorhynchus mykiss*), California roach (*Lavinia symmetricus*), Sacramento sucker (*Catostomus occidentalis*), western pond turtle (*Actinemys marmorata marmorata*), aquatic garter snake (*Thamnophis atratus hydrophilus*), Pacific treefrog (*Hyla regilla*), and western toad (*Bufo boreas*). Non-native bullfrogs (*Rana catesbeiana*), sunfish (*Lepomis sp.*), largemouth bass (*Micropterus salmoides*), and catfish (Ictaluridae) also occur within the study area, but these species are mainly restricted to reservoirs and are uncommon in lotic habitats (unpublished data).

Monitoring Movements

I monitored the movements and habitat use of adult *R. boylii* using radio telemetry and incidental recaptures during one spring breeding season (April-June 2004, S1) and two consecutive fall/winter non-breeding seasons (October-January 2004, FW1; and 2005, FW2). These periods encompassed a seasonal transition between the dry and wet season and were selected to maximize the probability of detecting seasonal movements (White and Garrott, 1990). Adult *R. boylii* were opportunistically captured at the beginning of each study season during visual encounter surveys (VES) and eye-shine surveys conducted along Red Bank Creek and intermittent tributaries. I attempted to restrict initial captures to a 1 km reach along Red Bank Creek. However, low captures occurred in this area during each season and surveys were expanded to a larger segment (~ 4 km) of Red Bank Creek and intermittent tributaries.

Visual encounter surveys were conducted during daylight hours by trained surveyor(s) walking both banks of a survey reach while visually searching the shoreline for adult frogs (Crump and Scott, 1994). Eye-shine surveys involved the same methods, but these surveys were nocturnal and thus surveyor(s) used a Nite Sport II light (Nite Light, Little Rock, Arkansas, USA) to visually detect frogs using light reflected from frogs' eyes (Corben and Fellers, 2001). Since *R. boylii* are diurnal and nocturnal (Van Wagner, 1996), both methods were employed to improve capture success and expedite radio-transmitter deployment.

Selection of study frogs was not random. A bias towards adult frogs was necessary to keep transmitter packages below 10% of a frogs' body mass, a standard limit used to minimize the potential effects from transmitter attachment on frog movement and behavior (Richards et al., 1994). I attempted to capture all adult frogs (~ 50 mm snouturostyle length) observed with a net or by hand. After initial capture, snout-urostyle length (SUL, ± 1 mm) was measured using calipers, mass was measured with a PesolaTM spring scale (± 0.5 g, Forestry Suppliers, Jackson, Miss.), and sex was determined based on sexual characteristics (e.g., nuptial pads on males). Frogs greater than 50 mm SUL were individually marked with passive integrated transponder (PIT) tags (BioMark, Inc., Boise, ID; (Donnelly et al., 1994). These tags were implanted subdermally via a small Vshaped incision made anterior to the sacral hump (Sweet, 1993).

Frogs exceeding the minimum weight requirement were fitted with a radiotransmitter, until all transmitters were deployed. I used BD-2 radio-transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) with a lifespan of three weeks (0.98 g) or seven weeks (1.35 g). Two sizes of radio-transmitters were used to allow for a wider size range of frogs to be monitored. Radio-transmitters were attached to R. boylii using a derivation of the lightweight beaded-belt method (Muths, 2003). I used beaded-belts (mean mass = 0.15 g) constructed of Czech glass seed beads (size 13) strung onto Stretch Magic[®] jewelry cord (0.5 mm diameter, Pepperell Braiding Company, Pepperell, MA). Belts were fitted around the frog's waist, inserted through a tube built into the anterior end of the radio-transmitter, tied off, and the knot was glued. Belts were sized loosely to permit free movement of the transmitter package around the waist but tight enough to prevent the belt from slipping off the frogs' legs. During PIT tag implantation and radiotransmitter attachment, frogs were immobilized using a device designed for restraining anurans (Bourque, 2007). Handling time during these procedures was ≤ 15 minutes, after which frogs were immediately released at the point of capture. When frogs were lost (i.e., predated or shed radio-transmitter) new study frogs were added as soon as transmitters became available.

I relocated radio-tagged frogs during daylight hours every 1-20 days (mean = 3 days) with a TR-4 Telonics receiver (Telonics, Inc., Mesa, Arizona) and an H-Adcock directional antenna. Frogs were relocated in a randomized sequence during each tracking day to avoid temporal sampling bias among individuals. Frog locations were recorded precisely with Global Positioning System (GPS; Geoexplorer 3, Trimble Navigation Ltd., Sunnyvale, California, USA) if individuals were visually detected, or to within 1 m when not visible (e.g., submerged or concealed by cover). All locations were post-processed using differential correction for a final accuracy of \pm 3-5 m. Locations were then compiled and entered into a Geographic Information System (GIS, ArcMap software, ESRI, Redlands, CA) to calculate distance measures.

Since skin injuries are a common problem reported from radio-transmitter attachment to anurans (Heyer et al., 1994), frogs were periodically re-captured to measure mass, inspect for injuries, and assess the integrity and fit of beaded belts. Beaded belts were refitted at the first sign of skin abrasion or replaced once wear of the elastic thread was noted. If abrasions did not begin to heal within ten days after resizing the beaded belt, the radio-transmitter was removed. Radio-transmitters and belts were removed from frogs 3-5 days prior to the scheduled battery expiration to ensure retrieval of transmitters. I also attempted to capture and mark all frogs encountered incidentally during relocation of radio-tagged frogs to maximize the probability of detecting gross movements within and between study seasons.

Movement between relocations, hereafter referred to as successive distance (SD), was measured as distance along the creek (meters) for each frog. Successive distance measures were used to identify activity areas (see below) and calculate movement rates. I also calculated network distance (NWD) by measuring the distance moved along the creek between initial and final capture for sedentary frogs and as maximum distance from initial capture for mobile frogs. I used NWD to assess the extent of *R. boylii* movements and make comparisons between sexes and seasons. Finally, I calculated net displacement (ND), the sum of successive distance measures, where upstream moves were assigned positive values and downstream moves were assigned negative values (Lowe, 2003). Net displacement was used to assess the directionality of movements. I did not use minimum straight-line distance, a common distance measure used in most movement studies, since the movements of monitored *R. boylii* were restricted to the stream network.

I simplified the movement path for each frog by categorizing locations into activity areas or stopover locations based on the degree of clustering among locations and the time spent at each location. An activity area was defined for a frog when the cumulative net displacement was < 35 m (a distance chosen arbitrarily after graphically screening the movement paths of all frogs) and residence was > 5 days. After identifying activity areas, the geographic coordinates for all locations within each area were averaged to produce a centroid. Once cumulative net displacement exceeded a threshold of 35 m an individual was assumed to have moved to a new spatial location and cumulative net displacement was reset to zero. New locations occupied for \leq 5 days were considered stopover areas.

After simplifying movement paths, I subsequently classified frogs into one of two categories based on the extent of movements observed. Frogs that made short-distance

movements (\leq 35 m, hereafter "localized movements") around the point of initial capture were classified as "sedentary" (Figure 2). In contrast, frogs that made directed movements (> 35 m) from the area where initially captured were classified as "mobile". Categorization of these movement patterns reflects behaviors observed and is not a permanent label assigned to the individual. I treated sedentary and mobile frogs separately when describing NWD but pooled data for population-level analyses.



Figure 2. Example of localized movements (black arrows) and designation of an activity area (broken circle) for *R. boylii* radio-tracked in the Red Bank watershed, showing Red Bank Creek (bold black line), initial capture location (black circle), relocations (white circles), and breeding site (gray polygon).

Habitat Measurements

Each time a frog was located, I measured physical and biological habitat characteristics potentially important to *R. boylii* for thermoregulation, foraging, hydration, and protection (Table 1). Creek meso-habitats were classified as riffle, run, glide, or pool using channel morphology, substrate composition, and flow velocity (McCain et al., 1990). Wetted width and water depth were obtained from measurements collected along a 0.5 m transect perpendicular to the creek channel at each frog location. Mean water depth was calculated from five depth measures collected at 16.6%, 33.34%, 50%, 66.67%, and 83.33% of the wetted width. Maximum water depth was recorded as the deepest point along the transect. Dominant aquatic substrate (within the wetted channel) and terrestrial substrate (within 3 m from the wetted channel) were classified as silt/fines (< 3 mm), sand (3-10 mm), gravel (10-64 mm), cobble (65-256 mm), boulder (>256 mm), or bedrock. The dominant vegetation within 5 m radius of each frog location was classified according to height (m) as herbaceous (< 0.5 m), under-story (0.5-2 m), mid-story (2-4 m), or over-story (> 4 m).

I measured four additional habitat variables in a GIS. Tree canopy closure (%) was estimated within a 30 m radius surrounding each frog location using data from the National Land Cover Database (NLCD; USGS, 2003). Stream order (Strahler, 1957), solar insolation, and solar duration were calculated from a 30-meter digital elevation model (DEM; USGS, 1999). Stream order for each watercourse in the study area was determined using the Watershed extension in Arc Map 9.1 software (ESRI, Redlands, California, USA). Based on field observations, stream order was a good indicator of

surface water availability and was used to produce three categories that generally described hydroperiod: stream order < 2 = ephemeral, 3-5 = intermittent, and > 5 = perennial. The DEM was also used to calculate the seasonal average incoming solar radiation (solar insolation) and average duration of exposure to solar insolation (solar duration) received within a 30 m area surrounding each frog location, assuming no cover. To obtain these data, solar insolation and solar duration were first calculated for each month of the year during which this study was conducted using the Solar Analyst extension (Helios Environmental Modeling Institute LLC, Lawrence, Kansas, USA) in ArcView 3.2 GIS software (ESRI, Redlands, California, USA). Monthly values were then averaged to produce a seasonal average, which I used for habitat analysis.

Areas used by radio-tagged frogs were also categorized as breeding or nonbreeding habitat. To identify breeding habitats, I conducted VES on perennial and intermittent waterways to locate and map egg masses during the 2004-2006 breeding seasons (April-May)¹. For each egg mass I measured the same physical and biological habitat characteristics recorded for each frog location (see above). Locations were recorded with a GPS, post-processed, and compiled into a GIS. Egg masses were often clustered within stream mesohabitats and those within 30 m of each other were merged to form a breeding site. Habitat characteristics were pooled among egg masses to produce mean site values. The size of breeding sites were bound by the wetted creek channel and a 5 m stream segment adjacent to egg mass on the upstream and downstream ends of the

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¹ I was unable to conduct breeding surveys of all intermittent and perennial waterways used within the study area due to the unpredictable extent of area used and due to unsuitable survey conditions (i.e., high water turbidity and scouring flows) during site visits. Therefore, activity centers in unsurveyed intermittent and ephemeral drainages were not included in habitat analysis.

breeding site. Frog locations within breeding sites were subsequently classified as breeding, and areas outside of breeding sites were classified as non-breeding.

To assess the use of terrestrial habitats by *R. boylii*, minimum distance to water was measured for each frog location. Distance to water was measured as the minimum straight-line distance of each frog location to the nearest flowing or standing water. These data were summarized to calculate mean and maximum values using the frog as the sampling unit.

Variable	Description
Stream habitat	Stream habitat category (McCain 1990): riffle (1), run (2), glide (3), pool (4), dry (5).
Stream width	Width (m) of the wetted creek measured perpendicular to frog location.
Mean depth	Average water depth (m) calculated from five water depth measures taken perpendicular to frog location.
Max depth	Maximum water depth (m) obtained from five water depth measures taken perpendicular to frog location.
Aquatic substrate	Size of dominant aquatic substrate: sand/fines (1), gravel (2), cobble (3), boulder (4), bedrock (5).
Bank substrate	Size of dominant substrate within 3 m of the wetted channel: sand/fines (1), gravel (2), cobble (3), boulder (4), bedrock (5).
Vegetation type	Category of dominant vegetation within 5 m radius of frog location: herbaceous (1), understory (2), midstory (3), overstory (4).
Vegetation cover ^{\dagger}	Proportion of vegetative cover derived from GIS, calculated from a 30 m area surrounding each frog location.
Avg. solar insolation [†]	Mean amount of direct solar radiation (Watt Hr/Month) calculated from a 30 m area surrounding each frog location.
Avg. solar duration ^{\dagger}	Mean duration of exposure to direct solar radiation (Hr/Month) calculated from a 30 m area surrounding each frog location.

Table 1. Description of meso-scale variables collected to characterize *R. boylii* habitat use.

† Estimated from GIS

Age Estimates

I used skeletochronology to estimate the age of *R. boylii* fitted with radiotransmitters. Skeletochronology is the study of growth rates in the mineralized bone of animals. This technique has been commonly used to estimate the age of amphibians with cyclic or continuous activity patterns (Homan et al., 2003; Kumbar and Pancharatna, 2001; Kusano et al., 1995; Measey, 2001; Rossell, 1998; Rozenblut and Ogielska, 2005; Sagor et al., 1998). Slower growth during dormancy or periods of reduced activity results in annual lines of arrested growth (LAG's), which can be counted to estimate the approximate time of metamorphosis (Castanet et al., 2003). This technique is analogous to counting the growth rings to estimate the age of trees.

To age radio-tagged *R. boylii* I collected two distal phalanges from the longest toe on the right rear foot at the time of radio-transmitter attachment. Samples were dried and sent to Matson's Laboratory (Miltown, Montana, USA) for histological staining (using hematoxylin & eosin dyes) and slide preparation. Prepared slides contained six 10 μ m sections from the mid-diaphyses of the proximal phalange. Two observers independently analyzed all samples, using a compound microscope, and the best section was used to count the number of visible LAG's. The first LAG represented the time from metamorphosis to the first winter (January, ~ 5 months) and the time following the last LAG was calculated as the number of months prior to toe collection. Time between lags was assumed to represent one year. Therefore frog age was estimated to the nearest month. Discrepancies in age estimates between observers were resolved through cooperative reanalysis to reach a final consensus (Rossell and Sheehan 1998). I used frog age to examine for differences in average seasonal movements among age groups.

Environmental Monitoring

I monitored ambient weather conditions during each study season to determine if associations existed with occurrence of frog movement. A terrestrial weather station was installed adjacent to Red Bank Creek to collect air temperature (±1°C) and relative humidity (±5%) at 30-minute intervals using a HOBO[®] H8 data logger housed in a solar radiation shield (Onset Computer Corp., Pocasset, MA). Precipitation was also collected using a HOBO[®] H7 event logger connected to a RG200 6-inch rain gauge tipping bucket (Global Water Instrumentation, Inc., Gold River, CA). Water temperature (±1°C) was collected using StowAway[®] Tidbit data loggers (Onset Computer Corp., Pocasset, MA) installed at five locations along Red Bank Creek.

I first summarized air temperature, water temperature, and relative humidity by calculating daily means. Daily means were then used to calculate mean 5-day averages for air temperature (M5AAT), water temperature (M5AWT), and relative humidity (M5ARH), calculated as the running average of the mean daily values for each day and the prior four days. I chose to use 5-day means to improve the interpretability of these data (Dunham et al., 2005) and to account for some of the variability in tracking frequency. I summarized precipitation data into daily rain (DR), cumulative seasonal rain (CSR), and cumulative 3-day rain (C3R). Cumulative seasonal rain was calculated for each day as a running total of rain recorded throughout the study season. Similarly, C3R

was calculated for each day as the running sum of rain recorded during the preceding three days.

Statistical Procedures

Statistical analyses were conducted using NCSS 2004 software ($\alpha = 0.05$; Number Cruncher Statistical Systems, Kaysville, UT), Excel (Microsoft Corporation), and PC-ORD (MjM Software Design, Glenden Beach, OR). For the valid application of parametric statistics, data transformations (i.e., log or square root) were used when necessary to ensure that basic assumptions of normality were met (Zar, 1999). When assumptions were violated, nonparametric statistics were used. Except for autocorrelation analysis (see below), frogs were selected as the sampling unit to avoid pseudoreplication and for making inferences about the population (Hurlbert, 1984). To describe movements between seasons and years I used all relocations (i.e., radio telemetry and incidental) recorded throughout the entire study. I made an *a priori* decision to exclude frogs with < 10 locations from statistical analyses because I had enough data for frogs with more locations. I made this decision prior to finding that study duration was not related to network distance traveled (linear regression: n = 72, R^2) = 0.0005, t = 0.18, P = 0.86). Movement data for excluded individuals has been provided in Appendices A-C.

General movements

Prior to conducting movement analyses, I tested for independence of observations (an assumption of most statistical tests) using a Kruskal Wallis ANOVA (Compton et al., 2002). This analysis tested the null hypothesis that successive distance was equal regardless of days elapsed between relocations (1-6 days). Relocations were statistically independent of time elapsed (Kruskal Wallis test: n = 100, df = 5, χ^2 = 8.05, P = 0.15), therefore I used all telemetry locations recorded for individuals. The Schoener ratio statistic (Schoener, 1981) was not used to assess autocorrelation because it is not appropriate for animals that exhibit shifting activity centers (Kernohan et al., 2001).

To describe and compare seasonal movement patterns I used radio-telemetry relocations and incidental recaptures for each tracking period. I used summary statistics to describe the general movements (i.e., extent, rate, and directionality) exhibited by adults. The high degree of variation in distance measures justified reporting median values. I tested for differences in NWD between sex and seasons (spring vs. fall) among females using a two-sample t-test (Zar, 1999). When comparing sexes I only used female movements recorded during the male tracking period (April 10-May 24). To assess directional bias of movements, I used ND measures and tested for skewness of the distribution using the D'Agostino skewness test (Zar, 1999). I then used a two-sample t-test to determine if skewness was different between sexes and seasons.

Habitat analysis

I conducted exploratory analyses to assess differences between breeding and nonbreeding habitats using Bray-Curtis Multiple Response Permutation Procedure (MRPP; PC-Ord 4.0; McCune and Mefford 1999). I restricted this analysis to the drainage scale, meaning that differences were only assessed for habitats within either perennial or intermittent drainages. I used this non-parametric procedure because it is designed to handle ecological data that violate parametric assumptions (McCune and Grace, 2002). This analysis calculates a matrix of Euclidean distance measures for the complete data set, an average distance within each group, and a weighted mean within-group distance (used to indicate the degree of contagion). These distances are used to generate two statistics: 1) the test statistic (*T*), which determines the degree of among-group separation, where more negative numbers indicate greater separation, and 2) the agreement statistic (*A*), which determines the within-group homogeneity compared to random chance. The agreement statistic can range from 0-1, where A = 1 when all within-group items are identical, A = 0 when within-group heterogeneity is equal to chance, and A < 0 when heterogeneity is greater than expected by chance.

When differences were detected between groups, I used univariate statistics to identify and describe the variable(s) responsible for group differences. Two-tailed t-tests were used to assess continuous variables and chi-square goodness of fit tests were used to assess categorical variables (Zar, 1999).

Age and size effects

Since the age class of frogs may influence mobility (Pilliod et al., 2002), I examined whether NWD traveled by adult *R. boylii* differed among size and age groups using a Kruskal-Wallis ANOVA test. This analysis was used to test the null hypothesis that the average distances traveled by frogs in each of four size groups (≤ 62 mm, 63-65 mm, 66-68 mm, and ≥ 69 mm) and age groups (< 3 years, 3 years, 4 years, and ≥ 5 years) were equal. Rejection of the null hypothesis would suggest that movement is associated with frog size and/or age. Males were excluded from this analysis due to insufficient sample size.

Weather triggers

To examine whether the timing of movements was associated with ambient weather conditions, I used t-tests or nonparametric tests to evaluate the ability of hypothesized predictor variables to distinguish between the binomial response variable (movement = yes or no). I considered variables with p-values < 0.2 as possible predictors (Hosmer and Lemeshow, 2000). Variables with unequal variance or failing to meet assumptions of normality were evaluated with the Aspen-Welch unequal-variance test or Mann-Whitney U-test, respectively (Zar, 1999). I then assessed multicolinearity among predictor variables using a Spearman-rank correlation matrix, where correlation coefficients (r_s) > 0.70 were considered colinear. Among multicolinear variables, I selected the variable presumed to have the greatest biological influence on the response variable for further analysis. Julian day was included in variable selection routines as a possible confounding variable for predicting frog movement.

Following variable selection, I developed *a posteriori* candidate logistic regression models. Candidate models were ranked using corrected Akaike Information Criterion (AIC_c) and Akaike weight (w_i) to determine the best model (Burnham and Anderson, 1998). To determine the relative importance of each independent variable in the best-ranked model, I used a chi-square test (Hosmer and Lemeshow, 2000). This test
compares the fit of the full model to the fit of a model after omission of each independent variable based on a deviance statistic. Relatively large deviance resulting from removal of an independent variable indicates a high degree of influence from that variable in the fitted model. To determine goodness-of-fit of the best model, I generated a Receiver Operator Characteristic (ROC) curve, which was used to calculate area under the curve (AUC) (Hosmer and Lemeshow, 2000). This metric measures the models' ability to correctly classify the binary response variable. An AUC of 0.5 suggests a model no better than random chance, 0.6-0.7 suggests acceptable discrimination, 0.9-0.8 suggests a model with excellent discrimination, and 1.0 indicates perfect fit of a model. Analysis of spring data included both sexes, and both 2004 and 2005 study seasons were pooled for analysis of fall/winter data. No data were reserved for model evaluation since the aim of this study was to describe relationships rather than make future predictions.

RESULTS

Seasonal Movements

Sample sizes and number of observations

I attached radio-transmitters to 79 *R. boylii* (11 males and 68 females) but only movement data from 70 individuals (9 males and 61 females, Appendices A-C) were used for analysis. The nine frogs excluded from analysis were either eaten, went missing, or shed the radio-transmitter less than 16 days from their initial capture. Among the frogs included in analyses, 16 were lost prior to scheduled removal of radio-transmitters either due to predation, shed radio-transmitter, or lost signals. Table 2 summarizes the morphological characteristics of all frogs fitted with radio-transmitters. Infrequent encounter of males meeting the required weight criterion for radio-transmitter attachment precluded this sex from being studied during the fall/winter study seasons. Three females were tracked for more than one study season: one during S1 and FW1 (A03) and two during both fall/winter seasons (B05 and B15).

I documented four predators of adult *R. boylii*. The aquatic garter snake (*Thamnophis atratus*) was a dominant predator responsible for deaths of eight frogs. One frog (female, SUL = 62.5 mm) was eaten by an adult bullfrog (*Rana catesbeiana*, female, SUL = 143 mm). Two other predators were not identified, but a "V" shaped laceration inflicted at night on one individual and tooth marks on the epoxy coating of a recovered transmitter suggested a nocturnal bird (e.g., owl) and a mammal, respectively.

As a result of frog loss and subsequent additions of new frogs during each study season, initiation dates, number of days tracked, and total number of locations varied among individuals. Variation in the deployment date of radio-transmitters was particularly high in S1 (April 10 - May 8) and low for both fall/winter seasons (FW1 = October 7-10 and FW2 = October 4-11). In S1, males were tracked for 20-31 days (n = 9, mean = 25 days) and females were tracked for 16-62 days (n = 20, mean = 40 days). In FW1 and FW2, tracking duration ranged from 32-102 days (n = 24, mean = 55.5 days) and 36–113 days (n = 20, mean = 72.7 days), respectively. A total of 1,388 tracking observations were recorded (S1 = 571, FW1 = 418, and FW2 = 399). In S1, male and female frogs were relocated 11-19 times (n = 9, mean = 15) and 11-34 times (n = 20, mean = 20), respectively. The number of relocations among females tracked during the two fall/winter seasons was similar, with 11-25 (n = 24, mean = 17) in FW1 and 11-25 (n = 20, mean = 20) in FW2.

Table 2. Morphological characteristics including sex (M = male, F = female), number of frogs (N), weight, mass %, snout-urostyle length (SUL), and age for *R. boylii* radio-tracked in the Red Bank Creek watershed. Values are means +/- standard error (minimum-maximum).

Study Season	Sex	N	Weight (g)	Mass %	SUL (mm)	Age (years)
S1 (April 10-May 24)	М	11	14.1 <u>+</u> 0.59 (11.3-18)	6.5 <u>+</u> 0.25 (5.0-7.8)	51.8 <u>+</u> 0.91 (46.5-56.0)	4.7 <u>+</u> 0.48 (2.8-6.8)
S1 (April 10-June 12)	F	23	26.7 <u>+</u> 1.31 (14.7-37.5)	5.0 <u>+</u> 0.27 (3.0-8.0)	64.9 <u>+</u> 1.13 (53.5-73.7)	3.9 ± 0.39 (1.8-5.8)
FW1 (Sept. 21-Jan. 16, 2005)	F	26*	32.1 <u>+</u> 1.2 (23.3-43.6)	4.9 <u>+</u> 0.15 (3.8-6.2)	66.4 <u>+</u> 0.67 (60.3-73)	3.9 <u>+</u> 0.39 (1.2-7.2)
FW2 (Oct. 7-Jan. 29, 2006)	F	22^	30.4 <u>+</u> 1.2 (23-41.7)	5.0 <u>+</u> 0.21 (2.0-6.5)	64.7 <u>+</u> 0.70 (60-71.8)	3.0 <u>+</u> 0.23 (1.2-4.2)

* One frog also tracked during S1 study season.

^ Two frogs also tracked during FW1 study season.

Spring males

Five (55.6 %) of the males monitored during S1 were mobile, and the other individuals (n = 4) were sedentary. The median NWDs for mobile and sedentary males were 149 m (range = 72-578 m) and 5.5 m (range = 2-13 m), respectively. Graphs of the movement histories of frogs suggested that mobile individuals were in the process of traveling to new activity areas following their initial captures (Figure 3 & Figure 4). Movements occurred during mid-April and were not restricted to rain events (Figure 3), but small sample size precluded analysis of associations with ambient weather. Mobile males generally established activity areas by early May. Based on ND measures, these males showed no significant directional bias in movement (D'Agostino skewness test: n = 9, *t* = -1.77, P = 0.076), although the majority (80%) of mobile individuals moved downstream from their initial capture locations. Among mobile frogs, only one (A26) was incidentally recaptured after the spring telemetry season. This frog was recaptured in October 2004 and was located at the same non-breeding habitat last occupied during the spring.



Figure 3. Movement histories of mobile male *R. boylii* radio-tracked during S1 in the Red Bank Creek watershed.





Spring females

The majority (80%, n = 16) of female *R. boylii* tracked during S1 were mobile, and the others (20%, n = 4) were sedentary. The median NWDs recorded for mobile and sedentary females were 525 m (range = 130-7,043 m) and 4 m (range = 2-14 m), respectively. No differences were detected in NWD traveled between males and females (Two-sample t-test: df = 18, t = 0.84, P = 0.41).

Among mobile females, many (63%) moved away from their initial capture locations shortly after (mean = 3 days) being fitted with radio-transmitters (Figures 5& 6), and most of them (n = 12) apparently completed post-breeding movements and established activity areas (i.e., summer foraging areas) by early to mid-May. However, four individuals were nomadic (i.e., showed no fidelity to any one area and moved continuously throughout the duration of the study season). One of them (A01) displayed impressive mobility, traveling 7 km during which she used intermittent tributaries (some of which were dry with only moist substrates) and crested a ridge (Figure 7A). These post-breeding movements were primarily unidirectional (Figures 5 & 7B), although two females migrated back to a previous point of capture (A03 and A14, see Figures 5 & 8A). Based on measures of ND, females displayed a strong upstream directional bias (D'Agostino skewness test: n = 22, t = 3.24, P = 0.001), with all but one mobile frog (93.8%) moving upstream (Figure 9).

Four gravid females were captured before deployment of radio-transmitters and prior to the start of breeding. Two of these frogs were sedentary between their initial





Distance from initial capture (m)







Figure 7. Examples of the longest movement (A) and other long range movements (B) exhibited by female *R. boylii* radio-tracked during S1 in the Red Bank Creek watershed. Symbols for lotic habitats, breeding sites, and frog locations with associated labels are the same as those used in Figure 4. Some movement paths include incidental captures (IC).



Figure 8. Examples of moderate movements and migrations exhibited by female *R*. *boylii* radio-tracked during S1 in the Red Bank Creek watershed. Symbols for lotic habitats, breeding sites, and frog locations with associated labels are the same as those used in Figure 4.



Net displacement (m)

Figure 9. Frequency distribution of net displacement for female *R. boylii* radio-tracked during S1 in the Red Bank Creek watershed. Positive values represent upstream moves and negative values represent downstream moves. Bins are of unequal sizes. The bin labeled -35-35 represents sedentary frogs.

capture and recapture, at which point each was fitted with a radio-transmitter. The other two frogs moved 54 and 74 m between first and second capture but were sedentary throughout their respective tracking periods.

Fall/winter females

No difference was detected between the movement distributions for females tracked in FW1 (n = 24) and FW2 (n = 20) (Kolmogorov-Smirnov test: P = 0.21), so these data were pooled. Twenty-four females (54.6%) were mobile (FW1 = 15, FW2 = 9), and twenty (46.4%) were sedentary (FW1 = 9, FW2 = 11). The median NWDs recorded for mobile and sedentary females were 332.5 m (n = 24, range = 60-3,693 m) and 8 m (n = 20, range = 0-32 m), respectively. Females tracked during fall/winter moved significantly shorter distances compared to females tracked in spring (Two-sample t-test: df = 62, t = -2.39, P = 0.01).

Mobile females remained at their initial capture locations for an average of 19 days in FW1 and 45 days in FW2. Departure from these areas occurred between mid October and early November in FW1 (Figures 10 & 11) and between early and late November in FW2 (Figure 12). After departing initial capture locations, 66.7% of *R. boylii* made a series of unidirectional movements before establishing new activity areas (e.g., Figure 13A). Six frogs moved throughout the remainder of the fall/winter season (e.g., C08, Figure 13B), and two frogs migrated back to their initial capture locations (e.g., C13 & C18, Figure 12). Assessment of female ND showed an overall downstream directional bias in movements (D'Agostino skewness test: n = 44, t = -3.62, P = 0.003;

Figure 14), even though the majority (68.2%) of females tracked moved upstream. Net displacement data were pooled because there was no difference in movement distributions between FW1 and FW2 (Kolmogorov-Smirnov test: P = 0.271).

Between season movements

Nine frogs were initially captured and/or recaptured outside the times when radiotracking occurred. The time elapsed between tracking seasons and incidental captures ranged from +/- 6 to 12 months. Four of these frogs were classified as sedentary based on telemetry locations, and incidental recaptures showed continued fidelity outside the tracking seasons (e.g., Figure 13A [B06] and Figure 15 [B05 and B15]). However, five frogs showed movements outside of the telemetry seasons. Table 3 summarizes and compares movement data obtained from radio telemetry and incidental captures for these individuals. Three of these frogs showed evidence of migratory patterns. The movement paths from radio telemetry data and incidental captures for three of these frogs have also been provided (Figure 15 [B09], Figure 13B [C08 & C09]).







Figure 11. Long-range movement histories for mobile female R. boylii radio-tracked during FW1 in the Red Bank Creek watershed.







Figure 13. Examples of long-range movements observed in FW1 (A) and FW2 (B) exhibited by female *R. boylii* radio-tracked in the Red Bank Creek watershed. Symbols for lotic habitats, breeding sites, and frog locations with associated labels are the same as those used in Figure 4. Some movement paths include incidental captures (IC).



watershed. Positive values represent upstream moves and negative values represent downstream moves. Bins are of Figure 14. Frequency distribution of ND for female R. boylii radio-tracked during FW1 and FS2 in the Red Bank Creek unequal sizes. Upstream and downstream movements < 35 m from initial capture represent sedentary frogs.



Figure 15. Examples of movement paths for female R. boylii radio-tracked during fall/winter seasons in the Red Bank Creek watershed. Symbols for lotic habitats, breeding sites, and frog locations with associated labels are the same as those used in Figure 4. Some movement paths include incidental captures (IC).

Table 3. Summary and comparison of distances moved from initial capture (DFIC) obtained from radio-telemetry and incidental recaptures (N = number of recaptures) for female *R. boylii* radio-tracked during the fall/winter seasons in the Red Bank Creek watershed. Positive DFIC values indicate upstream movements and negative values indicate downstream movements.

	R	ecapture d radio-tele	lata pre metry	Radio-te da	elemetry ta	Re	capture d radio-tele	ata post metry
Frog ID	N	Season	DFIC (m)	Season	DFIC (m)	N	Season	DFIC (m)
B02	0			FW1	475	1	FW2	-475
B09	0			FW1	-8	1	Spring 2005	239
B12	0			FW1	102	1	Spring 2005	-931
C08	0			FW2	1,334	1	Spring 2006	-1,334
C09	1	Spring 2005	3,713	FW2	-1,255	0		

Movement Rate

Movement rates were calculated separately for localized movements (i.e., movements within activity areas) and directed movements (i.e., movements ≥ 35 and away from activity centers) to provide a more accurate description and assessment of rates (Table 4). No differences were detected between sexes for localized (two-tailed ttest: t = 1.7, P = 0.09) or directed movement rates (two-tailed t-test: t = 0.4, P = 0.72) in S1. There were also no differences in the distributions of female movement rates between fall/winter seasons for either localized movements (Kolmogorov-Smirnov test: P= 0.08), or directed movement rates among females in S1 were significantly larger than in fall/winter (two-sample t-test: t = -2.14, P = 0.018), but no seasonal differences were detected between the log of directed movements (Aspin-Welch unequal-variance test: t =-1.59, P = 0.12). Upstream movements did not exceed 355 m/day, whereas, the absolute maximum downstream travel rate was 1,386 m/day.

	Į		Localize	ed mover	nent rates				Directe	d movem	ent rates		
Season	Sex	Z	Mean	SD	Min	Max	Z	Mean	Median	SD	Min	Max	Max ⁱ
S1	Μ	6	3	1.2	1.3	4.6	5	76.8	67.5	54.1	22.0	161.9	407
S1	Ц	21	4.4	2.4	1.5	11.5	16	85.3	70.5	43.9	21.4	159.4	355
FW1	Ц	24	3.9	2.8	1.4	14.4	16	104.0	28.2	149.6	10.7	513.8	1386
FW2	Ц	20	2.7	1.0	1.0	4.7	8	73.2	79.7	55.4	14.5	183.7	503
FW1&2	Ц	44	3.3	2.2	1.0	14.4	24	93.7	37.1	25.6	10.7	513.8	1386

Habitat Use

Breeding sites

A total of 64 breeding sites were identified during the 2003-2006 breeding seasons. Fifty-four (80.7%) of these sites were located along Red Bank Creek, and twelve were found on an intermittent tributary (Keystone Creek). Breeding-sites decreased significantly with distance upstream along Red Bank Creek (Pearson correlation: $r_p = -0.68$, P = 0.03). Breeding sites also decreased with distance upstream along Keystone Creek, but the correlation was not significant (Pearson correlation: $r_p = -$ 0.88, P = 0.12). Along the lower reaches of Red Bank Creek, where breeding site densities were highest, large floating algal mats were ubiquitous in the fall, but in the upper reaches and along tributaries, where breeding sites were sparse, floating algae were absent.

Spring males

Two general patterns of habitat use were observed among males. Most frogs (66.6%, n = 6) showed exclusive use of breeding sites. Four of them restricted activities to one breeding site, and two frogs moved between two breeding sites. One of these frogs (A22) moved from a breeding site on Keystone Creek to an alternate site on Red Bank Creek (Figure 4). The other pattern involved use of breeding and non-breeding habitats. Three males primarily used non-breeding habitats. These frogs generally made at least one brief visit (< 2 days) to a breeding site(s) before occupying non-breeding

areas (see A15 and A26, Figure 4). Movements between and away from breeding sites occurred from mid-late April, midway through the breeding season.

Spring females

Females tracked in S1 also used breeding and non-breeding habitats, but their use of breeding habitat was less prevalent and more variable compared to males. Three females (15% of all females) restricted their activities to the breeding sites where they were initially captured. Four frogs used breeding and non-breeding habitats. Three of these frogs transitioned from non-breeding sites to breeding sites in mid- to late May, towards the end of the active breeding season, where they remained into June (e.g., A17 and A34, Figure 8). The other frog (A03) migrated between a breeding site and non-breeding habitat (Figure 8A). The remaining thirteen females almost exclusively used non-breeding habitats and were generally more mobile; but brief use (< 5 days) of breeding sites occasionally occurred.

Fall/winter females

Patterns of habitat use were variable. Ten frogs (22.7%) restricted activities to the breeding sites where they were initially captured. Six frogs (13.6%) were observed using breeding and non-breeding habitats. Five of these frogs were initially captured at breeding sites and moved to non-breeding habitat. The other frog migrated between a non-breeding habitat and a breeding site. Twenty-three frogs (52.3% of all frogs tracked during both fall/winter seasons) primarily used non-breeding habitats, eight of which

used one locality. The remaining fifteen females were mobile and almost exclusively used non-breeding habitats. Breeding habitat use for five females (11.4%, two sedentary and three mobile) could not be determined because the areas used were not surveyed for egg masses.

Differences between breeding and non-breeding sites

I collected habitat data at 48 breeding and 15 non-breeding sites used by radiotracked frogs along Red Bank Creek during S1. Most breeding sites (88%) were at run or glide habitats, whereas non-breeding sites were in riffle (87%) or pool (13%) habitats. Along intermittent tributaries, I collected data at 9 breeding and 8 non-breeding sites (Appendix G). Glides and pools were the dominant habitat types used at both breeding and nonbreeding sites. No differences between breeding and non-breeding sites along the main channel were revealed by MRPP analysis. However, a significant difference was detected along Keystone Creek (Table 5). This difference was a main-effect from direct solar insolation and duration (Table 6), which were significantly less at breeding sites. Comparison between habitat types after removal of these variables resulted in no difference between groups (MRPP: A = -0.015, T = 0.312, P = 0.48).

During FW1 and FW2, I measured habitat variables at 10 breeding and 36 nonbreeding sites used by radio-tagged *R. boylii* along Red Bank Creek, as well as 4 breeding and 15 non-breeding sites along tributaries. No significant differences were found between breeding and non-breeding habitats for either of the two drainage types (Table 5). Table 5. Results of MRPP analyses comparing measured habitat characteristics at breeding and non-breeding habitats used by radio-tracked *R. boylii* in the Red Bank Creek watershed. The statistic (A) describes within-group heterogeneity compared to random expectation. A \approx 0 when heterogeneity within groups is less than random expectation.

Season	Drainage type	Ν	А	Test statistic (T)	P-value
S 1	Perennial	62	0.005	-0.347	0.252
S 1	Intermittent	17	0.227	-3.87	*0.008
FW	Perennial	46	-0.009	0.698	0.744
FW	Intermittent	19	-0.034	0.591	0.666

* Statistical significance at $\alpha = 0.05$

Table 6. Summary of univariate analyses quantifying differences between breeding and non-breeding habitats of *R. boylii* in spring along intermittent waterways in the Red Bank Creek watershed.

Variable	Test	Test Statistic	P-value
Habitat type	Chi-square	2.15	0.550
Stream width	T-test	1.49	0.159
Mean depth	T-test	-1.18	0.258
Max depth	T-test	-0.98	0.342
Aquatic substrate	Chi-square	1.42	0.840
Bank substrate	Chi-square	3.64	0.060
Veg. Type	Chi-square	3.06	0.420
Veg. Cover	Chi-square	2.00	0.160
Direct insolation	U-test	-3.42	0.004
Solar duration	T-test	-2.65	0.008

Terrestrial habitat use

Frogs were strongly associated with watercourses, but frequently used terrestrial habitats adjacent to wetted creek channels. During S1, males were located on land adjacent to surface water an average of 37.7% of the time and females 65.6% of the time. Females tracked during fall/winter seasons were located in terrestrial habitats 58.2% of the time. Frogs were located in water on all other occasions. Average distance from water was < 3 m for all seasons, but adults occasionally used terrestrial habitats 6.9-40 m from the stream channel (Table 7). Pooled across seasons, the distances moved from perennial (n = 64, mean = 2.52 m, range = 0.05-40 m), intermittent (n = 20, mean = 2.26 m, range = 0.01-40 m), and ephemeral (n = 7, mean = 8.57 m, range = 0.05-35 m) drainages were similar.

Table 7. Summary of average distance from water and maximum distance from water recorded for male (M) and female (F) *R. boylii* tracked in the Red Bank Creek watershed. Sample size (N), standard error (SE), 95% lower confidence limit (LCL), 95% upper confidence limit (UCL), and absolute maximum (Max^a) are shown.

			Ave	rage dis	stance (m)	Max	imum dis	stance (m)
Season	Sex	Ν	Mean	SE	Range	Median	LCL	UCL	Max ^a
Spring	М	9	1	0.16	0.58-1.85	1.45	0.95	3	6.9
Spring	F	20	1.2	0.13	0.33-2.53	2.72	1.9	3.9	10.7
Fall/winter	F	44	2.8	0.26	0.72-6.9	8.65	6.5	11.6	40
Total		73	2.1	0.18	0.32-6.9	4.6	3.7	7.4	40

Tributary use

Adult *R. boylii* used intermittent and ephemeral tributaries to Red Bank Creek during all study seasons, but the duration and timing of use was variable among seasons. One male (11%) and nine females (45%) used tributaries in S1. The male (A22) was initially captured on an intermittent tributary (Keystone Creek), which it used for nine days before moving to Red Bank Creek (Figure 4). Among females, three frogs used intermittent tributaries for the entire tracking period. Breeding was not observed along one of these tributaries (Abernathy Canyon Creek), which dried prior to October, suggesting that two of these frogs moved from Red Bank Creek after breeding and were ultimately forced to return to Red Bank Creek. The remaining six females presumably used tributaries following breeding on Red Bank Creek [see Figure 8 (A17, A14, A27 and A34) and Figure 7B (A25)]. Movements away from tributaries occurred in early to late May, which corresponded to the end of the breeding season and drying of these drainages.

During the fall/winter seasons a total of sixteen females (FW1 = 8 and FW2 = 8, 36.4% overall) were observed using intermittent and ephemeral tributaries. Timing and duration of use was variable among individuals. In October, ephemeral tributaries were dry and intermittent tributaries were predominantly dry except for small isolated pools. Movements to tributaries generally occurred once sufficient rains had fallen and these drainages contained standing surface water or began flowing. Three frogs were initially captured on an intermittent tributary (Keystone Creek) and used this drainage throughout

the fall and winter. The other thirteen frogs dispersed to intermittent and ephemeral drainages [(see Figure 15 (B16), Figure 13A (B06 and B07), and Figure 13B (C08 and C09)].

Age Estimates

Age was estimated for 62 *R. boylii* (9 males and 53 females, Table 2 and Appendices A-C). Overall, the average age of monitored individuals was 3.9 years (range = 1.2 to 7.2 years). There was no significant difference in age between sexes (two-sample t-test: t = -1.55, P = 0.14) or between seasons (spring vs. fall/winter) for females (two-sample t-test: t = -0.89, P = 0.38). Assessment of size and age effects on movements (NWD) revealed no significant differences among size groups (GLM ANOVA: df = 3, F = 0.41, P = 0.75), age groups (df = 3, F = 0.10, P = 0.96), or size-age interactions (df = 9, F = 1.11, P = 0.39).

Movement Triggers

Ambient weather was not a predictor of *R. boylii* movement during S1. Univariate tests showed no differences in ambient weather conditions preceding days when movements occurred compared to days without movement (P > 0.20). Therefore, no further analysis was warranted.

During the fall/winter seasons, ambient weather was a predictor of frog movement (Table 8). Correlation analysis revealed that M5AAT was multicolinear with Julian day (r_s = -0.88), ADAT (r_s = 0.90), ADWT (r_s = 0.92), and M5AWT (r_s = 0.92), and that

M5ARH was colinear with ADRH ($r_s = 0.77$). Julian day was also correlated with CSR ($r_s = 0.79$). Multicolinearity among temperature measures and Julian day was expected since these variables are influenced by a net reduction in solar insolation throughout the fall and because mean five-day averages were calculated from daily averages. I retained M5AAT and M5ARH for inclusion in candidate models because they were presumed to be the most biologically relevant variables.

Fourteen candidate logistic regression models were ranked by their corrected AIC_c values and Akaike weights (Table 9). The best-ranked model contained CSR, C3R, and M5ARH. Based on corrected Akaike weight, there was a 58.2% chance that this was the best model for predicting the occurrence of *R. boylii* movement given the variables and the data. This model was 1.2 times (20%) better than the next best model, which included M5AAT in place of C3R. All variables in the best model had a significant influence on the fit of the model, with CSR showing the strongest main effect (Table 10). The estimated logit for the best fit model was:

Logit (Y) = 5.61 - 0.061(C3R) - 0.019(CSR) - 0.056(M5ARH)

Table 11 shows parameter estimates for the best model. The area under the ROC curve was 0.88, indicating that regardless of classification cut-point the model was an excellent improvement over random chance for predicting the probability of movement and movement was regularly associated with C3R, CSR, and M5ARH (Figure 16). Examination of the sensitivity and specificity values resulted in an optimal cut-point of 0.55.

Interpretation of this model indicated that *R. boylii* movements were associated with humid or rainy weather. During early fall when CSR was low (< 22 mm), frogs were not likely to move until the first moderate rain event (C3R = 6-19 mm) and high M5ARH (> 81%). Once CSR became moderate (22-92 mm), frogs were more likely to move when C3R was high (> 19 mm) or M5ARH was high. Finally, movements were also likely to occur once more rain had fallen at the study site (CSR > 92 mm), unless M5ARH was low (< 52%) and C3R was less than 19 mm.

		M£	an	Mec	lian	Mini	mum	Maxi	mum	Standar	rd Error		
Variable	Units	Υ	N	Υ	Z	Υ	N	Υ	Z	Υ	N	Test statistic	P value
DR	mm	ł	ł	0.0	0.0	0.0	0.0	61.0	30.0	ł	ł	1.18^{\dagger}	0.23000
C3R	mm	1	ł	4.0	0.0	0.0	0.0	73.0	34.0	ł	ł	4.06^{\dagger}	0.00005
CSR	mm	ł	ł	89.3	10.7	1.0	0.0	145.8	145.8	ł	ł	4.42^{\dagger}	0.00001
ADWT	°C	8.3	10.0	ł	ł	3.0	1.0	13.0	18.0	0.53	0.70	-1.71	0.09000
M5AWT	°C	1	ł	10.0	10.0	4.0	2.0	12.0	20.0	ł	ł	-1.66 †	0.10000
ADAT	°C	8.2	11.9	ł	ł	1.0	2.0	14.0	20.0	0.51	0.82	3.80°	0.00030
M5AAT	°	8.5	11.9	!	1	3.0	2.0	14.0	20.0	0.49	0.84	3.53°	0.00080
ADRH	%	77.0	61.6	ł	ł	30.0	27.0	99.0	0.66	2.60	2.80	-4.04	0.00010
M5ARH	%	78.1	61.5	ł	1	53.0	30.0	92.0	87.0	2.00	2.50	-5.09	<0.00001
Julian	day	;	1	315.0	305.0	292.0	278.0	338.0	352.0	ł	ł	2.22^{\dagger}	0.02600
DR = dail M5AWT =	y rain, C = mean	C3R = cfive-da	cumulati vy averag	ive three-	day rain temperat	, CSR = ure, AD	cumulat: AT = ave	ive seaso erage dai	nal rain. ly air ten	ADWT =	= averag	ge daily water t AT = mean five	emperature, -day
average ai	r tempe	rature,	ADRH	= average	e daily re	slative h	umidity,	and M54	ARH = m	ean five-	day ave	erage relative h	umidity.

Variables	AIC _c	Wi	Rank
CSR, C3R, M5ARH	68.2	0.582	1
CSR, M5AAT, M5ARH	68.5	0.501	2
CSR, M5ARH	69.9	0.247	3
CSR, C3R	70.3	0.204	4
CSR, C3R, M5AAT	72.5	0.068	5
C3R, M5ARH	74.7	0.022	6
C3R, M5AAT, M5ARH	76.0	0.012	7
M5ARH	76.6	0.009	8
CSR	77.0	0.007	9
C3R, M5AAT	78.2	0.004	10
M5ARH, M5AAT	78.4	0.004	11
CSR, M5AAT	79.1	0.002	12
C3R	83.5	0.000	13
M5AAT	87.7	0.000	14

Table 9. Candidate models developed to predict the probability of *R. boylii* movement during fall/winter in the Red Bank watershed, showing corrected AIC values (AIC_c), Akaike weight (w_i), and rank.

Table 10. Results of chi-square test used to assess the statistical significance of each variable in the best-fit logistic regression model, showing degrees of freedom (df), deviance, chi-square statistic (χ^2), and probability of type I error (P).

Variable(s) Omitted	df	Deviance	χ^2	Р
All	3	96.8	35.0	< 0.0000
CSR	1	70.6	8.7	0.0032
C3R	1	65.7	3.9	0.0486
M5ARH	1	66.1	4.3	0.0382
None	3	61.8		
Table 11. Parameter estimates for the best ranked model predicting movement of *R*. *boylii* during fall/winter in the Red Bank Creek watershed, including standard error (SE), upper 95% confidence limits (UCL), and lower 95% confidence limits (LCL).

Parameter	Regression coefficient	SE	LCL	UCL
Intercept	5.607	2.060	1.568	9.6450
CSR	-0.061	0.047	-0.153	0.0300
C3R	-0.019	0.007	-0.032	-0.0060
M5ARH	-0.056	0.029	-0.113	-0.0001



Figure 16. Receiver Operating Characteristic (ROC) curve generated for the best logistic regression model for predicting movement of *R. boylii* during fall/winter in the Red Bank Creek watershed. Area under the curve is 0.88.

Effects From Radio-transmitter Attachment

Some *R. boylii* were injured as a result of radio-transmitter attachment. The majority of frogs (62% of all frogs studied) developed injuries to the skin along the area in contact with the beaded belt. The first signs of injury were detected an average of 16.6 days (N = 27, SE = 1.10, and range = 4-24) following transmitter attachment. Most injuries (68%) were minor, consisting of a depression in the skin to mild skin discoloration over one or both hips. Skin abrasion and lacerations were more severe but less common, accounting for 11% and 21% of the injuries, respectively. Belts fitted tightly tended to cause more severe injury than those fitted loosely, however loosely fitted belts still caused mild to moderate abrasions. Loosening the belt on frogs with moderate to severe abrasions generally resulted in healing within 7-10 days. The frequency and severity of abrasions were comparable to those reported in most radio-telemetry studies of anurans (Bartelt, 2000; Bartelt et al., 2004; Bull and Hayes, 2001; Griffin and Case, 2001; Holenweg and Reyer, 2000; Muths, 2003; Rathbun and Murphey, 1996; Richter et al., 2001).

DISCUSSION

Monitoring the movements and seasonal habitat use of *R. boylii* in the Red Bank Creek watershed provided insight into several aspects of this species' ecology. First, frogs in the upper Red Bank Creek watershed used separated habitats to acquire resources for breeding, foraging, and overwintering. Second, the extents and rates of movement I observed were greater than previously recorded for this species. Third, the travel routes of *R. boylii* were restricted to the linear stream network. Finally, movements were asynchronous, but were associated with seasonal changes in weather. These findings have important conservation implications for inland *R. boylii* populations.

Resource Acquisition

Males

Most males (66%, n =6) at Red Bank Creek generally restricted their activities to breeding sites during the breeding season, which suggests their behavioral emphasis is on acquiring mates. This high level of reproductive effort was expected because *R. boylii* are facultative breeders (Wheeler, 2007), meaning they are limited to breeding when stream conditions are favorable during a relatively short period in spring. Of these 6 males, 4 concentrated their efforts at small territories (< 13 m stream segments) and were faithful to individual breeding sites. The other 2 moved among different breeding sites. These individuals spent most of their time at a primary breeding site after brief use (< 3 days) of other breeding sites and were likely undergoing pre-breeding movements from overwintering sites. However, brief stops at breeding sites while dispersing to a primary breeding site may be a strategy to increase male reproductive success.

The high breeding-site fidelity of males at Red Bank Creek was congruent with that found for males at Hurdygurdy Creek in coastal northern California. At Hurdygurdy Creek, males showed high fidelity to a focal breeding site both within and between breeding seasons (Wheeler et al., 2006), and many individuals maintained territories throughout the breeding season (Wheeler, 2007). This consistency between studies suggests that a similar mate acquisition strategy exists among males in coastal and inland populations.

Three males made only brief visits (< 2 days) to breeding sites and established activity centers at non-breeding habitats before cessation of breeding activity. Because these males showed no breeding site fidelity and spent little time at breeding sites, they were likely unsuccessful at acquiring mates. However, it is also possible that these frogs departed breeding sites after successfully mating. Male *R. boylii* aggregate and individuals aggressively defend a breeding territory at breeding sites (Rombough and Hayes, 2007; Wheeler, 2007). Male aggregations were observed at Red Bank Creek breeding sites. If breeding territories were limited within sites, competition among males could have excluded inferior or tardy individuals from breeding sites and forced them to establish breeding territories at unsuitable habitats. Alternatively, maintaining a breeding territory is presumably costly, and after mating some males may choose to abandon their breeding territory in search of better foraging opportunities.

At Red Bank Creek it appears unlikely that individual males used their primary breeding sites after the breeding season. Despite multiple surveys (diurnal and nocturnal), males were not recaptured at their respective breeding sites during the subsequent fall. This finding suggests that males ultimately departed breeding sites to access feeding habitats and/or overwintering sites elsewhere in the watershed. By contrast, mark-recapture data at Hurdygurdy Creek suggested that males remained at breeding habitats after the breeding season to acquire resources other than mates (Wheeler, 2007). Male departure from breeding sites has only rarely been documented previously (Van Wagner, 1996; Wheeler et al., 2006; Yarnell, 2005), and its apparent infrequency may be an artifact of the study methods used (i.e., mark-recapture). Further study of individual males using radio-telemetry throughout an annual cycle would improve our understanding of their annual resource requirements.

Females 1 -

Many breeding sites at Red Bank Creek provided insufficient resources to support females year-round. All females were post-reproductive upon initial capture in spring, and most (85%) were found at non-breeding habitats. Assuming that Red Bank Creek females reproduce annually (as has been suggested for *R. boylii* at Hurdygurdy Creek; Wheeler et al. 2006), these females departed breeding sites shortly after breeding. Their continued use of non-breeding habitats in spring and early summer, and predominantly unidirectional movements away from initial capture locations, indicate that females at Red Bank Creek generally acquired post-breeding resources (e.g., food, shelter, and basking sites) away from stream meso-habitats where they breed. This finding agrees with evidence of post-breeding dispersal by females from a focal breeding site on Hurdygurdy Creek, California (Wheeler et al., 2006). Furthermore, the directional bias of movements in spring suggests that females obtain post-breeding resources upstream from breeding sites. The use of separate habitats to acquire different resources (e.g., breeding vs. non-breeding) is known as landscape complementation (Dunning et al., 1992), and may be important for female resource acquisition during spring and early summer at Red Bank Creek.

Some females (spring = 15 % and fall/winter = 22.7 %) resided at breeding habitats throughout their study duration, demonstrating that some meso-habitats supplied a full complement of resources (i.e., mates, oviposition sites, food, water, shelter, and basking sites). However, because specific oviposition sites were unknown for study frogs, it is possible that females bred at a site other than the breeding site where they were initially captured. Monitoring individuals for a complete annual cycle is required to resolve whether some individuals are truly resident.

Despite the common use of non-breeding habitats by post-reproductive females, the infidelity of individuals to single activity centers demonstrates that many nonbreeding habitats may supply insufficient resources. Mobile females (81%) commonly moved among different non-breeding habitats throughout the spring season, using either shifting activity centers, or moving in a nomadic fashion. Amphibians move within a habitat in relation to the spatial and temporal distribution of resources across the landscape (Pough et al., 2001). Therefore, if resources were driving movements and assuming the resource requirements (e.g., food, water, basking sites, and shelter) of females at Red Bank Creek were constant during spring, movements among disjunct habitats suggests that the abundance of at least one resource was limited at most stream habitats. The use of different habitat patches by individuals to improve acquisition of a specific resource is called landscape supplementation (Dunning et al., 1992), and may partially explain the infidelity of females at Red Bank to non-breeding habitats.

The varied patterns of habitat use among females during the fall-winter months demonstrates that frogs used different strategies to acquire overwintering resources based on the provisions supplied at initial capture locations. The high fidelity of some females (46.4 %, n = 20) to initial capture locations is evidence that many main channel habitats could provide adequate resources to sustain females throughout the rainy season (November - March). However, the common infidelity of many females (54.6 %, n = 24) to initial capture locations implies that many stream habitats used by females in the fall provided unfavorable overwintering resources. These frogs either move to different main channel habitats (24.6 %, n = 11), or to intermittent and ephemeral tributaries (30 %, n = 13) to acquire favorable overwintering resources. The use of tributaries provide protection from high intensity surface flows and mobile sediments in the main channel during the winter months (Kupferberg, 1996; Yarnell, 2005).

Despite the variable use of habitats, the downstream bias in female movements during fall/winter coincided with the increase of breeding sites downstream along Red Bank Creek. Although the timing of these movements did not coincide with the *R. boylii*

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breeding season (April-June) at Red Bank Creek, this finding suggests that females orient downstream to stage at overwintering habitats (e.g., tributaries) closer to breeding sites. Alternatively, the downstream bias may have been a result of females being displaced from summer foraging sites by pulse flows along the main channel during large rain events.

In general, I was unable to detect a significant difference among breeding and non-breeding habitats using measured habitat variables (Table 5). This result conflicted with the fact that resources at breeding sites (i.e., mates and oviposition sites) differed from those at non-breeding sites. In addition, the vast majority (88%) of main channel breeding sites were at glides and runs, whereas non-breeding sites were at either riffles (87 %) or pools (13 %; Appendix G). My inability to detect differences among breeding and non-breeding habitats at Red Bank Creek is in contrast with evidence of seasonal shifts in habitat use reported in other studies. At Clear Creek, California, adult females showed strong philopatry to pool habitats during the non-breeding season (Van Wagner, 1996). Females at Yuba River, California selected relatively deep slow flowing habitats (i.e., pools) or shallow fast flowing habitats (i.e., riffles) during the non-breeding season, and these habitats differed from oviposition sites (Yarnell, 2005). Scale is an important concept in ecology with profound effects (Wiens, 1989), and the similarity between breeding and non-breeding habitats at Red Bank Creek can likely be attributed to an inappropriate scale of habitat measurements to assess the resource needs of R. boylii. Yarnell (2005) collected fine-scale quantitative data on microhabitat characteristics within stream mesohabitats. Therefore, future studies on *R.boylii* ecology should assess

microhabitat characteristics to better understand resources important to post-reproductive females.

Extents and Rates of Movements

Males

The longest movement I observed for males (578 m) during the breeding season was similar to those previously reported. At Clear Creek, California (an inland stream) males moved upwards of 408 m (Van Wagner, 1996), and at Hurdygurdy Creek, California (a coastal stream) the longest movement was 560 m (Wheeler et al., 2006). Despite consistency in results between studies, I monitored males for a relatively short time frame (25 days) compared to the other studies (March-June). These movements presumably underrepresent actual seasonal movements of males at Red Bank Creek. Furthermore, based on the finding that average distance moved (April 10-May 25) was equal between sexes, males at Red Bank Creek likely make post-breeding movements comparable to females.

Females 1 -

The median (525 m) and maximum (7,043 m) distance traveled by females during spring at Red Bank Creek were considerably greater than distances reported by other studies. During the "pre-spawning/spawning" season at Clear Creek, *R. boylii* moved 54 m on average, with a maximum movement of 450 m (Van Wagner, 1996). Females at Hurdygurdy Creek had mean and maximum movements of 213 m and 446 m,

respectively (Wheeler et al., 2006). Finally, a radio telemetry study on the Feather River (an inland regulated river in northern California) reported movements up to 1,899 m during the pre-spawning season (Drennan et al., 2006). The variation in movement extent between studies may be a result of differences in the spatial and temporal arrangement of resources. However, differences in the study methods (radio telemetry vs. mark-recapture), timing (pre-breeding vs. post-breeding), and duration of time when individuals were studied undoubtedly contributed to differences among studies. The use of radio telemetry likely had the strongest effect on differences, because unlike markrecapture, this technique ensures scheduled resighting of individuals and can capture movements without a predefined spatial extent.

In the Red Bank Creek watershed, the median (333 m) and maximum (3,693 m) distances moved by females during the fall/winter seasons were also greater than distances reported for *R. boylii* elsewhere. The only study to investigate the movements of females during the "non-spawning season" found that frogs moved less than 27 m and those "non-spawning" movements were less than "pre-spawning/spawning season" movements (Van Wagner, 1996). By contrast, I found no difference in median distances traveled by females between seasons. Since Van Wagner (1996) had a restricted study area (a single 800 m linear stream segment), he was unable to detect movements to adjoining tributaries or beyond the search area, which I found to be common. The fall/winter movements I observed illustrate that *R. boylii* at inland watersheds can make extensive movements to overwintering sites during the rainy season (November-January).

The maximum travel rates (males = 407 m/day and females = 1,386 m/day) for *R*. *boylii* in this study demonstrated that this species can travel faster than previously thought. Drennan et al. (2006) reported maximum rates of 128 m/day for males and 317 m/day for females dispersing to breeding sites at the Feather River. Travel rates recorded for a population at Clear Creek reported maximum travel rates of 42 m/day for males and 46 m/day for females (Van Wagner, 1996). Again, the apparent differences in rates of travel between this and other studies are presumably a result of different methods (radio telemetry vs. mark-recapture) and timing (pre-breeding vs. post-breeding) in each study.

My results also suggested that movement rates may be affected by the direction of travel. The maximum rate reported for a frog moving upstream (355 m/day) was about 25% of the maximum downstream rate (1,386 m/day). This result implies that upstream movement is energetically more expensive than traveling downstream, and when dispersing upstream frogs generally travel 100 m/day. In contrast, rates of downstream movement could have been influenced by surface flow, and may be a strategy frogs use to conserve energy.

Movement Routes

Rana boylii has been considered a highly aquatic frog, seldom found more than a few meters from water (Kupferberg, 1996; Stebbins, 2003; Zweifel, 1955). However, anecdotal observations of *R. boylii* 50 m (Nussbaum et al., 1983) and 100 m (Welsh, H. H. per. comm.) from the stream channel have led to the supposition that postmetamorphic frogs use upland habitats during the winter months. Although this may be true for coastal

populations, I found no evidence that adults disperse upland at Red Bank Creek. Adults generally restrict their activities to within 2 m from watercourses among seasons. Therefore, upland habitats were not used by *R. boylii* as dispersal corridors, as commonly reported for many lentic-breeding anurans (Bartelt, 2000; Hodgkinson and Hero, 2001; Lemckert and Brassil, 2000), and adults of this species are presumably restricted to movement along the stream network. However, upland habitats > 2 m may still be important for some *R. boylii* during extreme weather events. Maximum lateral movements of 7-40 m coincided with relatively large precipitation events, and suggest that some frogs use upland habitats briefly as an alternative strategy to avoid scouring flows.

Movement Phenology

The asynchrony of movements among *R. boylii* during all study seasons was consistent with the findings of other studies on amphibian movement (Paton and Crouch, 2002; Paton et al., 2000; Regosin et al., 2005; Timm et al., 2007). In pond-breeding amphibians, temporal segregation of movement has been suggested as a strategy to avoid intraspecific competition and predation pressures (Blair, 1961; Wilbur, 1972; Wilbur, 1980). However, unlike lentic species where individuals tend to aggregate at isolated habitat patches, *R. boylii* habitat is arranged as a continuous linear network, and at Red Bank Creek individuals were scattered. Therefore, the spatial arrangement of *R. boylii* habitats may have limited intraspecific competition and predation pressures, and the asynchrony in movement I observed may be caused by variation in resource provisions at

the diverse mesohabitats (i.e., riffles, runs, glides, and pools) used by frogs. For example, habitats with more constant and abundant resources may have delayed movement, whereas, limited resources at other habitats could have prompted early movement once resources became scarce.

My findings that ambient weather influence the phenology of *R. boylii* movement provide further support of resource mediated movement in this study. Specific ambient weather conditions (i.e., wet and humid conditions) increased the probability of frog movement in the fall/winter. However, little movement after the first rains in early fall and frequent movement during desiccating ambient weather in spring suggested an indirect association. Frogs neglected to move after the first fall rains likely because these storms supplied insufficient rain to increase surface flows and change habitat quality (i.e., resource availability) at areas occupied by study frogs. The increased probability of R. *boylii* movement after 22 mm of rain seemed to be a threshold in the Red Bank Creek watershed. Rain above this threshold led to increased flow along Red Bank Creek and restored surface flow to intermittent and some ephemeral tributaries. The chronology of increased stream discharge on the main channel apparently made some habitats previously occupied by *R. boylii* unfavorable (e.g., submerged basking sites or refugia) and may be the factor causing the movement phenology in the fall/winter. The phenology of spring movements also appeared to be a direct response to changes in habitat quality. However, in this case habitat change resulted from a loss of water, as illustrated by those frogs that moved from remnant pools on tributaries to the main channel. Receding flows also changed main channel habitats throughout this study

season, but the specific change in resource provisions (e.g., food and shelter) that prompted these movements remains unclear.

The positive association of amphibian migrations with wet climatic conditions is often attributed to their thin permeable skin and resulting dependence on moist environments to ameliorate evaporative water loss (Stebbins and Cohen, 1995). In this study however, adult *R. boylii* commonly moved during hot dry conditions. Frogs ameliorated the risk of moving during desiccating conditions by restricting travel routes to the drainage network where moist microclimates were available, even along dry stream segments where substrates were saturated by hyporheic (i.e., subsurface) flows. This behavior is one example of how *R. boylii* has adapted to the dynamic hydrology of watersheds throughout the inland foothills of its range.

Conservation Implications

The movements of *R. boylii* at Red Bank Creek indicated that this population operates at the watershed-scale because frogs used a wide variety of habitats during relatively short periods of time (~ 2 months) and moved between main channel and tributary habitats. These findings support the implementation of whole water-catchment management strategies (Saunders et al., 2002) for species conservation throughout inland portions of the range. These strategies are designed to maintain dynamic natural fluvial processes and recognize the need to understand cumulative impact of land use throughout the watershed. The operational scale of *R. boylii* should not be inferred from other studies that used scale-dependent techniques (i.e., VES and mark-recapture) confined to single linear main channel study reaches, because most scale-dependent amphibian studies cover areas too small to capture a species' movement capabilities and population structure (Smith and Green, 2005).

The wide variety of spatially disjunct habitats (including intermittent and ephemeral tributaries) used at both individual and population-levels emphasize the ecological value of habitat heterogeneity for post-reproductive resource acquisition (e.g, food, shelter, and overwintering) at Red Bank Creek. High heterogeneity is also an important factor purported to support larger populations of *R. boylii* in the Yuba River watershed (Yarnell, 2005). Unregulated rivers and streams are naturally heterogeneous and dynamic environments (Vannote et al., 1980; Ward, 1989), whereas regulated streams and rivers are relatively homogeneous (Hampton, 1995). Managers of rivers with regulated flow regimes should therefore adopt management strategies that mimic the natural dynamics of unregulated local rivers and streams. This type of strategy has been proposed for the conservation of *R. boylii* egg masses and larvae (Lind et al., 1996). Additional evidence on the potential benefits afforded to adult life stages stresses the importance of natural fluvial processes to support viable *R. boylii* populations.

The upstream directional bias of *R. boylii* movements at Red Bank Creek could also help assess the extent of potential impacts to subpopulations from proposed projects. Several land use practices (e.g., urbanization, livestock grazing, road construction, water impoundments, gravel mining, agriculture, and wildfires) may adversely impact water quality and aquatic habitats in the Westside Sacramento River tributaries (Yee, 2004). Such land use practices may clearly impact *R. boylii* that use habitats downstream from a project area. However, the seasonal upstream bias and extent of *R. boylii* movements (7,043 m) is evidence that activities within a watercourse could also have far reaching impacts on individuals partially dependent on upstream habitats. Therefore, impact assessments for projects and management activities that may alter natural stream processes should use a radial footprint of at least 7 km surrounding project boundaries to include upstream watercourses, when consideration is given to *R. boylii*. A footprint of this size and shape would provide a more realistic understanding of the population segment likely impacted by landuse activities.

Empirical data on the use of upland and tributary habitat by *R. boylii* permits assessing the effectiveness of riparian buffers (e.g., equipment exclosure zones [EEZ], equipment limitation zones [ELZ], and watercourse and lake protection zones [WLPZ]) for protecting habitats used by this species. For example, under the California Forest Practice Rules (FPRs) perennial fish-bearing streams (i.e., Class I) are afforded the most protection (75-150 foot buffer widths), non fish-bearing streams with aquatic life (i.e., Class II) receive less protections (50-100 foot buffer zone width), and streams capable of sediment transport to Class I and II waters without aquatic life are given the least protections (25-50 foot buffer widths) (CDFFP, 2008). My finding that adult individuals will use all types of watercourses (Class I, II, and III) but rarely move > 11.6 meters (38.1 feet, 90% upper confidence limit) from watercourses at Red Bank Creek supports that the current minimum buffer widths for Class I (75 feet = 22.86 meters), II (50 feet = 15.24 meters), and III (25 feet = 7.62 meters) watercourses provide some protection to core terrestrial habitats for adult *R. boylii* in the Red Bank Creek watershed. Frogs that disperse to tributaries rarely move to tributaries nearest to their initial capture location, but they often move to one of the few intermittent streams habitats in the Red Bank Creek watershed. This finding suggests that intermittent streams provide more favorable overwintering resources compared to ephemeral tributaries. These drainages should therefore receive increased protection in managed watersheds. Efforts should be made to maintain their natural fluvial processes. For example, the construction of stock ponds along intermittent drainages should be avoided. This restriction would help maintain contiguous movement corridors for those adults using both main channel and tributary habitats. This would also minimize the potential for increased density and distribution of bullfrogs, an introduced predator of *R. boylii* (Moyle, 1973).

The maximum distance (7,043 m), maximum rate (1,386 m/day), and seasonal biases of adult *R. boylii* movements in the Red Bank Creek watershed could be used to understand the potential impact of infectious diseases within and among populations. Chytridiomycosis is an emerging infectious disease of amphibians caused by a fungal pathogen (*Batrachochytrium dendrobatidis*) that has been attributed to population declines and extinctions (Daszak et al., 2003). *Batrachochytrium dendrobatidis* has been detected in California populations of *R. boylii* (Fellers, 2005) and its potential spread is a conservation concern. Knowledge of the movements of adult *R. boylii* in the Red Bank Creek watershed could help develop realistic models to inform disease control strategies for infected populations.

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Appendix A. Morphometrics, age, and fate of *R. boylii* radio-tracked during S1 in the Red Bank Creek watershed, including sex (M = male, F = female), number of locations (N), study duration, weight, snout-urostyle length (SUL), mass %, age, and fate.

Frog ID	Sex	Ν	Study duration	Weight	SUL	Mass %	Age	Fate*
ç			(days)	(g)	(mm)		(years)	
A01	F	30	61	37.5	73.3	4.0	3.8	Released
A02	Μ	19	31	15.7	56.0	5.7	3.8	$Lost^1$
A03	F	35	64	27.8	67.5	5.5	1.8	Released
A04	F	28	51	36.7	73.7	4.0	4.8	Released
A05	F	11	16	35.0	73.0	4.0		Prey ⁵
A06	F	17	29	32.0	67.0	4.7	2.8	Lost ²
A07	F	32	62	28.0	67.0	6.0	4.8	Lost ²
A08	Μ	14	22	13.0	54.0	7.0	6.8	Prey ⁴
A09**	Μ	1	1	18.0	55.0	5.0		Prey ⁴
A10**	F	9	22	20.0	61.0	8.0		Prey ⁴
A11	F	21	52	31.3	71.0	5.0	4.8	Released
A12	F	26	50	29.5	62.5	5.5	5.8	Prey ⁶
A13	F	30	51	27.8	66.0	5.5	3.8	Released
A14	F	29	49	20.3	62.0	5.0	4.8	Released
A15	Μ	16	28	14.0	50.5	6.5	4.8	Released
A16	Μ	16	28	11.8	50.0	7.5	2.8	Released
A17	F	17	52	20.8	59.5	4.5	2.8	Lost ³
A18	Μ	16	27	12.3	48.0	7.3	6.8	Released
A19**	Μ	4	8	15.0	51.0	6.0		Prey ⁴
A20	F	16	31	29.7	65.0	3.0	5.8	Released
A21	F	14	23	18.2	59.0	5.4	2.8	Released
A22	Μ	14	23	15.6	55.0	6.6	3.8	Released
A23	F	14	36	23.6	63.3	4.2	1.8	Released
A24	F	17	70	31.3	68.7	3.0	2.8	Released
A25	F	11	28	17.8	55.3	5.0	2.8	Released
A26	Μ	15	26	11.3	46.5	7.8	3.8	Released
A27	F	22	38	25.0	64.0	6.5	3.8	Released
A28	F	11	26	14.7	53.5	6.0	3.8	Released
A29	F	13	64	33.0	67.7	3.0	3.8	Released
A30	Μ	11	22	14.0	52.0	6.5	3.8	Released
A31**	F	4	6	28.0	69.0	6.0		Prey ⁴
A32**	F	8	15	24.0	62.5	4.0	1.8	$Lost^1$
A33	Μ	12	20	14.0	51.5	6.0	5.8	Released
A34	F	17	29	22.5	60.5	7.0		Lost ²
Mean:		18	38	22.6	60.6	5.5	4.1	

¹Lost due to dropped signal, ²Lost due to beaded belt failure, ³Lost due to beaded belt failure but recaptured within study season, ⁴ Predation by *Thamnophis atratus*, ⁵ Predation by unknown predator, ⁶ Predation by *Rana catesbeiana*.

** Frogs not included in season means due to low number of locations (i.e., < 10).

Frog ID	Sex	N	Study	Weight	SUL	Mass %	Age	Fate*
-			duration	(g)	(mm)		(years)	
		20	(days)					
A03	F	20	64	41.2	72.0	3.8	2.2	Lost ¹
B02	F	14	50	43.6	73.0	4.0	3.2	Released
B03	F	18	50	30.0	66.0	5.0	2.2	Released
B04	F	18	50	31.5	67.0	5.3	3.2	Released
B05	F	18	54	25.5	63.0	6.2	2.2	Released
B06	F	19	57	33.3	68.0	5.0	6.2	Released
B07	F	24	102	27.0	63.0	5.9	6.2	Released
B08	F	18	54	31.0	66.5	5.0	2.2	Released
B09	F	18	54	27.0	63.0	5.8	5.2	Released
B10**	F	1	1	29.0	65.0	6.0		Prey ³
B11	F	15	53	28.8	65.0	5.4		Lost ¹
B12	F	17	54	23.9	60.7	4.0	3.2	Released
B13	F	17	53	39.4	70.0	4.0	6.2	Lost ²
B14	F	18	54	37.7	69.5	4.2		Released
B15	F	18	54	38.5	69.0	4.0	3.2	Released
B16	F	16	54	32.1	68.3	5.0	3.2	Released
B17	F	15	54	27.2	63.0	5.5	1.2	Released
B18	F	15	54	29.8	63.5	5.2	3.2	Released
B19	F	25	99	36.3	70.3	4.4	7.2	Released
B20	F	18	52	23.3	60.3	4.3	4.2	Released
B21	F	15	51	30.8	67.0	5.0		Released
B22**	F	6	21	26.5	67.0	6.0	3.2	Lost ²
B23	F	15	53	26.2	62.0	5.8	3.2	Released
B24	F	14	52	33.6	67.5	4.8	7.2	Released
B25	F	11	32	40.5	68.5	4.0	3.2	Released
B26	F	12	42	41.0	68.5	4.0	5.2	Released
Mean:		17	56	32	66	5	3.9	

Appendix B. Morphometrics, age, and fate of *R. boylii* radio-tracked during FW1 in the Red Bank Creek watershed, including sex (M = male, F = female), number of locations (N), study duration, weight, snout-urostyle length (SUL), mass %, age, and fate.

¹ Lost due to beaded belt failure, ² Lost due to slipped belt, ³ Predation by *Thamnophis atratus*.

** Frogs not included in season means due to low number of locations (i.e., < 10).

Appendix C. Morphometrics, age, and fate of *R. boylii* radio-tracked during fall 2005/winter 2006 in the Red Bank Creek watershed, including sex (M = male, F = female), number of locations (N), study duration, weight, snout-urostyle length (SUL), mass %, age, and fate.

Frog ID	Sex	Ν	Study	Weight	SUL	Mass %	Age	Fate*
			duration (days)	(g)	(mm)		(years)	
B05	F	23	55	38.6	71.8	4.2	3.2	Released
B15	F	15	52	41.7	70.1	2.0	4.2	Released
C01	F	20	55	30.2	65.8	5.3	3.2	Released
C03**	F	4	10	23.0	63.0	6.0		Prey ⁴
C04	F	22	59	25.5	61.5	6.0	3.2	Lost ²
C05	F	17	58	34.0	66.3	4.2	2.2	Lost ¹
C06	F	20	55	31.3	65.2	5.0	2.2	Released
C07	F	15	36	24.0	60.8	6.5		Lost ¹
C08	F	21	55	23.8	60.0	6.3	2.2	Released
C09	F	16	56	39.5	69.8	4.0	4.2	Released
C10	F	20	54	37.2	66.5	4.0	3.2	Released
C11	F	18	56	29.0	63.7	5.2	3.2	Released
C12	F	21	112	33.1	68.6	4.7	3.2	Prey ⁵
C13	F	23	113	29.1	63.6	5.1	4.2	Released
C14	F	20	59	25.7	62.8	5.0	2.2	Released
C15	F	21	113	27.8	62.8	5.7	4.2	Released
C16	F	21	113	28.5	62.9	5.4	2.2	Released
C17	F	21	112	25.7	62.2	5.9	1.2	Released
C18	F	24	112	28.6	63.7	4.9	4.2	Released
C20	F	25	87	24.0	60.1	4.4	3.2	Released
C21**	F	1	1	31.0	64.0	5.0		Prey ⁴
C22	F	11	42	36.8	67.3	4.0		Lost ³
Mean:		20	73	31	65	5	3.1	

¹ Lost due to beaded belt failure, ² Lost due to beaded belt failure but recaptured within study season, ³ Lost due to slipped belt, ⁴ Predation by *Thamnophis atratus*, ⁵ Predation by unknown predator.

** Frogs not included in season means due to low number of locations (i.e., < 10).

Appendix D. Summary of movement data; showing sex, number of locations (N), study duration, date range, cumulative distances (CD), network distance (NWD), net displacement (ND), movement pattern (M = mobile, S = sedentary), and resource use (P = perennial, I = intermittent, E = ephemeral); for *Rana boylii* radio-tracked during S1 in the Red Bank Creek watershed.

Frog ID	Sex	Ν	Study duration	Date range*	CD	NWD	ND	Movement	Resource
			(days)		(m)	(m)	(m)	pattern	use
A01	F	30	61	4/10 - 6/10	7043	7043	6169	Μ	P>I>E>P
A02	Μ	19	31	4/10 - 5/11	43	3	3	S	Р
A03	F	34	57	4/10 - 6/6	630	286	6	М	P>P
A04	F	28	51	4/10 - 5/31	424	130	130	Μ	P>P
A05^	F	11	16	4/11 - 4/27	416	382	382	М	P>P
A06	F	17	29	4/11 - 5/10	678	542	542	М	P>P
A07	F	32	62	4/11 - 6/12	3851	3669	3669	Μ	P>P
A08^	Μ	14	22	4/11 - 5/3	215	149	-149	Μ	Р
A09^	Μ	1**	1	4/12 - 4/13	0	0	0		
A10^	F	9**	13	4/12-4/25	80	2	2	S	Р
A11	F	21	52	4/12 - 6/3	1666	1654	1654	Μ	I>I
A12^	F	26	50	4/3 - 5/23	694	458	458	М	P>P
A13	F	30	51	4/16 - 6/6	128	2	-2	S	Р
A14	F	29	49	4/17 - 6/5	1026	501	-40	М	P>I>P
A15	Μ	16	28	4/17 - 5/15	185	149	-149	Μ	Р
A16	Μ	16	28	4/17 - 5/15	91	13	-13	S	Р
A17	F	17	52	4/18 - 6/9	423	379	-223	М	P>I
A18	Μ	16	27	4/18 - 5/5	132	72	72	Μ	P>P
A19^	Μ	4**	8	4/19 - 4/27	95	95	-95	М	P>P
A20	F	16	31	4/23 - 5/24	92	2	2	S	Р
A21	F	14	23	4/24 - 5/17	678	627	627	Μ	I>I
A22	Μ	14	23	4/24 - 5/17	628	578	-578	М	I>P
A23	F	14	36	4/24 - 5/30	2634	2386	2386	Μ	P>P
A24	F	16	49	4/24 - 6/12	3882	3610	3610	Μ	P>P
A25	F	11	28	4/25 - 5/23	1463	1441	1441	Μ	P>I
A26	Μ	15	26	4/25 - 5/21	594	548	-548	М	P>P
A27	F	22	38	4/26 - 6/3	556	508	184	М	I>P
A28	F	11	26	4/26 - 5/22	86	14	-14	S	Ι
A29	F	11	19	4/27 - 5/16	57	9	9	S	Р
A30	Μ	11	22	5/2 - 5/24	48	8	-8	S	Р
A31^	F	4**	6	5/2 - 5/8	166	166	166	Μ	P>I
A32	F	8**	15	5/2 - 5/17	393	373	-373	Μ	I>I
A33	Μ	12	20	5/4 - 5/24	20	2	2	S	Р
A34	F	17	29	5/4 - 6/2	318	272	-272	М	I>P
Median		16	29		424	333			
(min max)		(11-34)	(16-62)		(20-7043)	(2-7043)			

* Includes days tracked and incidental recapture(s). ** Frog not included in median due to low number of locations (i.e., < 10). ^ Animals lost due to predation events.

	~		~ 1		~~				
Frog ID	Sex	Ν	Study	Date range*	CD	NWD	ND	Movement	Resource
			duration		(m)	(m)	(m)	pattern	use
			(days)						
A03	F	19	51	10/4 - 11/24	177	17	17	S	Р
B02	F	14	50	10/5 - 11/24	831	475	475	М	I>I
B03	F	18	50	10/5 - 11/24	344	254	254	М	P>P
B04	F	18	50	10/5 - 11/24	159	21	21	S	Р
B05	F	18	54	10/6 - 11/29	75	1	1	S	Р
B06	F	19	57	10/6 - 12/2	1610	1483	-1048	Μ	P>I
B07	F	24	102	10/6 - 1/16	2931	2861	2861	М	P>I>E
B08	F	18	54	10/7 - 11/30	67	32	32	S	Р
B09	F	18	54	10/7 - 11/30	162	8	-8	S	Р
B10^	F	1**	1	10/7 - 11/8					
B11	F	15	53	10/7 - 11/29	527	527	527	М	P>P
B12	F	17	54	10/8 - 12/1	239	104	105	Μ	P>P
B13	F	17	53	10/8 - 11/30	213	185	185	Μ	P>P
B14	F	18	54	10/8 - 12/1	146	8	-8	S	Р
B15	F	18	54	10/9 - 12/2	123	9	-9	S	Р
B16	F	16	54	10/9 - 12/2	273	147	125	Μ	P>E
B17	F	15	54	10/9 - 12/2	55	23	23	S	Р
B18	F	15	54	10/9 - 12/2	306	266	266	М	P>P
B19	F	25	99	10/9 - 1/16	3593	3543	-2899	М	P>I
B20	F	18	52	10/10 - 12/1	468	384	-384	М	P>P
B21	F	15	51	10/10 - 11/30	3771	3693	-3693	Μ	P>P
B22	F	6**	21	10/10 - 9/31	741	741	741	М	P>P
B23	F	15	53	10/11 - 12/3	562	466	466	Μ	P>E
B24	F	14	52	10/23 - 12/14	212	158	158	Μ	I>I
B25	F	11	32	11/1 - 12/3	156	96	96	М	I>I
B26	F	12	42	11/2 - 12/14	104	12	12	S	Р
B30	F	3**	49	10/6 - 11/24	1602	1602	1602	М	
Median		18	54		226	153			
(min max)		(11-25)	(32-102)		(55-3771)	(1-3693)			

Appendix E. Summary of movement data; showing sex, number of locations (N), study duration, date range, cumulative distances (CD), network distance (NWD), net displacement (ND), movement pattern (M = mobile, S = sedentary), and resource use (P = perennial, I = intermittent, E = ephemeral); for *Rana boylii* radio-tracked during FW1 in the Red Bank Creek watershed.

* Includes days tracked and incidental recapture(s).

** Frog not included in median due to low number of locations (i.e., < 10).

^ Animals lost due to predation events.

Appendix F. Summary of movement data; showing sex, number of locations (N), study duration, date range, cumulative distances (CD), network distance (NWD), net displacement (ND), movement pattern (M = mobile, S = sedentary), and resource use (P = perennial, I = intermittent, E = ephemeral) for *Rana boylii* radio-tracked during fall 2005/winter 2006 in the Red Bank Creek watershed.

Frog ID	Sex	Ν	Study duration (days)	Date range*	CD (m)	NWD (m)	ND (m)	Movement pattern	Resource use
B05	F	23	55	10/7 - 12/1	170	0	0	S	Р
B15	F	15	52	10/10 - 12/1	151	15	-15	S	Р
C01	F	20	55	10/7 - 12/1	334	244	244	М	P>I
C03^	F	4**	10	10/8 - 10/18	24	6	-6	S	Р
C04	F	22	59	10/7 - 12/5	650	582	-472	М	P>E
C05	F	17	58	10/7 - 12/4	62	2	2	S	Р
C06	F	20	55	10/8 - 12/2	192	80	48	М	P>E
C07	F	15	36	10/8 - 11/13	160	2	2	S	Р
C08	F	21	55	10/8 - 12/2	1406	1334	106	М	P>I>E
C09	F	16	56	10/10 - 12/5	1399	1285	-1255	М	P>I
C10	F	20	54	10/9 - 12/2	111	5	5	S	Р
C11	F	18	56	10/9 - 12/4	415	281	281	М	P>E
C12	F	21	112	10/9 - 1/29	99	31	-31	S	P>P
C13	F	23	113	10/8 - 1/29	295	60	5	М	P>P
C14	F	20	59	10/8 - 12/6	823	729	-667	М	P>I
C15	F	21	113	10/8 - 1/29	165	7	7	S	Р
C16	F	21	113	10/8 - 1/29	84	2	-2	S	Р
C17	F	21	112	10/9 - 1/29	182	28	28	S	P>P
C18	F	24	112	10/9 - 1/29	399	131	-15	М	Р
C20	F	25	87	10/10 - 1/5	175	20	20	S	Р
C21^	F	1**	1	10/19 - 10/20					
C22	F	11	42	10/21 - 12/2	68	4	4	S	Р
Median (min max.)		21 (11-25)	57 (36-113)		179 (62-1406)	46) (0-1334)			

* Includes days tracked and incidental recapture(s).

** Frog not included in median due to low number of locations (i.e., < 10).

^ Animals lost due to predation events.

	Red Bank	k Creek	Intermittent creeks			
Habitat Variable	В	NB	В	NB		
Number of sites	48	15	9	8		
Stream width (m)						
Mean	6.41	5.60	2.10	1.70		
SE	0.21	0.31	0.16	0.16		
Range	4-10	4-7.6	1.5-3	1-2.6		
Mean water depth (m)						
Mean	0.32	0.15	0.12	0.20		
SE	0.01	0.01	0.03	0.07		
Range	0.08-0.6	0.09-0.24	0.02-0.03	0.0-0.58		
Max water depth (m)						
Mean	0.31	0.25	0.21	0.30		
SE	0.02	0.02	0.05	0.08		
Range	0.1-0.76	0.17-0.49	0.05-0.52	0.11-0.76		
Avg. insolation (WH/pixel)						
Mean	4670	4710	4395	4620		
SE	18	20	52	68		
Range	4324-4829	4500-4848	4166-4538	4166-4749		
Avg. solar duration (Hours/month)						
Mean	389	396	353	388		
SE	3	2	6	9		
Range	338-407	2.4-374	332-377	356-410		
Vegetative Cover (%)						
Median	0	0	0	41		
Range	0-51	0-63	0-57	0-50		
Stream habitat (%)						
Riffle	13	87	11	13		
Run	45	0	11	0		
Glide	43	0	44	25		
Pool	0	13	33	63		
Aquatic substrate (%)						
Soil	0	0	0	0		
Sand	4	0	11	25		
Gravel	28	7	44	38		
Cobble	49	27	33	38		
Boulder	13	20	0	0		
Bedrock	6	47	11	0		
Bank substrate (%)						
Soil	13	7	56	38		
Sand	11	13	0	0		
Gravel	11	0	Õ	Õ		
Cobble	17	13	Õ	38		

Appendix G. Characteristics of breeding (B) and non-breeding (NB) habitats used by *R*. *boylii* during S1 in the Red Bank Creek watershed.

Boulder	15	40	0	0
Bedrock	33	27	44	25
Riparian Vegetation (%)				
Herbs	53	87	56	50
Understory	15	13	33	13
Midstory	23	0	11	13
Overstory	9	0	0	25