MATING STRATEGY AND BREEDING PATTERNS OF THE FOOTHILL YELLOW-LEGGED FROG (*RANA BOYLII*)

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Abstract.—The Foothill Yellow-legged Frog (*Rana boylii*) has declined across much of its native range in California. Improper stream management may lower egg mass survival and reduce the availability of suitable breeding habitats. We collected data during six breeding-seasons (2002-2007) along an unregulated stream in northwestern California. We monitored temporal reproductive patterns at a breeding site and used mark-recapture and behavioral observations to spatially and temporally track individuals and investigate aspects of the mating strategy. The duration of breeding activity lasted three to seven and a half weeks. Day within the breeding-season and stream flow influenced breeding activity. Male frogs congregated at the breeding site during the reproductive season but females arrived asynchronously. Male frogs showed fidelity to individual sites within the breeding area. The daily operational sex ratio of adults was male-biased, while the overall breeding-season operational sex ratio was female-biased. Males in amplexus were larger than males never observed in amplexus, providing evidence of a non-random mating pattern. These frogs showed plasticity in temporal breeding patterns and were not exclusively prolonged or explosive breeders. Frog behaviors at the breeding site were more typical of prolonged breeding anurans. Both timing and duration of breeding were closely linked to the natural hydrologic cycle, indicating that anthropogenic variations of stream flows may suppress the reproductive behavior and annual output of these frogs.

Key Words.—Foothill Yellow-legged Frog; mating strategy; northwestern California; *Rana boylii*; reproductive ecology; temporal breeding patterns

INTRODUCTION

The Foothill Yellow-legged Frog (*Rana boylii*) occurs in rivers and streams of Oregon and California (Stebbins 2003) and is one of a few obligate stream breeding ranid frogs in the United States. Streams are stochastic in nature and the abiotic factors that influence the reproductive ecology of stream breeding frogs are different from those of lentic species. *Rana boylii* attach egg masses to substrates in shallow stream habitats with low water velocities such as river bars that can have limited spatial and temporal availability (Zweifel 1968; Hayes and Jennings 1986; Fuller and Lind 1992; Lind et al. 1996; Kupferberg 1996). Frogs may use the same stream habitats that provide suitable conditions for breeding activity each year (Fuller and Lind 1992; Kupferberg 1996). One major threat to *R. boylii* populations is the artificial regulation of stream flows in dammed river systems. Improperly managed stream flows can have direct (i.e., scouring and stranding of egg masses) and indirect (i.e., elimination of suitable breeding habitat) consequences on the reproductive output (Lind et al. 1996). Lind et al. (1996) and Kupferberg (1996) each demonstrated the importance of key abiotic processes in the successful annual reproduction of this species.

Understanding mating systems and their relationship to abiotic processes is important in species conservation (Caro 1998). A variety of ecological mechanisms including temporal breeding patterns, operational sex ratios, and breeding population densities influence the evolution of mating systems (Emlen and Oring 1977; Wells 1977a; Arak 1983b). Limited seasonal availability of suitable breeding habitat combined with males' access to females affects anuran breeding activity patterns (Emlen and Oring 1977; Wells 1977a).

Wells (1977a, 2007) described prolonged and explosive breeding as two basic patterns of anuran reproduction (extremes of a temporal continuum), with behavioral differences associated with these patterns. Prolonged breeding occurs over a period of more than a month and explosive breeding takes place over a period of a few days to a few weeks (Wells 1977a). Prolonged breeders tend to have a more male-biased daily operational sex ratio compared to explosive breeders (Sullivan et al. 1995). Behavioral differences include the tendency to aggregate, complexity of the vocal repertoire, competition intensity, spatial organization, and mate selection (Wells 1977a).

In this study, we examined timing of breeding activity in relation to abiotic factors and mating behaviors that we believed were important in characterizing the mating strategy used by a robust breeding population of *R. boylii*. In particular, we assessed whether: (1) frogs exhibited a prolonged or explosive temporal breeding pattern and how it related to stream flow and date; (2) frogs aggregated at breeding sites during the reproductive season; (3) male frogs vocally and/or

128

FIGURE 1. Male Foothill Yellow-legged Frog (*Rana boylii*) from Hurdygurdy Creek, Del Norte County, northwestern California, USA, marked with beaded belt; identified as 1-green/1-white.

physically maintained and defended areas within a breeding site; (4) operational sex ratios were biased; and (5) the size of males and females of mating pairs indicated size-assortative or large-male advantage mating patterns.

In addition to describing the mating strategy, aspects of this study may provide valuable information relevant to conservation. A comprehensive understanding of the annual variation and the effect of stream flows on breeding activity in a natural flow regime is important in conservation planning and managing for this species. *Rana boylii* breeding habitats have limited spatial and temporal availability and protection of these habitats should be a primary objective; however, the seasonal distribution of reproductive male and female frogs relative to breeding sites warrants some consideration. Understanding the social structure and spatial organization of a breeding population may be important in establishing how factors such as breeding habitat patch size influence the maintenance and evolution of the mating strategy (Trumbo and Eggert 1994; Wong et al. 2005). Additionally, knowledge pertaining to a species' mating system (e.g., operational sex ratios and mating patterns) provides information on the effective

population size and the genetic diversity of a breeding population (Nunney 1993).

MATERIALS AND METHODS

Study site.—We conducted field work on the lower 2 km of Hurdygurdy Creek, Del Norte County, northwestern California, USA, a fifth-order tributary to the South Fork Smith River. Hurdygurdy Creek was located in mixed hardwood/Douglas-fir (*Pseudotsuga menziesii*) forest with cool wet winter and warm dry summer seasons. Alder and willow (*Alnus* and *Salex* sp.) were the primary riparian species along the reach and at the primary breeding site studied. Rainfall at the nearest gauging station (Gasquet Ranger Station, Smith River National Recreation Area, 17.7 air km north) averages 280 cm annually (range = 152-330 cm). During the study period, ambient air temperatures ranged from 6 to 30°C and water temperatures ranged from 6 to 18°C. The geomorphology of Hurdygurdy Creek revealed that this creek has experienced disturbance events characteristic of a natural winter high flow regime such as annual debris flows, flooding, and some braided channel migrations. However, major mesohabitat types along the reach were consistently maintained across years. Stream discharge is variable, ranging from one cubic meter per second (CMS) in the summer to over 100 CMS in the winter (McCain 1994). Our census reach was a 1,560 m section of creek located approximately 300 m upstream from the South Fork Smith River confluence. The primary breeding site used in this study was located approximately 877 m upstream from the confluence. This 20 m^2 area was within a 40 m wide braided channel that contained shallow (< 1 m) glide and riffle habitat.

Timing of breeding activity.—We monitored the onset and duration of *R. boylii* breeding activity to determine where this species fell on the continuum between prolonged and explosive temporal breeding. We surveyed for egg masses every one to nine days during the springs of 2002 through 2007 except during two periods of extremely high stream discharge that followed rain events (21 April 2004 and 19 May 2005). We recorded the location, oviposition date and embryonic development stage (Gosner 1960) for each egg mass. We estimated oviposition dates based on larval development for egg masses that were not laid during our observation periods. We monitored the stages of development for several egg masses over successive days and created a curve to estimate developmental progression over time. Egg masses developed at an approximate rate of two stages during the first two days, four stages during the third day, one stage during days four through eight, and one stage every two days during days nine through 13 (Gosner stage 16). These rates
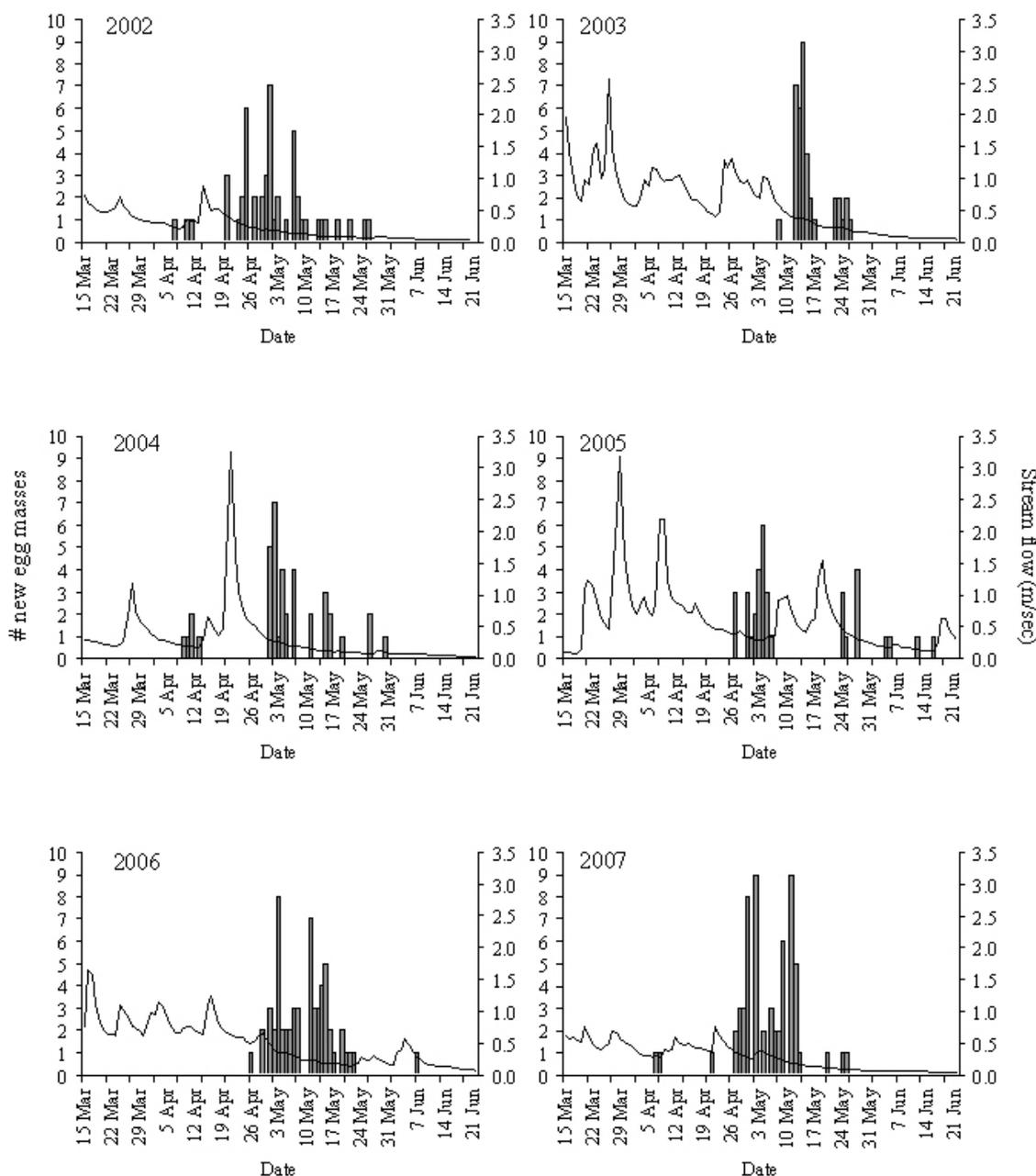
FIGURE 2. *Rana boylii* breeding activity at the primary breeding site of Hurdygurdy Creek, Del Norte County, California**,** USA and the estimated stream flow during the breeding-season. Bars represent the number of new egg masses and lines represent stream flow values.

differed from those previously reported (Zweifel 1955); however, because rate of embryonic development is highly temperature-dependent and hence site specific, we assumed that these rates were more accurate for this study. We could not accurately estimate the oviposition dates for egg masses that we observed very late in development (Gosner stage ≥ 17); therefore, we eliminated these egg masses from the analysis (three in 2003, three in 2005, and four in 2007).

In order to relate the onset and duration of breeding activity to stream flow, we obtained water discharge data for the mainstem Smith River from the USGS stream flow database (http://waterdata.usgs.gov/ca/nwis). We measured stream velocity (to the nearest 0.1 m/s) using a digital flow meter (Hach/Marsh-McBirney, Frederick, Maryland, USA) at a reference site at Hurdygurdy Creek several times throughout the 2003 season to validate using Smith River discharge data as a surrogate measurement. Linear regression analysis confirmed that

TABLE 1. Breeding-season date, duration, and stream flow data for Hurdygurdy Creek, Del Norte County, California, USA for 2002-2007.

Year	Breeding Initiation Date	Breeding End Date	Breeding-season Duration (days)	Mean Stream Flow (m/s)	Min Stream Flow (m/s)	Max Stream Flow (m/s)
2002	7 April	26 May	50	0.18	0.03	0.87
2003	8 May	26 May	19	0.49	0.06	1.31
2004	9 April	30 May	52	0.28	0.03	3.24
2005	27 April	16 June	51	0.57	0.13	2.19
2006	26 April	7 June	42	0.43	0.08	1.24
2007	7 April	25 May	49	0.24	0.04	0.76

Hurdygurdy flow measurements were strongly related to Smith River discharge data ($r^2 = 0.95$, $P < 0.0001$, n = 23). We then used the resulting regression equation, Y = 0.0044X - 0.0404, to obtain daily flow estimates for Hurdygurdy Creek using the Smith River data. We plotted annual Hurdygurdy Creek flow estimates and number of new egg masses to examine trends in the data and used a generalized additive model to examine the effects of stream flow and day on breeding activity (measured as the number of new egg masses). We used stream flow, day within breeding-season (from 1 April to 20 June), and sampling year as covariates used in the non-parametric regression model. We used a generalized additive model because we suspected that the relationships between independent variables and the response variable would be nonlinear.

We used Spearman rank correlation analyses to examine associations between pairs of the following variables: the total number egg masses, first and last dates of oviposition, length of breeding-season (number of days from first to last date of oviposition), stream flow on the first date of oviposition, and mean, minimum and maximum stream flows during the breeding-season (from 1 April to 20 June) for the six years. We set alpha at $P = 0.1$ for all analyses (Schrader-Frechette and McCoy 1993).

Breeding site aggregations.—To assess whether frogs formed aggregations during the reproductive season, we quantified the distribution of adult frogs along the creek, both during and following the breeding period. In 2002, we conducted stream censuses, which typically took two days, during the active breeding period (6 April-13 May 2002) and several times following the cessation of breeding (15 June-14 September 2002). We visually searched both stream banks with one surveyor on each side. They walked slowly upstream, searching the banks and mid-channel emergent rocks for frogs. We conducted one census during the first week of breeding activity at the study site (6-7 April), one census midway through the breeding-season (12-13 May), and three censuses following the breeding-season (15-16 June, 24-25 July, 13-14 September).

We captured all adult frogs observed with a net or by hand and held them in a re-sealable storage bag (S.C. Johnson & Son, Inc., Racine, Wisconsin, USA) with a small amount of creek water in order to prevent desiccation and overheating until processing. We weighed frogs to the nearest 0.5 g using a Pesola spring scale (+/- 0.1), measured snout-to-urostyle length to the nearest mm (repeated three times for accuracy) using hand-held calipers (General Tools & Instruments Co., LLC., New York, New York, USA) and recorded their gender if we observed secondary sexual characteristics (enlarged nuptial pads indicated a male, distended abdomen indicated a gravid female). We marked adult frogs with 12.45 mm Passive Integrated Transponders (PIT) tags (Biomark Inc., Boise, Idaho, USA) that we inserted subcutaneously through a v-shaped incision on the dorsal side (Pope 1999). We identified previously captured and marked frogs by reading their PIT tags with a scanner (Avid Identification Systems, Inc., Norco, California, USA and Biomark Inc., Boise, Idaho, USA).

We recorded the locations of frog captures, tadpoles, and egg masses using location codes and a map developed by Lind et al. (2004), which consisted of mesohabitat type (e.g., pool, riffle, run, glide; McCain et al. 1990) and the length of each mesohabitat. A habitat unit refers to a specific mesohabitat along the stream reach. We classified each habitat unit as a breeding (n = 15) or non-breeding (n = 40) site. Because we may not have located some egg masses along the reach during surveys, we defined breeding sites as those habitat units in which we observed at least one egg mass or tadpoles in at least one of the study years. Though it was possible that habitat may have changed status (breeding/non-breeding) from one year to the next, previous research indicated that *R. boylii* use the same breeding areas in successive years (Fuller and Lind 1992; Kupferberg 1996).

We used randomization t-tests (with 10,000 iterations, $\alpha = 0.10$) to examine differences in the number of adult captures within breeding and non-breeding habitats during the reproductive (April-May) and post-reproductive seasons (June-September). We assessed male and female captures separately.

Spatial organization and aggression.—To examine inter-male spacing, we monitored the location and behavior of individual male frogs during the 2003 breeding-season at the primary breeding site over 17 days between 17 May and 5 June 2003. We marked
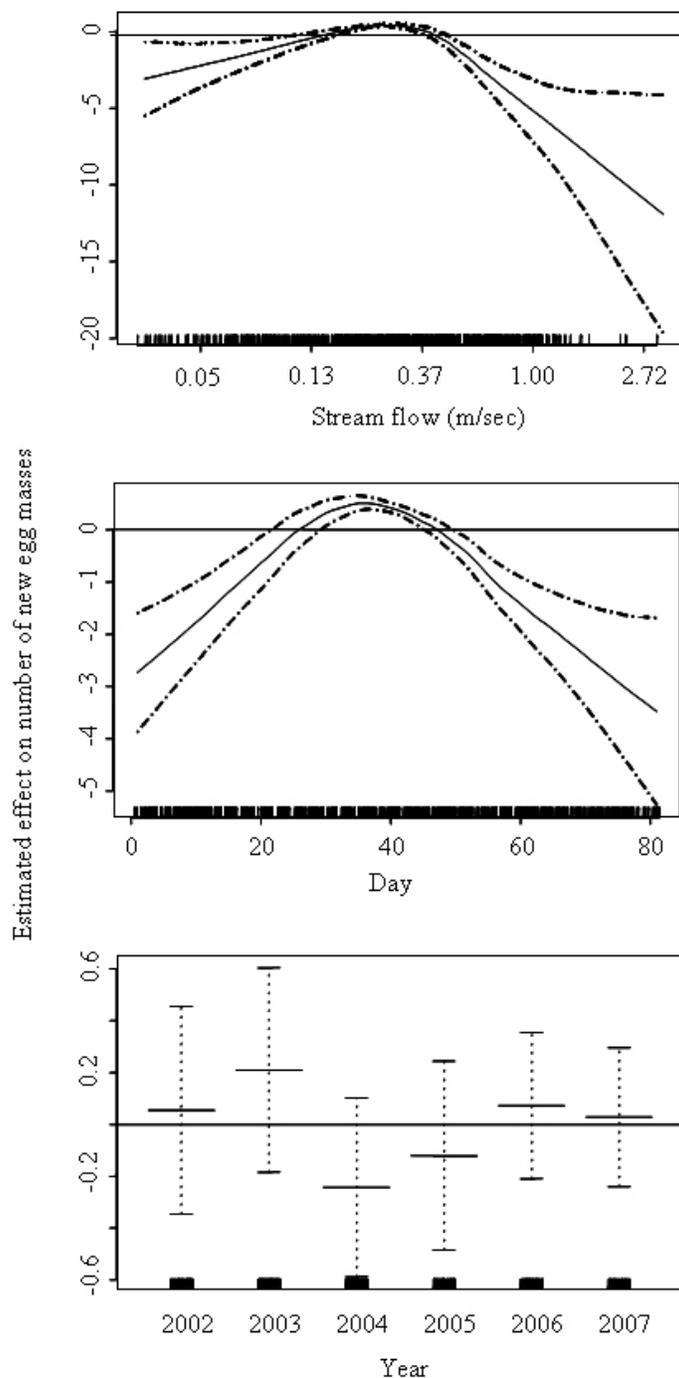
FIGURE 3. Estimated effect of stream flow, day within breeding-season and year on breeding activity of *Rana boylii* from Hurdygurdy Creek, Del Norte County, California. Dashed lines represent approximate 95% confidence intervals and hatch marks on the horizontal axis represent data points. The effect is significant ($P < 0.01$) when confidence intervals fall above or below the effect line.

male frogs with uniquely colored beaded belts (Fig. 1) made of nylon jewelry cord (Pepperell Crafts, Pepperell, Massachusetts, USA) and glass seed beads (Ornela Co., Czechoslovakia; modified from Woolbright et al. 1990). This allowed visual identification during behavioral observations without further handling. We observed marked frogs in agonistic interactions, calling and amplexus, indicating that the belts did not hinder their activities. We recaptured frogs regularly, examined them for skin lacerations and removed beaded belts at the end of each breeding-season. We did not recapture all frogs at the end of each breeding-season;

TABLE 2. Results of generalized additive model relating day and flow to number of new egg masses of *Rana boylii*.

Parameter	Value
Null Deviance	990
DF† (null model)	485
Model (residual) Deviance	443
DF† (full model)	474
Deviance increase ‡	
Stream Flow	170 (31)*
Day Within Breeding-season	201 (37)*
Year	5 (1)

†DF = degrees of freedom.
‡Deviance increase: increase in deviance resulting from dropping the selected variable from the model. The percentage increase in deviance is given in parentheses, and was calculated as (deviance increase/(null deviance-model deviance)) x 100 (Knapp 2005).
*$P < 0.0001$.

consequently this method may have resulted in lower survival. However, we selected this method in order to minimize the amount of disturbance during breeding activities.

During 2003, we mapped the primary breeding site using a 20-m transect run through the area. We set rebar near the left and right stream banks creating a transect perpendicular to the creek within the area used for breeding activity. We positioned a metric tape between the two pieces of rebar to represent the x-axis and used a second metric tape, representing the y-axis, to measure the upstream/downstream distance from the x-axis. We then recorded and mapped the artesian coordinates of the wetted channel of the point bars, emergent rocks and alder (*Alnus* sp.) shoots within the breeding site, and all egg masses. Based on these landmarks, we systematically recorded the locations of individual male frogs each hour for two to nine hours a day for three weeks (17 May 2003 through 5 June 2003).

We converted all x and y-coordinates of individual male frog locations to Northing and Easting coordinates and entered them into ArcView to establish site fidelity and home range sizes. To test if male frogs had fidelity to particular locations within the breeding area, we performed a Monte Carlo random walk test. In this analysis, the mean square distance from the center of activity was compared to 100 randomly generated paths for each individual. An individual was classified as site faithful if the actual movement paths were lower than the lower bound of the 95% confidence interval of the random mean square distances (Hooge et al. 1997). Additionally, we determined standard 50% kernel home ranges (core area used) for each individual male frog. The core area was considered the center of activity (i.e., where an individual spent 50% of its time) within the entire range of all recorded locations. We used only males with > 10 location points in statistical analyses (range = 11-86 locations, mean = 40). Considerable controversy exists over the number of location fixes

required to obtain accurate kernel estimates. Borger et al. (2006) claimed accurate estimates with only 10 fixes, while Seaman et al. (1999) reported that at least 30-50 fixes were required for reliable kernel estimates. Our study site was small and the observed movements within this area were short, thus a minimum of 10 fixes seemed reasonable for estimating accurate kernels. Site fidelity and home range sizes were calculated using the Animal Movement 2.0 extension (Hooge and Eichenlaub 2000. Animal Movement Extension to ArcView ver. 2.0. United States Geological Survey, Alaska Science Center-Biological Science Office, Anchorage, Alaska, USA. http://www.absc.usgs.gov/glba/gistools/animal_ mvmt.htm) in ArcView 3.2 (ESRI 1999).

We recorded all aggressive encounters and calling activity and the identification of the participants. Aggressive encounters included chasing, physical wrestling, and acoustic duels (alternations of vocal responses that were usually observed prior to physical wrestling) between males. We defined the frequency of aggressive behavior as the number of observation periods that we observed an individual being aggressive divided by the total number of observation periods for that individual. Frequency of calling activity was the number of observation periods that we observed an individual calling divided by the total number of observation periods for that individual. We collected data on above water calling activity only; we did not document the frequency of underwater calling activity, which is well established in this species (MacTague and Northen 1993; Ziesmer 1997). We used Pearson product-moment correlation analysis ($\alpha = 0.10$) to examine associations between home range size, frequency of aggressive behavior, and frequency of calling activity.

Operational sex ratios.—To test if the operational sex ratio was gender-biased, we determined the number of males and egg masses (an index of female occurrence) for each observation date (2002 and 2003 only), and overall breeding-season (2002-2006). Because females of this species are presumed to lay only one clutch of eggs per season (Zweifel 1955), the number of egg masses represented the number of reproductive females observed.

We calculated number of breeding females (# of egg masses) per number of breeding males to examine gender-biased skew in daily and overall breeding-season operational sex ratios (Sullivan et. al 1995). Operational sex ratio values less than one indicated that a breeding population was male-biased, values greater than one were female-biased and values equal to one were not gender-biased. We used exact binomial tests for goodness-of-fit ($\alpha = 0.10$) to analyze differences between the observed sex ratios and an expected 1:1 sex ratio. We established daily operational sex ratios for

TABLE 3. Daily operational sex ratios of *Rana boylii* and test results. Sex ratio was calculated as the number of new egg masses (representing the number of females) divided by the number of males on each day. Exact binomial tests for goodness-of-fit were used to analyze for statistical differences between the observed sex ratios and an expected 1:1 sex ratio.

Date	No. of Egg Masses	No. of Males	Sex Ratio	*P*
7 April 2002	1	6	0.17	0.125
27 April 2002	2	8	0.25	0.109
2 May 2002	1	10	0.10	0.012
3 May 2002	2	8	0.25	0.109
5 May 2002	1	8	0.13	0.039
7 May 2002	5	10	0.50	0.310
10 May 2002	1	7	0.14	0.070
13 May 2002	1	6	0.17	0.125
18 May 2002	1	4	0.25	0.375
12 May 2003	7	19	0.37	0.029
13 May 2003	6	12	0.50	0.238
14 May 2003	9	15	0.60	0.307
15 May 2003	4	11	0.36	0.118
16 May 2003	2	13	0.15	0.007
17 May 2003	1	10	0.10	0.011
22 May 2003	2	14	0.14	0.004
23 May 2003	2	20	0.10	< 0.001
24 May 2003	1	15	0.07	< 0.001
25 May 2003	2	11	0.18	0.022
26 May 2003	1	21	0.05	< 0.001

each day in which males and new egg masses were observed.

Mating patterns.—In 2002 and 2003, we recorded the sizes of males and females in amplexus in order to determine whether these frogs exhibited size-assortative (e.g., large females pair with large males) or large-male advantage (e.g., females pair with large males regardless of their own size) mating patterns. Both of these non-random mating patterns may be considered evidence of female mate selection. We captured and identified all pairs observed in amplexus. For accuracy and to maintain consistency in methods for comparisons, we used snout-to-urostyle data from earlier or subsequent captures of males (i.e., caliper measurements of males when not in amplexus). We used a standard metric ruler instead of calipers to measure females because it was difficult to obtain accurate caliper measurements when in amplexus. We rarely obtained caliper measurement data of females not in amplexus because we most frequently captured them when they were in amplexus. We released pairs following processing.

To test whether mating was random with respect to male size, we used Pearson product-moment correlation analysis ($\alpha = 0.10$) to determine if frog pairs captured in amplexus were of similar size (i.e., exhibited size-assortative mating; 2002 and 2003 were analyzed separately) and used t-tests ($\alpha = 0.10$) to compare the difference between the size of male frogs never observed

in amplexus and those observed in amplexus (2003 data only).

RESULTS

Timing of breeding activity.—During the six years of study, the onset of breeding activity started as early as 7 April (2002 and 2007) and as late as 8 May (2003) (Table 1; Fig. 2) and was closely associated with the mean annual stream flow ($r = 0.88$, $P = 0.02$). The median duration (number of days from first to last egg mass) was 49.5 days (range = 19-52 days; Table 1, Fig. 2) and was associated with stream flow on the first date of breeding activity ($r = -0.83$, $P = 0.04$). Across the six breeding-seasons, the mean annual stream flow was 0.37 m/s (SE = 0.06), the minimum annual stream flow was 0.06 m/s (SE = 0.02) and the maximum annual stream flow was 1.60 m/s (SE = 0.39; Table 1). In order of decreasing importance, the resulting model for timing of breeding indicated that of those variables tested, day within breeding-season and stream flow had highly significant effects ($P < 0.0001$) on the probability of observing new egg masses (Table 2). Response curves indicated that the number of new egg masses was highest after the 30th day of the breeding-season (approximately May 1st), and when stream flow was between 0.10 and 0.60 m/s. (Fig. 3). Year did not have a significant effect (Fig. 3). The total number of egg masses was closely associated with maximum annual stream flow ($r = -0.89$, $P = 0.02$).

Breeding site aggregations.—In 2002, we captured 25 adult frogs (22 males, three females) prior to and during the reproductive season (April-May), and 27 adult frogs (nine males, 18 females) in the post-reproductive months (June-September) along the study reach. We captured a higher number of males in breeding habitats (mean = 1.20, SE = 0.87, n =15) than non-breeding habitats (mean = 0.10, SE = 0.07, n = 40) during the reproductive season ($t = 2.04$, df = 53, $P = 0.05$). There was an insufficient number of females captures (n = 3) to test for differences in mean captures during the reproductive season. We captured a higher number of males in breeding habitats (mean = 0.33, SE = 0.19, n = 15) than non-breeding habitats (mean = 0.10, SE = 0.06, n = 40) during the post-reproductive season ($t = 1.56$, df = 53, $P = 0.07$). There was no difference in the number of female captures in breeding habitats (mean = 0.47, SE = 0.17, n = 15) and non-breeding habitats (mean = 0.28, SE = 0.12, n = 40) during the post-reproductive season ($t = 0.88$, df = 53, $P = 0.33$).

Spatial organization and aggression.—We classified 15 of 22 male frogs observed at the primary breeding site during the 2003 reproductive season as site faithful (68%) based on their movements. The number of male locations recorded within the breeding site ranged from
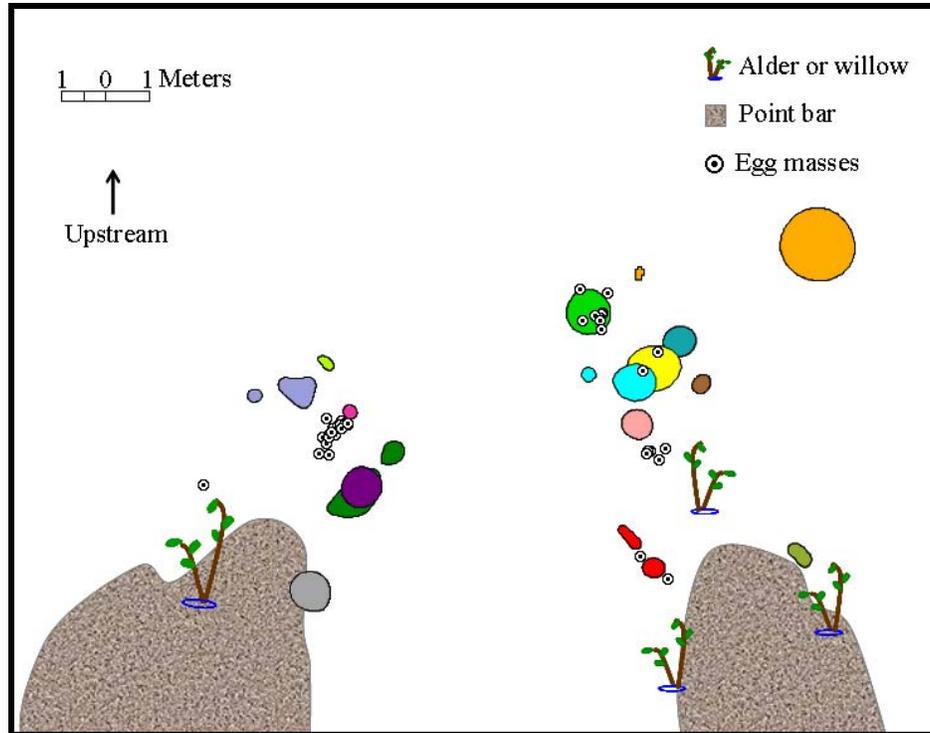
FIGURE 4. Locations of the home ranges (50% kernel core areas) of 15 individual male Foothill Yellow-legged Frogs (*Rana boylii*) in 2003 (sampled 17 days between 17 May 2003 and 5 June 2003) at Hurdygurdy Creek, Del Norte County, California, USA. Different colors represent individual home ranges.

11 to 86 observations per individual and these were not correlated with individual male home range sizes ($P = 0.66$). There was also no significant correlation between the number of days observed (out of 17 days) and size of home range ($P = 0.17$). A map of the 50% kernel core areas, for frogs classified as having site fidelity, demonstrated that individual males had attachment to small individual regions within the breeding area (Fig. 4). In some cases there was overlap of these male home ranges (Fig. 4). For site faithful individuals, mean male frog home range size was 0.58 m^2 (SE = 0.10, n = 15) during the 17 day observation period. There was a significant association between frog home range size and frequency of aggressive behavior ($r = 0.62$, $P = 0.01$) and frequency of aggressive behavior and frequency of calling activity ($r = 0.59$, $P = 0.001$).

Operational sex ratios.—In 2002, we observed a median of six individual males (range = 1-10 males, n = 18) and zero females (range = 0-3 females, n = 18) per day within the breeding period at the primary breeding site (first to last date of oviposition). In 2003, we observed a median of 13 individual males (range = 5-21 males, SE = 0.95, n = 29) and zero females (range = 0-3 females, n = 29) per day at this site.

In both years, the number of males was greater than the number of new egg masses (representing the number of females) on all observation days. Daily operational sex ratios ranged from 0.10 to 0.50 in 2002 and ranged from 0.05 to 0.60 in 2003 (Table 3). In 2002, the daily operational sex ratio was significantly male-biased on three of nine days (Table 3). In 2003, the daily operational sex ratio was significantly male-biased on eight of 11 days (Table 3). For the overall breeding-season, the number of egg masses was greater than the number of individual males in all years. The overall breeding-season operational sex ratio ranged from 1.09 to 1.81 (Table 4) and was significantly female-biased in 2002 and 2006, but not in other years (Table 4).

Mating patterns.—Snout-to-urostyle lengths of males in amplexus ranged from 71-110% of their female partner's snout-to-urostyle length. There was no correlation between male and female snout-to-urostyle lengths of pairs in amplexus in 2002 or 2003 ($P = 0.82$ and 0.53; respectively). Male frog size was significantly different between males observed in amplexus (mean = 52.2, SE = 1.16, n = 10) and males never observed in amplexus (mean = 49.0, SE = 0.97, n = 21), with amplectant males having larger mean snout-to-urostyle lengths than non-amplectant males ($t = -2.01$, df = 29, $P = 0.05$). We observed four of the five largest males

TABLE 4. Breeding-season operational sex ratios of *Rana boylii* at Hurdygurdy Creek, Del Norte County, California and test results. Sex ratio was calculated as the number of egg masses (representing the number of females) divided by the number of males. Exact binomial tests for goodness-of-fit were used to statistically analyze differences between the observed sex ratios and an expected 1:1 sex ratio.

Year	No. Males	No. Females	No. Egg Masses	Estimated Breeding Population	Sex Ratio	*P*
2002	27	8	49	76	1.81	0.02
2003	32	13	41	73	1.28	0.35
2004	34	8	39	73	1.15	0.64
2005	35	5	38	73	1.09	0.82
2006	34	7	59	93	1.74	0.01
2007	--	--	65	--	--	--

(snout-to-urostyle length > 55.0 mm) in amplexus at least once and up to three times.

DISCUSSION

Temporal breeding patterns and breeding site aggregation.—In general, studies on anuran reproductive ecology have focused on lentic (still water) breeding species. A number of abiotic factors (e.g., temperature, amount of rainfall, and timing of snowmelt) that limit the availability of ephemeral habitats, such as temporary vernal pools, may influence the timing of breeding activity in many of these species (Wells 1977a, 2007). In lentic breeding species, temporal breeding patterns such as onset and duration of activity may be easily defined because of the high predictability of suitable breeding conditions of ponds and lakes. In contrast, stream environments are less predictable and lotic breeding species, such as *R. boylii*, have a different set of abiotic factors that influence their reproductive ecology.

Variation in the temporal breeding patterns of *R. boylii* has been previously documented (Kupferberg 1996). In a 16-year study of *R. boylii* breeding activity on the South Fork Eel River, California, USA, the initiation of oviposition occurred earlier in low base-flow years than high discharge years, and the duration of breeding activity was highly variable (range = 18-63 days, mean = 34.25, SD = 10.95, n = 16; Sarah Kupferberg, pers. comm.). Kupferberg (1996) attributed the annual differences in the length of the breeding period to the presence or absence of spring rains during the reproductive period. More recently, Rombough and Hayes (2007) suggested that *R. boylii* in Linn. Co., Oregon is an explosive breeder with a short reproductive season, and with most egg masses laid within one week. The geographic location (northernmost extant population) and physical attributes of the stream, as well as a limited availability of suitable breeding habitat, may explain the rapid breeding-season in this population (Christopher Rombough, pers. comm.).

In this study, we observed similar variation in the onset and duration of breeding activity, which was highly correlated with base-flows and related stream velocities during the breeding-season; variables that change primarily in response to spring rains in the Smith River system. Breeding occurred earlier in low base-flow years (7 April 2002, 9 April 2004, and 7 April 2007), and later in high base-flow years (8 May 2003, 27 April 2005, and 26 April 2006). Initiation of breeding activity was associated with mean annual stream flow, and duration was related to stream flow on the first date of breeding activity. With the exception of 2003, breeding activity lasted approximately six to seven weeks, a duration characteristic of prolonged breeders (Wells 1977a). In 2003, activity was somewhat explosive, lasting fewer than three weeks. Results suggested that frogs are more likely to breed after 1 May. Kupferberg (1996) found that warming air and water temperatures influenced the initiation of oviposition in her *R. boylii* population. While the significant effect of day on breeding activity in this study may be a consequence of abiotic conditions, such as increasing air and water temperatures, it is also possible that the relative state of egg development within gravid female frogs influences this onset.

Earlier studies demonstrated that high stream velocities may dislodge *R. boylii* egg masses from oviposition substrates and that these frogs have evolved a strategy to avoid egg mass scour by altering the timing of oviposition and multiple scale breeding site selection (Lind et al. 1996; Kupferberg 1996; Lind 2005). Some stream-breeding anurans reproduce during the dry season, presumably to avoid high discharge flooding of breeding areas caused by heavy rainfall (Aichinger 1987; Kam et al. 1998). In all years except 2003, breeding activity ceased for a brief period of time during rain events that increased stream flows (Fig. 2). In a study on breeding activity of a Japanese stream breeding frog, heavy rainfall reduced activity, which was attributed to a lack of suitable calling sites (i.e., emergent stones within the breeding area; Fukuyama and Kusano 1992). In this study, the submergence of male calling sites, in addition to lack of underwater sites with suitable low velocities for oviposition (Wheeler et al. unpubl. data), may explain the interruption in reproductive activity. In

addition to a lack of spring rain events during the breeding-season in 2003, the shorter breeding period could also be due to the delay in conditions suitable for initiating breeding activity (Fig. 2). The delay may have forced arriving frogs to wait for appropriate flow conditions before commencing breeding. In any event, the season was shorter and appeared explosive compared to other years.

Our model indicated that frogs at the Hurdygurdy Creek site are more likely to breed when stream flows are between 0.1 and 0.6 m/s, though stream flow was not a good predictor of when breeding activity occurred, but rather when it did not. If flows exceed optimal conditions due to spring rain events during the breeding-season, activity can be suspended until flows recede (Fig. 2), which may lengthen the overall duration of the breeding period, as occurred in most of our study years. Additionally, there was no year effect, indicating that reproductive output is similar between years. However, the total number of egg masses was negatively associated with maximum annual stream flow and model results did not account for egg mass mortality as a result of scouring or stranding (Lind et al. 1996; Kupferberg 1996).

In all years, the onset of breeding activity occurred when stream flow was at or below 0.6 m/s, the upper value of the model (Fig. 3). However, at the microhabitat scale (individual oviposition sites) mean stream velocity was 0.11 m/s (SE = 0.03) with a 95% confidence interval of 0.04-0.17 m/s, a range that is considerably lower than 0.6 m/s (Wheeler et al. unpubl. data). Clearly, 0.6 m/s is much higher than optimal flow conditions for oviposition; therefore, this value may be a good predictor for oviposition at the tributary or mesohabitat (e.g., run, riffle, pool) scale but not at the microhabitat scale for this *R. boylii* breeding population. Annual flow variation and site specific attributes (e.g., hydrology and geomorphology) may also influence oviposition site microhabitat conditions and egg mass survival (Kupferberg 1996). More research is needed to understand the tolerance of flows that egg masses can withstand.

Our observations, coupled with previous studies indicated that *R. boylii* show plasticity in temporal breeding patterns; the duration may be prolonged, explosive, or reflective of some period within the extremes of this temporal continuum. These frogs appear to be highly adaptable and able to breed when local conditions are favorable; however, the effects of early or late season breeding on survival and recruitment are unknown.

River bars provide shallow stream habitats with low water velocities that *R. boylii* repeatedly use for breeding activity (Fuller and Lind 1992; Kupferberg 1996). In this study, males in particular aggregated at breeding sites during breeding activity but also used these habitats for activities other than reproduction (e.g., basking sites). Aggregation to particular breeding sites during the breeding-season may increase an individual's probability of finding a mate (Wells 1977a). In contrast, we observed females in breeding and non-breeding habitats regardless of season, providing evidence of a more dispersed distribution during both seasons. While the importance of maintaining breeding habitats for the persistence of *R. boylii* is obvious, these frogs use other areas during and outside of the breeding-season. Protection of breeding and non-breeding habitats during and following the breeding-season is important in species management.

Streams are dynamic ecosystems and their ecological integrity relies on a natural flow regime. Organisms that use streams may require various habitats that have limited spatially and temporally availability, depending on the flow regime (Poff et al. 1997). One geomorphic response to modifications of stream flows resulting from dams and diversions is the reduction of the formation of river bars, which are important structural foundations for aquatic and riparian communities in stream ecosystems (Poff et al. 1997; Trush et al. 2000). Appropriate timing of flow releases in regulated systems is critical to riverine species that avoid or use specific flow conditions to complete certain life-history activities, such as reproduction. Alteration of natural flows can therefore have direct and indirect impacts on the species' reproductive success (Lind et al. 1996). Assessing the influence of abiotic factors on the temporal breeding patterns of these frogs in unregulated stream systems is important in understanding the adaptations that allow their persistence in stochastic stream environments. Modeling exercises, such as this one, assist in predicting temporal breeding patterns and may facilitate species management. In addition to eliminating breeding habitats and lowering suitability of microhabitat conditions for oviposition, improper regulation of stream flows may alter breeding activity by advancing or delaying onset, shortening or lengthening duration and inundating calling sites.

Aspects of the mating system.—Within small aggregations, males call to attract females from stationary positions, and may defend display sites (i.e., calling sites), territories, oviposition sites, or courtship areas (Wells 1977a, 2007). Areas defended by males may or may not contain resources such as oviposition sites (Wells 1977a, 2007; Howard 1978b; Halliday and Tejedo 1995). Territories that contain limited resources that vary in quality may influence female mate choice and male mating success (Wells 1977b). The term home range for this study referred to the locations within the larger breeding area that were maintained by individual male frogs (Fig. 4). Based on our observations, a majority of individual breeding male frogs exhibited site

attachment. They used the same small area (< 1m² in most cases) to call from within the greater breeding area. These observations along with the behaviors described below indicated that male *R. boylii* maintained and defended individual sites within the primary breeding area that were not generally associated with egg deposition sites.

In this study, male-male interactions occurred and aggressive behavior may have been induced by calling activity. Aggressive interactions observed between *R. boylii* males were similar to behaviors in other species (e.g., *R. clamitans*; Shepard 2004). Aggressive behavior in *R. clamitans* could be a means for territorial defense or a mechanism to maintain individual distance (Halliday and Tejedo 1995; Shepard 2004). Inter-male spacing may enable males to avoid acoustic interference and also may allow females to distinguish and locate preferred males (Pierce and Ralin 1972; Halliday and Tejedo 1995). Fukuyama and Kusano (1992) observed male *Buergeria buergeri* sitting on stones in streams and defending these calling sites from other males. Male frogs at our study site had attachment to particular sites and males with larger home ranges were more aggressive. Emergent rocks within home ranges appeared to be display or acoustic sites that males used as calling perches to attract females.

Although the ratio varied, the daily operational sex ratio was male-biased. However, the overall breeding-season operational sex ratio was female-biased. This female-biased sex ratio and the lack of female aggregation suggest that females arrived at the breeding site at various times throughout the breeding-season while the males maintained a constant presence. Asynchronous arrival of females and male-biased daily operational sex ratios are indicative of prolonged breeding (Wells 1977a, 2007). As such, a male-biased operational sex ratio should increase the intensity of female selection (Sullivan et al. 1995).

Two potential non-random mating patterns that we examined were size-assortative mating and selection for larger males. In several studies, females selected males that were a proportion of their size in order to minimize the distance between the pair's vents, maximizing fertilization (e.g., Howard 1978a; Arak 1983a; Howard and Kluge 1985; Robertson 1990; Bourne 1993). In other studies, females selected larger males (e.g., Howard 1978a; Ryan 1980; Berven 1981). Size may be indicative of male quality with mating with higher quality mates leading to increased reproductive success (Sullivan et al. 1995; Tsuji 2004). Results from this study did not indicate positive size-assortative mating, but indicated that larger males had greater mating success. The mating success of large males may result from male-male competition, female choice, or a combination of these behaviors (e.g., Wells 1977a; Arak 1983a; Howard and Kluge 1985). Although there is

evidence for female choice in many anuran species, Arak (1983b) emphasized that interpreting female choice is confounded by many factors. In this study, we rarely observed females at the breeding site; hence, we did not observe female mate sampling. Furthermore, our sample size was low and the result was barely significant (t = -2.01, df = 29, P = 0.05), and while we standardized data collection techniques and repeated snout-to-urostyle measurements to ensure accuracy, measurement error probably accounts for some of the variability. Regardless, observations of inter-male spacing, male territorial and calling behaviors, size differences of amplectant and non-amplectant males, male-biased daily operational sex ratios, along with documented complex vocal repertoire of this species (MacTague and Northern 1993; Ziesmer 1997) inferred that females may actively select mates.

Although the length of the breeding patterns varied, many of the behaviors that we observed were typical of prolonged breeders. These include small breeding aggregations, site attachment, asynchronous arrival of females, male-biased daily sex ratios, and potentially female mate selection. Contrary to our findings, Rombough and Hayes (2007) observed several attempts of physical and non-vocal competition between male *R. boylii* for females by displacement of amplectant males. They suggested that males of this population may actively seek out and physically compete for females (Rombough and Hayes 2007), behaviors that are generally observed in explosive breeders. Their observations imply that females in their study population did not exhibit active mate choice. Inconsistencies in mate acquisition behaviors may have been attributed to differences in the duration of the breeding-season or breeding population densities at their more northern latitude. Moreover, variation in mate acquisition may occur within species, populations and individuals (e.g., calling versus searching behavior; Wells 2007). In this study, we occasionally observed males trying to displace males in amplexus, which may be evidence of alternative mating tactics (see Wells 2007).

The mating strategy of many prolonged breeders may be analogous to lek or resource-defense mating strategies (Wells 1977a, 2007). Wells (2007) suggested that lek mating may be the predominant mating system among aquatic, prolonged breeding anurans. In a resource-defense polygyny mating system, male territories or display sites provide a resource such as oviposition sites. In a lek mating system, males display at stationary locations to attract females and display sites do not offer resources (Hoglund and Alatalo 1995). For example, in the lekking frog *Buergeria buergeri*, females pair with males at their calling sites (emergent rocks in streams) and carry them to different locations prior to laying eggs under rocks (Fukuyama et al. 1988). In this study, most of the oviposition sites were not within any male home

range (Fig.4) and we observed females in amplexus preparing and laying eggs on substrates outside the amplectant males' calling site (Wheeler et al. 2003). This indicated that males were not defending high quality oviposition sites. Rombough and Hayes (2005) also suggested that females carefully assessed and selected oviposition substrates following pairing. Frogs did not provide parental care, female frogs visited the breeding area where males congregated to breed, and males called from stationary locations presumably to attract females; all of these behaviors are characteristic of leks.

Currently, egg mass counts are used as an index for the relative abundance in monitoring efforts for this species. Although the number of egg masses accurately represents the number of reproductive females, the effective population size can not be estimated based on egg mass count unless it is assumed that the operational sex ratio is 1:1. Estimating the effective population size also requires data on the number of reproductive males (Nunney 1993). Our results suggest that the breeding-season operational sex ratios were female-biased and variable, ranging from 1.09 to 1.81, where 1.00 represents a 1:1 ratio. Thus, an accurate effective population size can not be determined exclusively based on egg mass counts. The effective population size is also affected by the mating system, particularly variance in the reproductive success of individuals (Nunney 1993). Further research would help in classifying the mating system of *R. boylii*; however, our results suggest that there is a skew in male reproductive success. This skew would result in an even smaller effective breeding population.

Numerous studies have indicated that females are attracted to characteristics of male vocalizations such as call frequency, rate, and duration (Howard 1978a; Ryan 1983; Robertson 1986) and males may assess a rival's size based on vocalization characteristics, and alter call behavior or intensity of aggression accordingly (e.g., Davies and Halliday 1978; Arak 1983a; Robertson 1986; Given 1987). *Rana boylii* exhibits five distinct vocalization types (MacTague and Northen 1993; Ziesmer 1997), but the functions of these vocalizations are still unknown. Research on female preferences for specific call types and call attributes in *R. boylii* using playback experiments would further our understanding of the role of vocalizations in sexual selection. The degree of sexual selection varies by mating system; it is intense in lek mating systems, with few males receiving most of the matings (Hoglund and Alatalo 1995).

Paternity analysis of egg masses to examine male mating skew, in combination with oviposition site or male location data, may provide quantitative and reliable information regarding the amount of variation in male reproductive success, female mate choice, and effective population size within a breeding population. Because mating strategies evolve from multiple selective pressures such as population density and the distribution of suitable substrates for egg mass deposition, results from this study may be highly site specific and should be investigated and confirmed for this species at multiple localities. Given the unique and specific reproductive behaviors and their demonstrated linkages with physical site attributes associated with dynamic lotic systems, it is clear that the conservation of this frog will require that particular watershed conditions, should they be manipulated for impoundments or flood management, be modified only within the parameters of the natural flow regime (Poff et al. 1997).

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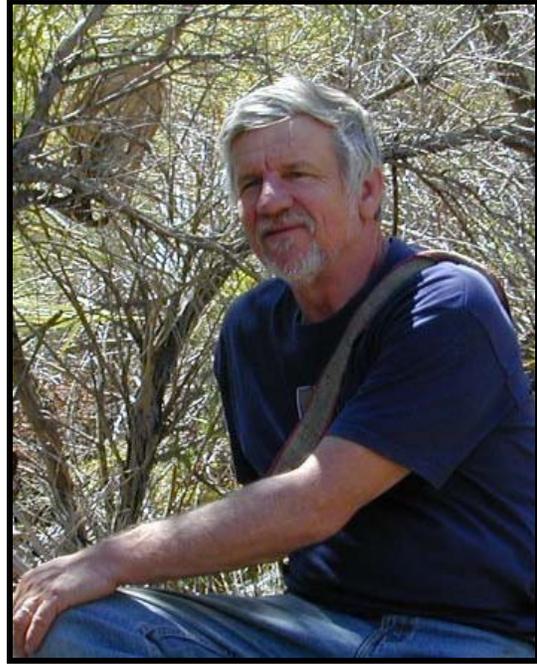
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