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Male Mating Behavior in *Hyla regilla*

STEPHEN A. PERRILL

Three male mating tactics (calling, site-specific; non-calling, satellite; and opportunistic) are described and all three resulted in mating success. On 38 nights, a census of satellite to calling males was taken and a mean of 17% of the calling males were found in a satellite association. Satellites were observed for extended periods and on three occasions they were seen intercepting and amplexing females approaching calling males. No significant differences were found between the size of males captured in amplexus compared to the expected distribution of successful males, and there was no relationship between snout–vent lengths of males and females in amplexus.

A NURAN amphibians are good subjects for studies in behavioral ecology. They can be observed at close range with no apparent effect on their behavior and experimental manipulations cause few disturbances. Since Wells (1977a) reviewed social behavior in anurans, there has been a steady flow of research.

The focus of most studies of mating behavior in anurans has been on calling by the male. A large body of data has accumulated on call properties of a number of anuran species. In *Hyla regilla*, Snyder and Jameson (1965) describe four different kinds of calls and Moore (1979) describes a modified form of one of these calls. The functions of *H. regilla* calls in social contexts have been the subject of a number of studies (Awbrey, 1978; Straughan 1975; Whitney, 1980, 1981; Whitney and Krebs, 1975a, b).

This study considers three mating tactics similar to those described for *Rana catesbeiana* (Howard, 1978): 1) calling, territorial males; 2) non-calling, satellite males (called "parasite males" by Howard); and 3) opportunistic males. The issues assessed include: 1) the frequency of the three strategies; 2) the ratio of satellite to calling males; 3) the comparative mating success of the three strategies; 4) the viability and consistency of the satellite strategy; and 5) the factor(s) that influence the adoption of a particular strategy by an individual frog.

METHODS

The study site, located in La Jolla, California, was a canyon drainage ditch, two meters wide and eight meters long. The outlet end of the ditch was dammed by vegetation which resulted in semi-permanent standing water approximately 0.5 m deep. Following heavy rains, water spills out of the ditch thereby increasing the size of the study area twofold. Following two or more weeks without rain, the standing water in the ditch is significantly reduced and dried up on one occasion. The dominant vegetation surrounding the ditch is pampas grass (*Cortaderia atacamensis*). Some of the frogs spend their days in the clumped bases of these plants.

This study, performed on 84 nights from 27 Jan. 1981 to 21 May 1981, began when the frogs became active around dusk. Observations were made between 1700 and 2300 PST. Male frogs were toe-clipped and numbers were freeze-branded on their backs for field identification. Females captured in amplexus were toe-clipped to check for multiple egg clutches (Perrill and Daniel, 1983). Snout-to-vent measurements were made on males and females.

Three male behavioral patterns are described: 1) territorial males, defined as calling males that restrict their behavior to a defended call site having a 10 cm radius; 2) satellite males, defined as non-calling males which maintain a low posture within 25 cm of a calling male and often orient toward the calling male; and 3) opportunistic males, defined as males which move around in the study area adopting both satellite and calling tactics and which are often chased away by territorial males.

RESULTS

A large sample of the population was marked. Eighty-five females had a mean snout-to-vent length of 39.5 mm (range = 32 to 47 mm, SD = 3.73) and 82 males had a mean snout-to-vent length of 35.3 mm (range = 29 to 42 mm, SD = 3.06). Thus, a significant size difference existed between males and females ($t = 8.06$, $df = 165$, $P < .001$). Large female body size is an adaptation associated with the females' ability to hold

TABLE 1. THE BEHAVIORAL STRATEGY OF 27 MALES OBSERVED ON 10 OR MORE NIGHTS.

| Male number | Size (mm) | Total number of nights observed | Percent of number of nights (based on total # of nights observed) | | | | |
			Calling	Satellite	Not calling	Switching	Amplexing
1	36	35	48.6	0	37.1	14.3	0
2	30	12	33.3	8.3	33.3	16.7	8.3
4	37	33	54.6	0	30.3	9.1	6.1
5	35	17*	76.5	0	17.7	0	5.9
7	35	16	50.0	0	31.3	18.8	0
8	32	14	85.7	0	7.1	0	7.1
10	38	39*	97.4	0	0	0	2.6
11	36	13	38.5	7.7	46.2	0	7.7
15	32	13	38.5	0	7.7	53.9	0
17	33	12	66.7	0	16.7	16.7	0
20	35	43*	74.4	2.3	9.3	4.7	9.3
21	32	18	66.7	5.6	11.1	16.7	0
23	34	47*	85.1	0	4.3	6.4	4.3
24	37	13	61.5	7.7	15.4	15.4	0
29	34	13	53.9	0	7.7	30.8	7.7
31	35	19	57.9	0	21.1	10.5	10.5
32	38	11	81.8	0	0	0	18.2
34	37	23*	78.3	0	13.0	4.3	4.3
36	39	18	72.2	5.6	16.7	5.6	0
40	30	12	50.0	16.7	25.0	0	8.3
41	35	13	15.2	7.7	30.8	38.5	7.7
42	37	12	66.7	0	16.7	0	16.7
43	35	20	80.0	0	10.0	0	10.0
51	33	11	81.8	0	9.1	9.1	0
52	39	14*	71.4	0	14.3	0	14.3
56	35	13	61.5	0	15.4	7.7	15.4
74	34	10	80.0	0	10.0	0	10.0
Mean	34.93		64.4	2.3	16.9	10.3	6.5

* Displacement experiment done.

more eggs (Salthe and Duellman, 1973). Age also influences body size in anurans and this may contribute to the sexual dimorphism in the breeding population if females mature later than males. I was unable to determine the ages of frogs and sexual differences in maturation are unknown in *H. regilla* [although Jameson (1956) suggests that males and females both mature in a single season].

Of the 82 marked males, 27 were observed on ten or more nights (Table 1). None of the males sustained a consistent satellite tactic from night to night. The column in Table 1 labeled **Switching** refers to males which changed from calling to satellite and/or satellite to calling on a given night. The column labeled **Not-Calling** identifies frogs observed not calling; but since they could not be clearly associated with a calling male, they are not considered satellites. Many

of the males (27 of 57) observed in amplexus on a given night were found calling the following night. Two of three males found in amplexus on two consecutive nights were in the pond calling on the third night. There was never any indication of males not in amplexus trying to displace amplexed males, or females attempting to reject amplexed males. Therefore, males found in amplexus were considered successfully-mated.

The number of satellite males versus the number of calling males was determined on 38 nights (Table 2). The mean percent of calling males in a satellite association was 17.02 (range = 0 to 42.9%, SD = 7.85). Unmarked males are included in these counts. There was never more than one satellite associated with a calling male. The number of satellites is represented conservatively in these counts because non-calling

TABLE 2. FREQUENCY OF SATELLITE MALES.

Date	Time (PST)	Number of males		Percent of calling males in a satellite association
		Calling	Satellite	
2/3	1920	20	3	15.0
2/5	1906	23	3	13.0
2/11	1855	19	0	0
2/26	2000	20	4	20.0
2/27	1936	22	1	4.6
2/28	2045	20	5	25.0
3/1	1900	24	5	20.8
3/8	1918	14	2	14.3
3/9	1920	17	3	17.7
3/10	1915	9	1	11.1
3/11	1925	7	0	0
3/12	1950	6	1	16.7
3/15	2030	11	2	18.2
3/16	1930	14	2	14.3
3/20	1930	33	5	15.2
3/21	1900	28	5	17.9
3/22	2105	15	2	13.3
3/23	1915	16	3	18.8
3/24	2000	14	2	14.3
3/25	1915	10	2	20.0
3/26	1950	6	1	16.7
3/27	1920	8	2	25.0
3/29	1930	18	4	22.2
3/30	2000	15	2	13.3
3/31	1940	13	4	30.8
4/5	1950	14	3	21.4
4/6	1945	10	3	30.0
4/7	1930	7	3	42.9
4/20	2015	26	3	11.5
4/21	2015	22	3	13.6
4/22	2000	22	2	9.1
4/23	2000	27	4	14.8
4/24	2015	28	3	10.7
4/26	2040	24	5	20.8
4/27	2115	14	3	21.4
5/6	2130	25	5	20.0
5/8	2100	28	5	17.9
5/10	2130	28	4	14.3
	Total	677	110	646.6
	Mean	17.82	2.95	17.02
	SD	7.34	1.43	7.85

TABLE 3. OBSERVATIONS ON SATELLITE MALES.

Animal number	Size (mm)	Date	Distance from calling male (cm)	Time as satellite (min)
38	30	2/3	25	41
2	30	2/5	10	38
		3/8	10	42
15	32	2/11	10	40
		2/28	10	24
		3/4	15	30
		3/21	10	40
54	32	2/26	10	35
29	34	2/28	15	9
		3/22	5	80
		3/23	20	70
		3/24	20	80
60	30	2/28	5	24
61	29	3/1	5	32
		3/21	5	29
62	32	3/1	15	32
21	32	3/6	20	66
		3/9	10	38
		3/21	5	10
51	33	3/7	5	34
17	33	3/8	10	20
		3/21	10	20
69	35	3/12	30	65
		3/31	10	70
63	35	3/15	5	50
		3/16	5	25
		3/22	10	39
70	32	3/15	10	70
23	34	3/16	10	37
		3/31	20	45
71	36	3/25	20	70
24	37	3/27	5	75
56	35	3/29	10	40
20	35	3/29	5	70
40	30	4/6	5	45
41	35	4/20	5	50
		4/21	10	90
		4/23	8	120
		4/24	10	45
36	39	5/7	20	90
58	39	5/10	5	70

males not clearly associated with calling males are not included.

Twenty-three males were observed in satellite posture for extended time periods ranging from 9 to 120 min (Table 3). Five of these satellites were observed on two separate nights; two were observed on three nights; and three were observed on four nights. The mean size of the 23 males is 33.4 mm (range = 29 to 39 mm). On three occasions, I observed satellites successfully amplex females [Moore (1979) observed two instances in which satellite males intercepted and successfully amplexed females that were approaching calling males].

On numerous occasions, I heard and observed territorial males defend their sites from other males with trill calls. Four times I saw

TABLE 4. DISPLACEMENT OF SITE-SPECIFIC MALES
FROM THEIR CALL SITES.

Animal number	Date	Number of nights seen at call site	Distance displaced (m)	Time to return (min)
23	3/16	47	1.5	24
	3/20		4	9
	4/6		1	<1
12	3/16	8	1.5	88
34	3/16	23	1.5	17
	3/16		2	22
52	3/21	14	2	10
	3/21		5	78
51	3/23	11	8	16
10	3/23	39	9	15
5	3/24	17	8	11
20	3/27	43	2	2

physical encounters that involved butting and wrestling between two males resulting in the territorial males chasing off the intruder.

Eight territorial males calling consistently from a particular call position were displaced to other areas of the study site (Table 4). One male was displaced three times; two were displaced twice; and five were displaced once. All of the males returned to their original call site and resumed calling. En route, males often passed by a number of other calling males.

The size distribution of 35 males captured in amplexus was compared to the expected distribution of successful males and no significant difference was found between these two groups (Fig. 1). The number of males in each size class (successful and unsuccessful) was multiplied by the overall mating success (43.2%), to determine the expected distribution.

Also, there was no relationship between snout–vent lengths of males and females captured in amplexus ($r = -0.0363$, df $= 104$, $P > 0.05$). This supports the suggestion by Woodward (1982) that in anurans, assortative mating by size is not a general phenomenon.

DISCUSSION

The three patterns of male mating behavior described for *Rana catesbeiana* (Howard, 1978) appear to be similar to the behavior of *Hyla regilla*. Brattstrom and Warren (1955) suggest that *H. regilla* are not territorial because they do not defend an area. However, Fellers (1979a) and Jameson (1957) discuss territorial behavior
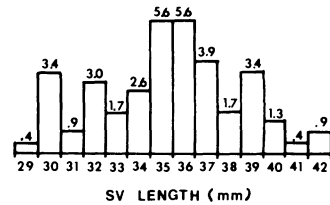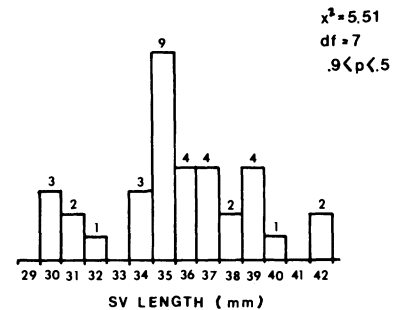

Fig. 1. Observed and expected size distributions of successful males.

in *H. regilla* and the site-specific males I observed defended their sites with trill calls, butting and wrestling. Awbrey (1978) found that frogs within 20 cm of each other resulted in at least one member starting slow trill calls and my observations support his data. Whitney and Krebs (1975b) and Fellers (1979a) observed *H. regilla* employing advertisement calls at distances not less than 40 cm; I, however, regularly observed males using mating calls at distances of 20 to 30 cm. Chorus densities must influence this distance significantly and frog densities at my study site were often very high due to the restricted borders of the drainage ditch. In addition, Whitney (1980) points out a distinction between the use of the encounter call at the beginning of calling bouts as observed by Fellers (1979a) in a Los Angeles, California population and his Vancouver, British Columbia population in which the encounter call was absent at the beginning of bouts. Further, the displacement experiments (Table 4) suggest that territorial males have a strong connection to a par-

ticular location. These displacement experiments are consistent with a mark recapture study (Jameson, 1957) in which 16 males were marked and 15 were found to restrict their movements to a radius of 1.8 m with most of the frogs moving only 5 to 10 cm over a period of 17 days.

Whitney (1981) reports that territorial males treat satellite males as females and often attempt to amplex them. In *H. cinerea* also (Perrill et al., 1978) when identified as not female, the territorial male chased satellites as well as opportunistic males away with trill calls and/or butting and wrestling.

"Bout leaders" have been described in *H. regilla* (Whitney and Krebs, 1975b; Moore, 1979) and Whitney and Krebs (1975b) demonstrate that females mate preferentially with bout leaders. An early objective of my study was to identify these leaders in order to discern differences in mating success and to see if satellites were more attracted to bout leaders than to other calling males. I was unable to identify bout leaders which could be caused by the restrictive borders of the study site and a higher-than-normal density.

The extended observations on 23 satellite males suggest that the satellite tactic is an adaptive behavior for *H. regilla*, that some males are more persistent than others in this tactic and that males of all sizes perform this behavior. In addition, a number of the males was seen switching tactics from calling to satellite and vice-versa. A variety of potential variables could be responsible for these switches (Perrill et al., 1982).

The proportion of satellite to calling males in *H. regilla* ($\bar{x} = 17.02$) is very close to the value obtained for *H. cinerea* ($\bar{x} = 16.74\%$, Perrill et al., 1978). Fellers' (1979a) population census of *H. regilla* on six nights found approximately 20% of the calling males associated with silent males.

It is difficult to determine relative mating success in reference to the different male tactics. Six of the eight site-specific males tested in displacement experiments (Table 1) were observed in amplexus. Three of the six mated twice and one mated on four different nights. The opportunistic males were also successful in obtaining mates. Fellers (1979a) suggests that non-calling male hylids are subordinate males not interested in intercepting females moving to calling males. On three occasions, I saw satellite males snatching females as they moved toward calling males. Perrill et al., (1978) showed that satellites successfully intercepted females in 43%

of 30 field experiments and Miyamoto and Cane (1980) obtained similar results (38% success rate) in a tropical hylid, *Hyla ebraccata*. Because of the high density and inability to isolate satellite relationships from other frogs, it was not possible to perform such experiments in my population of *H. regilla*. It is clear in my study that all three tactics result in mating success; however, many more data are needed to demonstrate differential success rates among the tactics.

Finally, some recent research on the influence of anuran male size on mating success suggests that large size is the most important feature determining mating success (Fairchild, 1981; Gatz, 1981; Howard, 1978, 1980; Ryan, 1980; Wilbur et al., 1978; Woodward, 1982). However, Sullivan (1982) shows that *Bufo woodhousei australis* females prefer males which call persistently, regardless of male size. Fellers (1979b) demonstrates that perch site is a critical factor in determining mating success and shows that larger males are not significantly more successful than smaller individuals. Wells (1977b) indicates a size advantage for males in *Rana clamitans* but suggests that male size is not as important as the quality of the territory in influencing female choice. Larger males are not more successful in mating in *H. cinerea* (H. C. Gerhardt, pers. comm.) or in *H. regilla* (Moore, 1979). My study of *H. regilla* shows that a number of factors, including the tactic employed, influence mating success and that large males may not experience significantly greater success than other size classes.

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