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WATER TEMPERATURE AT OVIPOSITION SITES OF
RANA LUTEIVENTRIS IN NORTHEASTERN OREGON

Evelyn L. Bull[1] and Jay F. Shepherd[2]

ABSTRACT.—Water temperature at which Columbia spotted frog (*Rana luteiventris*) eggs were deposited and developed was determined at 18 oviposition sites in northeastern Oregon in 2000. Mean daily water temperature on the day of initial egg deposition ranged from 7.6°C to 16.0°C with a mean of 9.6°C. Maximum water temperatures on the 1st day of egg deposition ranged from 9.8°C to 20.2°C and averaged 15.5°C. Eggs were not deposited on days when maximum water temperature was below 9.4°C. Duration of egg deposition ranged from 1 to 20 days at the 18 sites. Embryos hatched after 12–21 days. Mean and maximum daily water temperatures were significantly correlated with number of days to hatching.

Key words: Columbia spotted frog, embryonic temperature tolerance, northeastern Oregon, Rana luteiventris, *ranid.*

Knowledge of the breeding biology and thermal requirements of ranids is essential for a broad understanding of each species and its individual abilities to adapt to environmental fluctuations common during the breeding season. Little information is available on water temperature for breeding and embryonic thermal requirements of ranid frogs in the northwestern United States, and most literature is based on laboratory studies. Moore (1939) reported temperature tolerance of eggs for 5 ranid species in the eastern United States and found that embryonic temperature sensitivities are correlated with environmental temperatures during the breeding season. Embryos of the earliest breeding species develop faster and tolerate lower temperatures than other ranids that breed later in the year under warmer conditions. Ryan (1941) explored the effects of previous exposure to one temperature on the subsequent development rate of *Rana pipiens* eggs at another temperature.

Temperature tolerance limits are temperature ranges at which 50% or more of the embryos develop normally (Brown 1967). The species of ranids that occur in the northwestern United States for which there is information on temperature limits include *R. aurora aurora* (4–21°C; Licht 1971), *R. sylvatica* (6–24°C; Herreid and Kinney 1967), *R. cascadae* (6–27°C; Sype 1975), *R. pretiosa pretiosa* (6–28°C; Licht 1971), *R. luteiventris* (6–28°C;

Johnson 1965), and *R. pipiens* (5–28°C; Moore 1939). Average water temperature on the 1st day of egg deposition has been determined to be 7–9°C for a population of *R. sylvatica* (Herreid and Kinney 1967). Both *R. aurora aurora* and *R. pretiosa pretiosa* are known to breed when water temperature of breeding ponds reaches 6°C at a depth of 61 cm (Licht 1971). Although basic breeding biology of *R. luteiventris* is known (Turner 1960, Morris and Tanner 1969, Cuellar 1994), no comprehensive field studies have been conducted to document temperature at oviposition of this species. Our objective was to determine water temperature on days when oviposition occurs in *R. luteiventris* in natural breeding sites within the Blue and Wallowa Mountains.

METHODS

During spring 2000 we monitored water temperature at 18 oviposition sites of *R. luteiventris* in 12 breeding ponds (ponds 4–9, 11–16; Table 1) in the Grande Ronde River watershed in Union County and in 4 breeding ponds (ponds 1–3, 10; Table 1) along the Wallowa River in Wallowa County in northeastern Oregon. Ponds 6 and 7 each contained 2 oviposition sites. Eleven of the 12 ponds were within 300 m of the Grande Ronde River, and 1 pond (pond 16) was 1600 m from the river. The surface of these ponds typically froze in

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Table 1. Initial and last day of egg deposition (interval in days); number of days on which eggs were deposited; number of egg masses deposited at that oviposition site; and mean, minimum, and maximum water temperature (°C) on the day that eggs were first deposited at 18 oviposition sites of *R. luteiventris* in northeastern Oregon, 2000.

Site	Dates of egg deposition	No. days eggs deposited	No. egg masses	Water temperature		
				Mean	Min.	Max.
1	22 Mar–7 Apr (17)	12	47	10.1	4.2	17.9
2	22 Mar–10 Apr (20)	11	16	16.0	12.9	20.2
3	27 Mar–5 Apr (10)	3	5	12.1	6.2	19.8
4	1–11 Apr (11)	6	11	8.8	4.2	17.1
5	3–9 Apr (7)	5	7	9.3	5.0	16.8
6A	3–8 Apr (6)	6	15	9.3	5.4	16.0
6B	4–8 Apr (5)	4	9	8.3	4.2	13.3
7A	4–7 Apr (4)	2	3	10.0	2.5	19.8
7B	5–12 Apr (8)	8	28	8.7	5.0	14.9
8	6–14 Apr (9)	7	17	7.9	6.6	11.4
9	8–9 Apr (2)	2	7	10.9	6.2	18.7
10	8–22 Apr (9)	6	8	9.3	5.8	14.9
11	9–18 Apr (10)	5	7	8.4	4.2	14.5
12	13–22 Apr (10)	5	5	9.4	6.2	11.8
13	14–27 Apr (14)	6	6	7.6	5.8	9.8
14	14–23 Apr (10)	7	10	–	–	–
15	21 Apr (1)	1	1	8.2	6.6	11.8
16	28 Apr– 2 May (5)	4	9	9.3	4.6	14.9

November and thawed between March and May depending on elevation. Elevation of these ponds ranged from 924 m to 1810 m. Four ponds were within 200 m of the Wallowa River, 3 remained ice-free, and all were at about 960 m elevation. The 16 ponds ranged in size from 60 to 28,500 m². All breeding ponds had permanent water (primarily from springs), except pond 9, which dried.

Data loggers (Onset Computer Corporation) recording water temperature at 1-hour intervals were placed at each oviposition site at least 2 weeks prior to the date that egg deposition had occurred in past years; the exact location of oviposition sites had been determined in a previous study (Bull and Hayes 2000). Data loggers were submerged 3–5 cm below the surface of the water, as this is the depth where egg masses typically were found. The oviposition sites were checked twice a week until frogs appeared at the site, after which they were checked daily to record the number of frogs and egg masses seen. The time that sites were checked was recorded. New egg masses were identified with a numbered flag along their edge. Oviposition sites were checked daily until eggs hatched (stage 20; Gosner 1960) or until no new egg masses were deposited for a week, at which time data loggers were removed.

Mean, maximum, and minimum temperatures were calculated for the day that egg depo-sition was initiated at each oviposition site. We determined the average of the mean, maxi-mum, and minimum daily water temperatures from onset of egg deposition until hatching, Spearman's rank-order correlation coefficients were used to test for significant correlations between number of days to hatching and aver-age of the mean, maximum, and minimum water temperature during that time period.

Results

The 1st egg masses were deposited at the 18 oviposition sites between 22 March and 28 April (Table 1, Figs. 1, 2). Frogs were observed at 16 of 18 oviposition sites 1–12 days ($\bar{x}$ = 6.2, s = 3.49, n = 16) before eggs were de-posited. Amplexing pairs were observed at 6 oviposition sites 1–9 days ($\bar{x}$ = 3.2, s = 3.06, n = 6) before eggs were deposited. Mean daily water temperature on the day eggs were deposited ranged from 7.6°C to 16.0°C, with a mean of 9.6°C for 17 oviposition sites. Because the oviposition site at pond 14 was 8 m from the one used in previous years, we did not know temperatures prior to or on the day of egg deposition. The data logger was moved to the new oviposition site when eggs were first deposited. Minimum water temperature the night following egg deposition ranged from 2.5°C to 12.9°C and averaged 5.6°C. Maximum water temperature on the day eggs
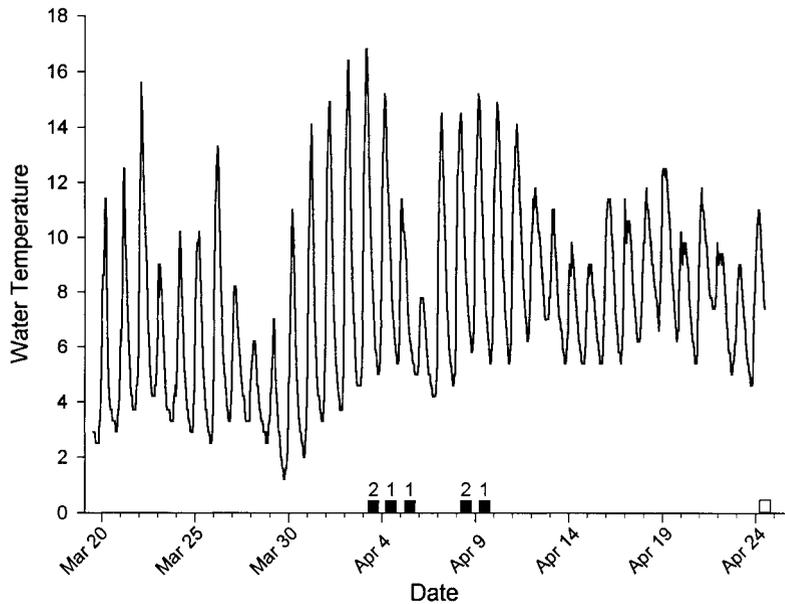
Fig. 1. Water temperature (°C) by date at oviposition site of *R. luteiventris* at pond 5 in northeastern Oregon, 2000. Solid squares signify the days that eggs were deposited with the number of egg masses listed above each square. The open square signifies the day that the eggs first hatched.

TABLE 2. Number of days to hatching (stage 20) and the average of mean, minimum, and maximum daily water temperatures (°C) during embryonic development at 13 oviposition sites of *R. luteiventris* in northeastern Oregon, 2000.

Oviposition site	No. days to hatching	Water temperature		
		Mean	Minimum	Maximum
1	15	9.7	3.8	19.0
2	16	15.7	12.7	21.7
3	14	11.3	6.1	20.3
4	16	10.2	5.6	16.7
5	21	8.9	5.8	12.7
7A	13	10.4	4.4	19.0
7B	13	10.7	6.7	15.7
10	19	8.5	5.9	11.7
11	21	8.0	5.8	10.6
12	18	9.9	6.9	13.5
13	17	8.9	5.8	12.5
14	18	8.9	5.8	13.3
16	12	11.0	5.5	19.3

were deposited ranged from 9.8°C to 20.2°C and averaged 15.5°C.

Duration of egg deposition ranged from 1 to 20 days at the 18 oviposition sites. Four of the ponds had 3–5 oviposition sites, which actually lengthened the duration of breeding in these ponds because some of the oviposition sites were used later than those we monitored (pond 1: 24 days, pond 3: 13 days, pond 7: 20 days, pond 16: 7 days). Egg deposition did not occur on cold days when the maximum water temperature was below 9.4°C. Egg deposition was observed on 5 occasions between 0900 and 1430 hours, although it also occurred outside this time period because newly deposited eggs (i.e., eggs in a very small cluster) were observed prior to 0900 on several occasions.
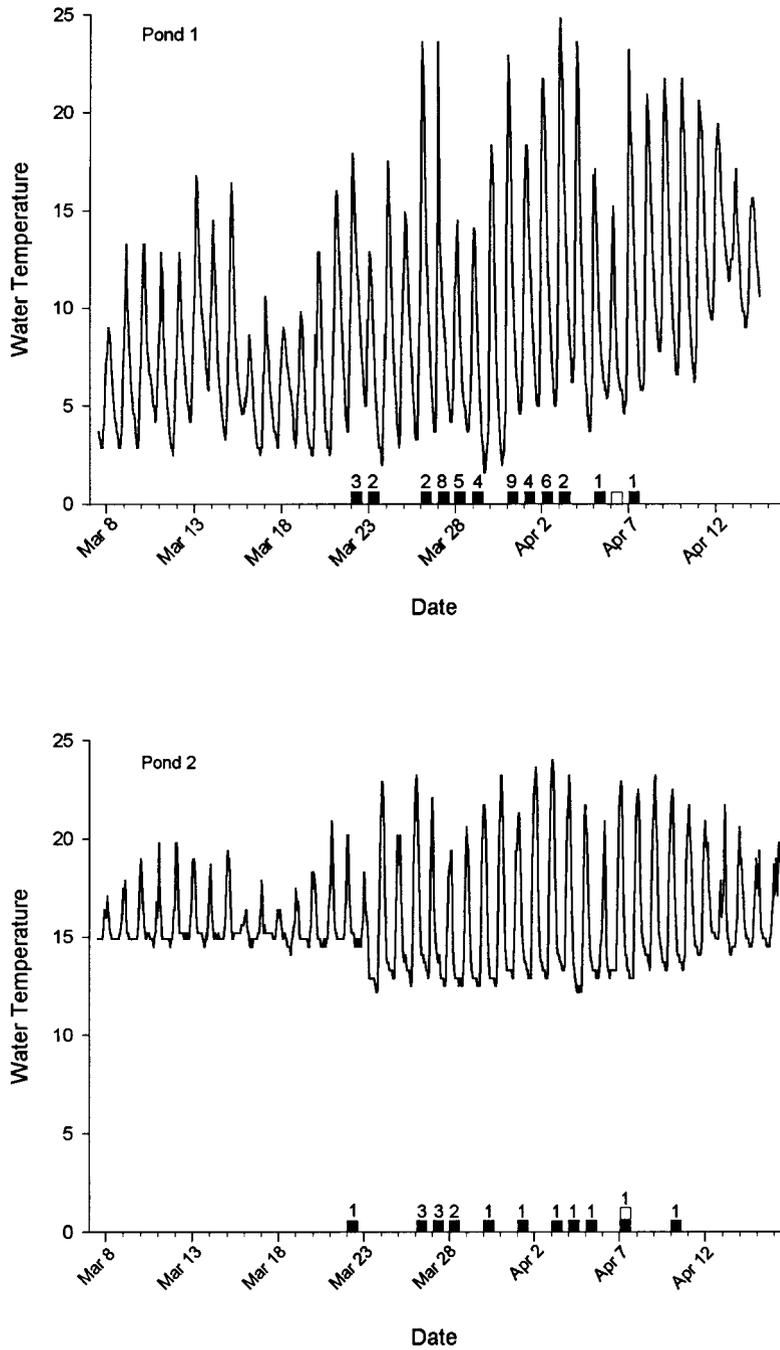
Fig. 2. Water temperature (°C) by date at oviposition site of *R. luteiventris* at ponds 1 and 2 in northeastern Oregon, 2000. Solid squares signify the days that eggs were deposited with the number of egg masses listed above each square. The open square signifies the day that the eggs first hatched.

Hatching occurred 12–21 days after deposition (Table 2). Mean and maximum daily water temperatures were significantly correlated with number of days to hatching (mean: $r = -0.7944$, $P = 0.001$; maximum: $r = -0.7732$, $P = 0.002$, $n = 13$; Table 2). Minimum water temperatures were not correlated with hatching time. Hourly recordings of water temperatures did not drop below 1°C at night at any of the sites. More than 50% of the embryos survived to hatch at each oviposition site, except pond 9, where the embryos were eaten by leeches.

DISCUSSION

Egg deposition was initiated at the oviposition sites when mean water temperature was 7.6–16.0°C, and maximum water temperature was 9.8–20.2°C. These temperatures were above the minimum embryonic thermal temperature (6°C) reported for *R. luteiventris* by Johnson (1965). It appears that maximum water temperatures had to be at least 9.8°C for egg deposition to occur; no egg deposition occurred when maximum water temperatures were below that level. Johnson (1965) predicted that a water temperature of 15–16°C would be required for breeding in *R. luteiventris.*

The minimum water temperature on the 1st night following egg deposition was below the minimum embryonic thermal temperature at 11 of 18 sites. It is known that embryos are able to withstand cold temperatures (1°C) for several hours (Licht 1971, Sype 1975), and the temperature tolerance of embryos increases with age (Brown 1967). We observed deposition of eggs in the morning or early afternoon; this timing provides warm temperatures for the newly fertilized eggs and allows embryos to undergo several hours of rapid development before being exposed to cold overnight temperatures (Licht 1971). In addition, water temperature within a cluster of ranid egg masses may be higher than the surrounding water (Herreid and Kinney 1967, Licht 1971, Sype 1975).

Although water temperature appears to be the primary factor determining timing of egg deposition, we suspect other factors may exert some influence. Ponds 1 and 2 were within 300 m of each other, and egg deposition occurred on 22 March in both of them. Yet, ponds 1 and 2 had mean water temperatures of 10.1°C and 16.0°C, respectively (Fig. 2). If water temperature was the sole factor determining oviposition, egg deposition should have occurred sooner in warmer pond 2 than in pond 1. Photoperiod, distances between overwintering and breeding sites, and water temperatures at overwintering sites (which could determine when frogs leave these sites) are additional factors that could affect timing of egg deposition. Further research on the effect these other factors play in breeding activity seems merited.

Temperature is the major factor influencing the developmental rate of amphibian embryos. Averages of the daily mean and maximum water temperature were significantly correlated with the amount of time until hatching in our study. The 12–21 days required for hatching in this study differed from data for *R. luteiventris* reported by Johnson (1965). In laboratory situations with water at constant temperatures, Johnson found that embryos reached stage 20 after 476.5 hours (19.9 days) at 10°C and after 197.2 hours (8.2 days) at 15°C. Herreid and Kinney (1967) reported that *R. sylvatica* embryos greatly increased their speed of development with small temperature increases at low water temperatures. Overall development time of embryos of *R. dalmatina* and *R. temporaria* was a logarithmic function of temperature (Riis 1991).

Information on breeding ecology is fundamentally important in developing an overall picture of how disturbance factors influencing water temperature may affect the reproduction of amphibians in an ecosystem. The temperature at which breeding occurs is particularly important because temperature tolerances of embryos are more sensitive than those of larvae or adults (Moore 1939). The variable nature of water temperatures affects not only the timing of breeding, but embryonic development and survival as well. Knowledge of water temperature at breeding can be used to determine the timing that population monitoring at oviposition sites should occur.

ACKNOWLEDGMENTS

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