

## Comparative breeding behavior of the red-legged frog (*Rana aurora aurora*) and the western spotted frog (*Rana pretiosa pretiosa*) in southwestern British Columbia

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The breeding behavior of *Rana aurora aurora* and *R. pretiosa pretiosa* from an area of sympatry in southwestern British Columbia is described and compared. A 7-ac field near White Rock, B.C., was closely observed during the 1968 and 1969 breeding seasons.

Both species arrived at breeding sites and began breeding activities within 2 weeks after emergence from hibernation in February and March. They both used the same temporary pond and slow-moving stream, and breeding occurred simultaneously.

Male *pretiosa* gather into small groups with individuals vocalizing within inches of each other. The mating call is given in air as the frogs float on the surface of water only a few inches deep at the margins of the pond and river. Male *aurora* call several feet apart while completely submerged in 2 ft or more of water, and 3 ft or more from the pond and river edges. Descriptions of the mating calls of both species, as well as a call peculiar to amplexic male *aurora*, are given.

Female *pretiosa* spawn mainly during daylight and the eggs are placed on top of, or immediately adjacent to, the first mass present. As many as 26 separate masses were laid on top of one another in the same place, unattached to vegetation in only a few inches of water. Female *aurora* spawn only at night and deposit their eggs attached to submerged vegetation in a minimum of 12 in. of water, and at least 3 ft from the pond and river shore; masses are several feet apart. The eggs of both species are laid in those areas where conspecific males vocalize.

Peculiar aspects of both species' breeding behaviors are discussed, as well as those factors leading to successful reproductive isolation. Observations of breeding *aurora* in allopatry indicate no major differences from those on *aurora* sympatric with *pretiosa*.

### Introduction

In southern British Columbia, the red-legged frog, *Rana aurora aurora*, and the western spotted frog, *R. pretiosa pretiosa*, are reported to occupy complementary geographical areas, with *pretiosa* found east of the Coast Range, and *aurora* restricted to the extreme southwestern coast, west of the Coast Range (Carl and Cowan 1945). Recently, however, both species have been found coexisting in well-established populations in the Lower Fraser Valley of British Columbia, about 40 mi south of Vancouver. As part of an intensive investigation of the ecology of these species where they are sympatric, I made special efforts to closely observe their breeding behavior.

Relatively little has been published concerning the breeding behavior of these species, and the notes of early naturalists (Dickerson 1913) are essentially only incidental observations. Storm (1960) provided some information on *aurora* near Portland, Oregon, and Svihla (1935) presented brief notes on *pretiosa* in eastern Washington. Some aspects of the breeding

biology of *pretiosa* at 7800 ft in Wyoming were reported by Turner (1958).

One general aim of this report is to provide more complete information on the breeding behavior of these infrequently studied anurans of the Pacific Northwest. Comparison of the breeding behavior of these two closely related species occurring in the same habitat should help in an understanding of how they can continue to exist as independent breeding populations, that is, what the reproductive isolation is between the two species, and how each species has become adapted for reproductive success in the same environment.

Aspects of the breeding biology of these species subsequent to egg deposition are not included here, but will be presented in a separate report.

### Materials, Methods, and Study Areas

Information has accumulated on both species during the breeding seasons of 1968 and 1969. Most material is based on data from the locality where both species are sympatric, but two other areas where only *aurora* is found were also observed.



for known differences between the two localities. Precipitation records for both years are from the airport station.

Unless otherwise specified, the behavior described is based on observations at the LCR study area, where both species are sympatric. However, observations made at other localities were valuable in determining whether the LCR *aurora* population differed because of sympatry with *pretiosa*.

During both years, breeding *aurora* were observed in two other localities. One is a small pond at sea level adjacent to Beaver Lake in Stanley Park, Vancouver, B.C. The pond, formed by overflow from a large lake, is about 15 by 40 ft, and 6-18 in. deep. The water is clear and allows good visibility of the few frogs that breed in it. Most breeding occurs in the deeper, muddy lake nearby.

The second area is Marion Lake, in the University of British Columbia Forestry Reserve, about 1000 ft in elevation near Haney, B.C. The lake is 32 ac in area, with a mean depth of 8 ft. The water is very clear and allows good vision of the several hundred *aurora* that breed in it. A thick coniferous forest extends to the lake on all sides.

Frog vocalizations were recorded with a Uher M 514 microphone and an LC-10 hydrophone (Atlantic Research Co.), together with a Uher 4000 Report-L tape recorder. Calls were analyzed on a Sonagraph (Kay Electric), adequate tests being made to ensure that calls were not distorted if recorded with different equipment.

The intensity of calls (in decibels (db) re 0.0002 dynes/cm<sup>2</sup>), as they occur in the natural environment, were measured with a Scott Type 450 sound level meter.

**Results**

In the Lower Fraser Valley and the LCR study area, weather conditions in early spring of 1969 were very different from those of the same period in 1968. A prolonged cold wave (setting a 50-yr record) in 1969 kept the river and field under ice until late February, and sub-freezing temperatures occurred almost nightly until the second week of March. As seen in Fig. 1, the air and water temperatures which existed during the last week of February in 1968

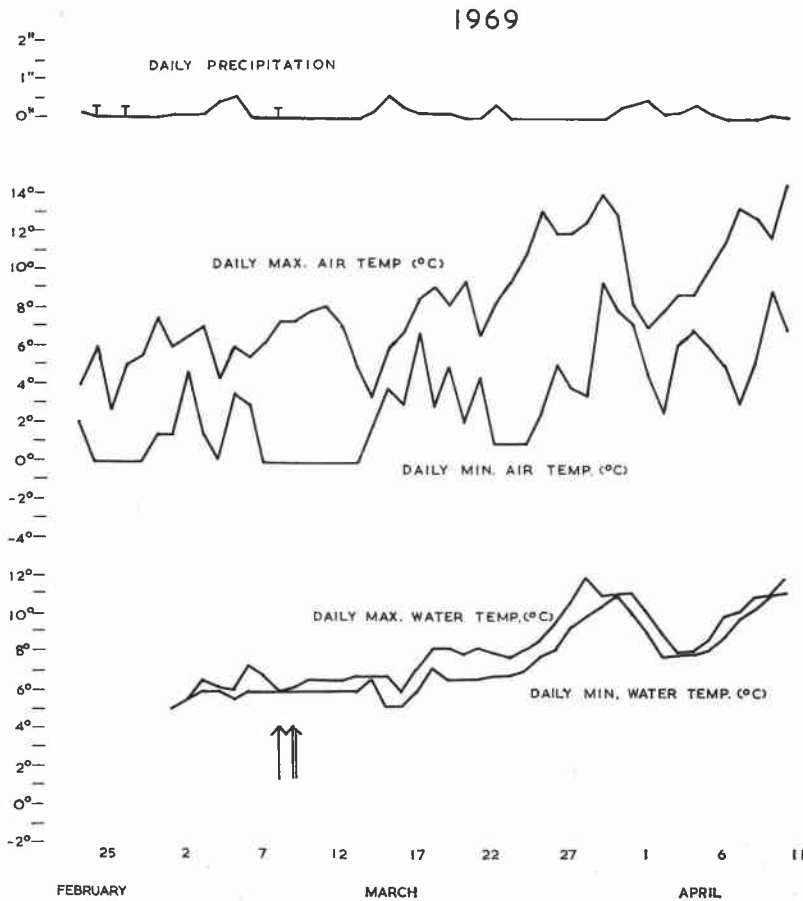


FIG. 1 (Part 2)

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were not encountered until the second week of March in 1969. The onset of breeding by both species was delayed for almost 2 wk in 1969, a fact which provides evidence that there exists temperature thresholds necessary for initial breeding activity.

*Prebreeding and Breeding Behavior of Rana aurora aurora*

(a) *Emergence from Hibernation and Migration to Breeding Sites*

The first *aurora* appear as soon as ice and snow begin melting from the river and field. Frogs have been found overwintering in both river and woods, and the duration of ice cover primarily affects the time of emergence. In 1968, the last ice melted about 14 February, and daily searches were first successful on 24 February when several males were caught. In 1969, frogs were first caught on 3 March, the unusually prolonged ice and cold having delayed emergence. The temperature data for both years (Fig. 1) indicate that *aurora* first become active when the air has been at least 5 °C for several days. If temperatures fall below this after emergence, the frogs apparently become inactive. (Subadult frogs did not appear for the first time until several weeks after breeding terminated and air temperatures were daily above 10 °C.)

Very soon after emergence, *aurora* begin to move to breeding sites. Most movements occur at night and seem to be stimulated by cloud cover and precipitation, conditions under which warmer temperatures prevail. On clear days, some frogs were caught active during daylight hours, but most were found during dusk, before the rapid drop in temperature accompanying the onset of darkness. In both years, by about 1 week after emergence, several dozen males had arrived at the breeding sites.

The breeding sites were in the northern ends of the pond and adjacent portions of the river.

(b) *Prespawning Activity at Breeding Sites*

Males arrived first at the pond and river breeding sites and remained concealed, often in full sunlight, near sedges and bulrushes. No feeding activity was noticed at this time, and the frogs quickly entered the water when approached. In the first week after emergence, no female *aurora* were found at the breeding sites, but several were found 150–300 ft away in the field.

Males were at the breeding sites at least 1 week before they began to vocalize. Not a single call was heard in a full week of almost round-the-clock observations, yet more males were found at each search. This suggests that the males find these sites and orient to them without use of vocal cues from other males already at the sites.

Although the males are not vocal when first gathered at the sites, experiments show that they will persistently and tenaciously clasp a female *aurora*, or any other animal of suitable size, if given a chance. Male *aurora*, collected from breeding sites before calling had initiated, and placed with female *aurora* (or *pretiosa*) in aquaria, quickly assumed amplexus. At Stanley Park, about 1900 h on 19 February, 1968, a pair of *aurora* was caught in amplexus, and on 20 February, about 2000 h, at Stanley Park, a male *aurora* was seen tightly clasped with a male salamander, *Ambystoma gracile*, which finally broke free after a 10-min struggle. Thus calling and initiation of a "chorus" is not a necessary prerequisite for sexual arousal in male *aurora*.

(c) *Vocalizations at Breeding Sites*

Male *aurora* began calling after about 1 week at the breeding sites. After several days of listening with no indication of vocal activity, in 1968 the calls were first heard on the afternoon of 28 February, and the afternoon of 8 March in 1969. Stimuli responsible for initiating the calling are uncertain, but warming temperatures seem especially important. In both years, the water and air temperatures were above 6 °C for several days before calling started. Temperatures in the pond where frogs had gathered had not fallen below 6 °C for 5–7 days before initial vocal activity (see Fig. 1).

Unpaired male *aurora*, at every breeding site observed, emit their mating call while completely submerged under water 7 in. to 3 ft in depth (up to 5 ft in Marion Lake). They normally remain stationary on the bottom or concealed in tufts of submerged vegetation. Of numerous males observed in daily and nightly recording sessions, only two were observed to call above water, and they did only briefly before submerging again. Males call several feet apart and remain motionless on the substrate or in vegetation. At indefinite intervals they surface for air, and may swim a few inches

above water, usually returning and submerging very near the spot from which they surfaced.

The mating call of *aurora* is very low in volume and has little carrying power. The calls given underwater, as they normally are, are barely audible in air; if the frog is calling in several feet of water, no sound at all can be detected in air, and a hydrophone is necessary to detect the calls. Frogs calling near the surface in shallow water produce calls heard, at most, 20–30 ft away in air. Mating calls given above the water cannot be heard beyond 50 ft. Males calling in about 2 ft of water at 12.8 °C emit calls which carry about 30 ft underwater, as verified by use of a hydrophone.

The intensity of calls given above water by a male 2 ft away from the sound meter reached a maximum of only 3 db. The call is less intense if given underwater and measured directly above the calling male at the water surface.

The calls have a definite ventriloquial effect and at first appear to emanate from frogs vocalizing some distance away. They are almost completely masked by the loud "chorus" of the Pacific treefrog, *Hyla regilla*, which often call simultaneously. (For comparison, note that a single *Hyla* calling 15 ft away from the sound meter gives calls having a maximum intensity of 10 db.)

Observations at Marion Lake emphasize the unusual behavior of calling male *aurora*. On 8 April, 1969, at 2100 h, I listened in air for sounds of male *aurora* I knew to be present in the lake. Not a single call was heard from any position around the lake or from a boat in the center of the lake. However, on listening beneath the water with a hydrophone, the mating calls of several hundred *aurora* were heard. The entire lake, beneath the water, resounded with the calls of frogs submerged at depths up to 5 ft. The same series of events was repeated the next day.

At the LCR locality, *aurora* males were found to call during the day, but most were vocal during the night and early morning. When calling has begun for a season, it may continue nightly until breeding has terminated. Low air temperatures at night do not seem to affect the males calling submerged in the warmer water.

Mating calls are emitted at indefinite intervals, but there seem to be cycles of maximum intensity in a "chorus" throughout the night.

Males call more frequently when other males move near them. When two males approach, they rapidly repeat their mating calls in quick succession, doing so until they attempt mutual amplexus, emit release calls, and swim away. Any movement near a calling male stimulates him to call more often, at times up to 30 sec almost without cessation.

The mating call of unpaired male *aurora* has not been described previously by analysis with the sound spectrograph. The call consists of either two, three, four, or five notes, but almost all calls are three or four notes. A sonagram for a typical mating call given by a male 58 mm (snout to vent) calling submerged in water 9 °C is seen in Fig. 2.

Each individual note consists of five to six separate pulses. There is a rise in pitch and intensity on the last notes in a series. The dominant frequencies of the notes lies between 450 and 1300 Hz, and the notes may extend to 7.5 kHz. A call with four notes lasts about 1 sec (0.90–1.00 for 12 calls from three males in water at 9 °C). A five-note call lasts about 1.25 sec. The call can be compared to a repeating series of the sound 'uh', with more emphasis placed at the end of the series: uh uh uH UH.

#### (d) Behavior of Amplexic Pairs

Male *aurora* clasp females in an axillary position as described by Storm (1960), and as seen in other ranids. The male holds very tightly and it requires some effort to remove him from a female. While clasping, the male emits a single call note, about once every second. As the male gives this note, his throat pulses and his abdomen contracts, causing him to pull slightly backwards as he grips the female. He makes this sound with his mouth directly behind the female's tympanum.

This single note is very constant in structure and is essentially a burst of energy between 750 and 1500 Hz (Fig. 3). The spectral characteristics of the note fall within the range of dominant frequencies of the mating call (Fig. 2). The note is unpulsed and lasts only 0.05 sec. It is extremely low in volume and cannot be heard beyond 1–2 ft from an amplexic male in a very quiet room. It is at most 1 db in intensity when measured 6 in. away. However, the note is emitted directly into the female's ear and consequently may be more intense for her.

Males clasped with receptive females emitted this sound continually. Without cessation, a male continually repeated this note almost every second for a full hour during which he was observed. It is given both underwater and in air, if the amplexic pair is placed out of water. Males also give this call when clasped with females which are unreceptive and attempting to gain their release, but when the female becomes very active, the male ceases and emits a different kind of call as described by Licht (1969). Males from all populations studied gave the single note when clasped, and it seems to be a normal part of their vocal repertoire during breeding.

The second type of call amplexic males emit is a series of one to eight notes which differ in temporal and structural pattern from the mating call of unpaired males (see Figs. 7, 8 in Licht 1969, and Fig. 2 in this report). This amplexic call has been recorded from males clasped with unreceptive females both in the field and laboratory, but it is not yet certain that this call is given by males clasped with receptive females. However, there is some preliminary evidence that it may. A hydrophone was held near a pair of *aurora* in 2 ft of water at Marion Lake. The male did not give this amplexic call as the female remained still, but as she began to swim a few inches, the male began vocalizing. When she stopped swimming, he stopped calling. On another occasion, in the laboratory, a male *aurora* was clasped with a female *pretiosa* which remained quiet and did not struggle. She was thus a 'simulated' receptive female *aurora*. They were left alone in a darkened room and not disturbed, but recordings were made of all vocalizations. The male spontaneously emitted amplexic calls (series of one to eight) at intervals. Subsequent observations indicated that the male called whenever the female *pretiosa* began to swim.

Sonograph analyses of male *aurora* release calls (those calls given by males when they come physically in contact with other males, and identifying the caller as male) and male amplexic calls reveal much similarity. The release calls are highly variable in both spectral and temporal pattern and are not easily quantified. Males are in varying states of excitement when they emit the release calls, but in general they are more intense (more energy) and more rapidly

repeated than the amplexic calls. Although they cannot be considered the same call types, the amplexic call seems to be a modified version of the male release call.

A male *aurora* is quickly forced to release an unreceptive female *aurora* which undergoes elaborate and extensive behavior to gain her release. When placed in aquaria with 2 in. of water, an unreceptive female can secure her release in less than 1 min (Licht 1969). Further tests were conducted with unreceptive females placed in tanks containing water 1 or 2 ft deep. Under these circumstances, when clasped by a persistent male *aurora*, the female attempts to gain her release by continually rolling over in the water and issuing release calls. Persistent males will maintain their grip for as long as 15 min, but eventually relax their clasp on the female. The same females, when placed in only 2 in. of water, can gain their release within a minute, owing to their ability to use the substrate to maneuver more easily.

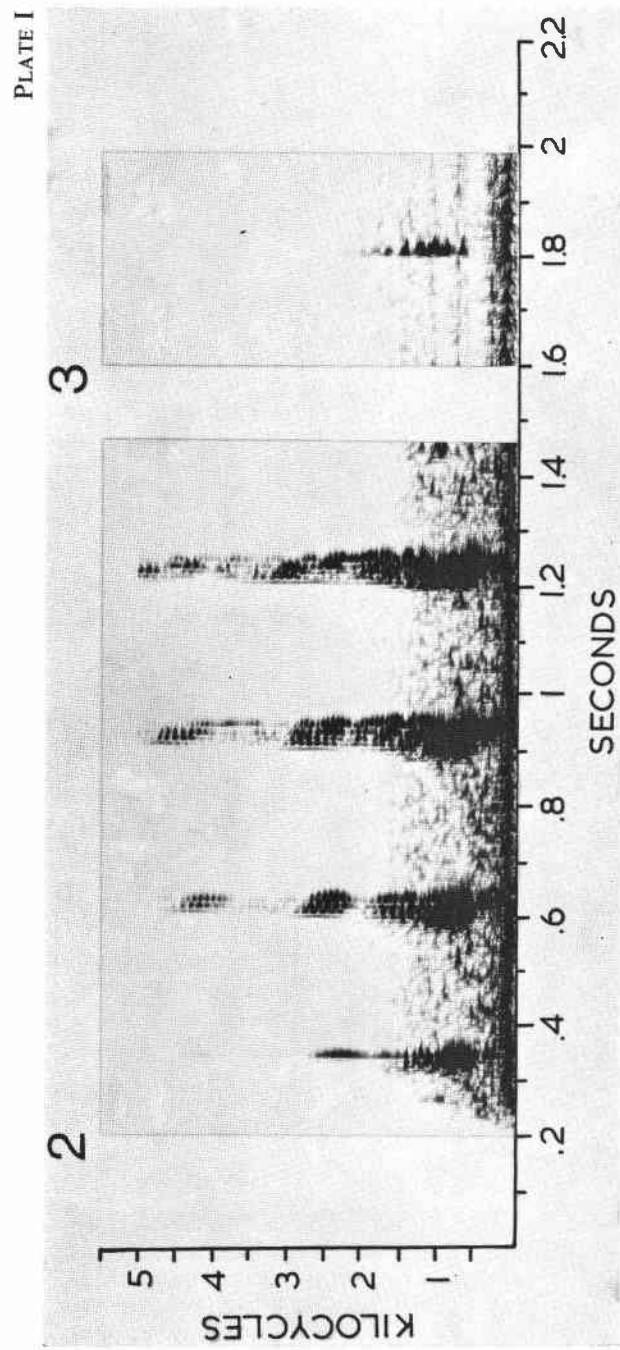
#### (e) Spawning Behavior

During both years at the LCR, the initiation and termination of egg laying was precisely determined. Egg laying started on the night of 28 February and ended on 13 March in 1968, and in 1969, it began on the evening of 15 March and stopped on 3 April. Once egg laying began it was intensive, and most females spawned within 2 weeks after the first egg mass was found

TABLE I

Numbers of new *R. aurora* egg masses found on each search at the Little Campbell River during the 1968 and 1969 breeding seasons

1968		1969	
Date	No. masses	Date	No. masses
February 26	0	March 12	0
27	0	13	0
28	1	14	0
29	5	15	1
March 1	2	16-22	0
2-5	2	23	3
6	0	24	0
7	4	25	5
8	1	26	3
9	0	27	10
10	8	28-31	0
11	0	April 1	0
12	8	2	0
13	5	3	11
14	0	4	0
15	0	5	0



Figs. 2, 3. Sonograms of male *auroora* vocalizations. Fig. 2. Mating call of an unpaired male submerged in water 9 °C. Fig. 3. Single note emitted once a second by a male clasped with a female.

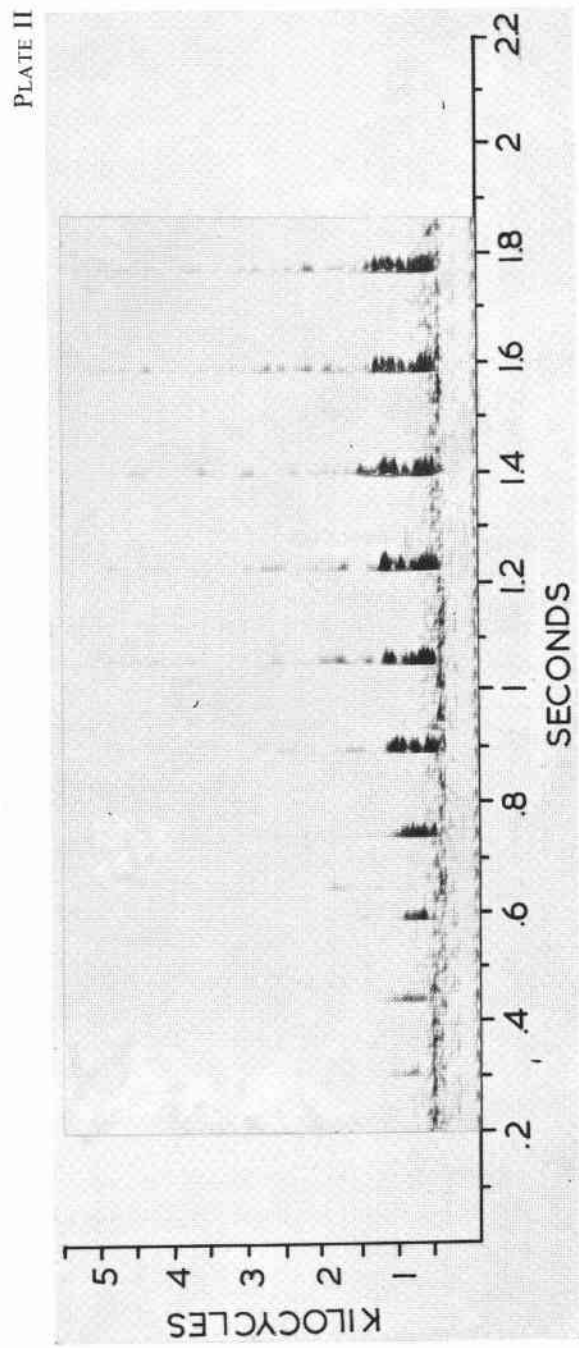


FIG. 4. The mating call of an unpaired male *pretiosa* floating in water 12.4°C.



(Table I). Weather data seen in Fig. 1 indicate that water temperature of 7.0 °C is sufficient for spawning and that once this minimum is reached, most eggs are deposited. In 1969, only one egg mass was deposited before the pond reached at least 7.0 °C.

In both seasons, all eggs were deposited overnight as determined by dusk and dawn visits to the LCR site. Although males may vocalize during the daylight hours, the females apparently spawn only during the dark (it is unknown whether they respond to the male call during the night or day).

Egg masses were attached to stalks of submerged vegetation (*Typha*, *Carex*, and *Potamogeton*) at minimum depths of 12 in. and as deep as 3 ft (up to 5 ft in Marion Lake). The eggs are placed in quiet water with little or no flow, and in areas exposed to sunlight for most of the day. Masses were usually 2 ft or more apart from each other, but at each distinct site at the LCR, the eggs are laid in the same general vicinity. For example, 10 masses were deposited within 20 sq. ft in the river. The eggs often become covered with a film of debris and may be difficult to distinguish, but if one mass is found, a careful search will reveal others nearby.

In the LCR pond, *aurora* deposits its eggs in the center where water is deepest (2–3 ft), and about 3–15 ft from the pond edge. In the river, the eggs are laid in water 2–4 ft deep, close to the main channel at the deepest part of the overflow. No *aurora* mass was found within 4 ft of the shoreline and submerged less than 18 in. deep. The oviposition sites are those at which males vocalize.

In the LCR locality in 1968, the first *aurora* mating calls were heard on 28 February and the last egg mass laid on 13 March. In 1969, these dates are 8 March and 3 April. Thus the effective breeding season lasted 15 days in 1968 and 27 days in 1969.

### *Prebreeding and Breeding Behavior of Rana pretiosa pretiosa*

#### (a) *Emergence from Hibernation and Migration to Breeding Sites*

Emergence from overwintering sites begins as early in the year as the winter thaw permits. Frogs were first caught on 21 February, 1968, and 3 March, 1969. Air temperatures of 5.0 °C is evidently the minimum necessary for initial

activity, but several males seen basking in the sun probably had higher body temperatures.

The males arrive first at breeding sites and on arrival they remain in shallow water at the edges of the pond and along the margins of the river overflow. From 3 to 9 March, 1969, about 18 or more males gathered into two separate areas. About eight males were within a 3-ft square area at the edge of the pond where bulrushes provided cover. Ten or more males were within a similar area along the shallows of the river, about 65 ft away from the pond. A few solitary males were caught scattered along the river and pond borders about 10–20 ft from the main groupings, and they remained apart from the aggregations before calling started. All males were basking in the sun or floating on the water surface.

#### (b) *Vocalizations and Male Behavior at Breeding Sites*

Calling by unpaired males at breeding sites began on 29 February, 1968, and on 9 March, 1969. The first calls were noted in the afternoon when the air temperatures were about 12 °C in direct sunlight at the calling sites. Calling continued throughout the afternoon and into the evening, but ceased on some nights when temperatures were near freezing. Within a day or 2 after calling began, solitary males initially found away from the main aggregations, and individually marked by toe clipping, were recaptured within the groups of males.

Males called from within 1 ft of each other, and as many as six may cluster into an area 2 ft square. They called while floating on the water surface with their heads up, or sitting above the water on mats of vegetation: they were not observed to call underwater. They remained in the shallows of the pond or river overflow in water only 2–6 in. deep, and virtually all males faced toward shore as they called.

On the first few days after calling began, the males in close proximity constantly clasped each other. Whenever a male moved, it attracted the attention of a nearby male which swam towards it and attempted amplexus. After breaking apart, both males would remain still for many minutes until they would again attempt amplexus or move apart. After several days of this behavior, these bouts of mutual amplexus were no longer seen, and thereafter the males remained within

inches of each other, vocalized, but did not clasp.

The mating call of *pretiosa* males is usually a series of short bass notes from 6 to 9 in number, but notes of 4 to 26 in a series are also given. About noon, on 26 March, 1969, when the water was 13 °C, I counted the notes of 163 calls given by seven males. Twenty-seven had 6 notes, 48 had 7 notes, 47 were 8 notes, and 23 had 9; the rest were either 4, 5, 10, or 12 notes. However, it was observed that as a male approached another frog, the number of notes increased, and reached as many as 26 before that call ceased. Playback of recorded calls on tape loops to nearby males continually evoked prolonged calls from them.

The call of *pretiosa* is low in volume and carries only 50–100 ft at most. The first two or three notes in a call are barely audible, but the intensity increases with each succeeding one. A male calling 4 ft away from the sound meter gave mating calls which were 4–5 db. The call of *Hyla regilla* completely masks the low bass notes of *pretiosa*.

A sonagram of a typical call with 10 notes is seen in Fig. 4. Each note is unpulsed and lasts about 0.03 sec. At 11.4 °C, the interval between notes within a call is 0.11–0.14 sec, and a call of seven notes lasts 1.10–1.22 sec. Each note contains dominant frequencies between 0.5 and 1.5 kHz, and the last notes within a call extend, with reduced energy, to about 5.5 kHz.

(c) *Behavior in Amplexus and Spawning*

Before amplexus, females find their way to the breeding sites and there remain within range of the males' mating calls. They remain apart from the males until ready to spawn. For example, in 1969, four females were found about 75 ft from the pond several days before the males began to give mating calls, and three were recaptured in the same area on successive days. One female first caught on 3 March was caught again in amplexus on 12 March, in the pond 60 ft from where she was originally found.

During both years, eight amplexic pairs of *pretiosa* were encountered, and all but one pair were found in bright sunshine in midafternoon, with air temperatures about 15–16 °C. Pairs remained very still in shallow water only 2–5 in. in depth, with the male's back often three-quarters out of water. No calls from amplexic male *pretiosa* were detected, although two males

gave rapid 'trills' when first grasping a female and assuming amplexus: the clasp is axillary as in other ranids. Unreceptive female *pretiosa* secure their release by use of release calls and abdominal vibrations.

The first egg masses in 1968 were deposited on 1 March, and in 1969 on 13 March. Subsequent egg masses appeared within several days as seen in Table II. The eggs were mostly deposited during midafternoon, but during the night as well.

In each area where males called, the eggs were deposited in one spot. The masses were usually deposited on top of, or immediately touching, a mass already present. For example, clusters of 26, 19, and 11 masses were found in areas less than 2 ft square. The smallest number found together was five. The masses are not attached to any vegetation and are deposited in such shallow water that only the bottom half of each is submerged while the tops are exposed directly to the air.

This clustering phenomenon is directly due to the behavior of both the male and female. On four different days, males were observed calling from the surface of the egg jelly, while other males were calling only inches away. More striking evidence is that females may actually seek out egg masses already present on which to deposit new ones. On 20 March, 1969, a female was observed depositing the first eggs in an area where males had been calling for several days.

TABLE II

Numbers of new *R. pretiosa* egg masses found on each search at Little Campbell River during 1968 and 1969 breeding seasons

1968		1969	
Date	No. masses	Date	No. masses
February 26	0	March 12	0
27	0	13	15
28	0	14	0
29	0	15	0
March 1	3	16	1
2–5	10	17	0
6	0	18	0
7	15	19	9
8	0	20	1
9	0	21	18
10	2	22	0
11	0	23	10
12	0	24	0
13	0	25	0
14	0	26	0

The next day there were 18 new masses surrounding or touching that one. I moved all 19 masses to an identical spot 4 ft away. On 23 March, two other masses had been added to the surface of the others and a third mass was deposited only 3 in. away. No new masses were added to the new or original sites on subsequent days, but these preliminary manipulations suggest that there are in female *pretiosa* specific behavioral adaptations for grouping of egg masses.

Sites used for egg laying in 1969 were within 1 ft of those used in 1968. A third new site in the river was also used in 1969. As will be discussed, two sites were within 10 ft of those used by *aurora*, although the specific area chosen differed in several respects.

In 1968, the effective breeding season was 11 days, and 15 days in 1969, as determined by the first day of calling and last day of egg laying.

### Discussion

#### *The Behavior of Rana aurora*

The breeding behavior of *aurora* is peculiar in several respects. The fact that the males usually give their mating calls while completely submerged in several feet of water is unlike the calling behavior of other North American ranids. Storm (1960) also noted that in Oregon, *aurora* may call underwater.

This behavior renders the mating call of little value in attracting females or other males to the breeding sites from long distances. At best the mating call is not heard beyond 40 or 50 ft (Storm 1960, and present results). Males of most species of *Rana* in eastern North America call immediately upon reaching breeding sites, and their loud calls are believed to aid in enlarging the numbers of both sexes at breeding aggregations (Bogert 1960). However, given the nature of the mating call and the unusual calling sites of *aurora* males, this function seems unlikely. It appears that both male and female *aurora* find their way to breeding sites without use of vocal cues from mating calls. Most males had already arrived at the LCR breeding sites before any vocalizations had begun. Olfactory and visual cues are used by other ranids for orientation and homing (Oldham 1967; Ferguson *et al.* 1968), and may be important for migrating *aurora*.

The situation at Marion Lake provides strong evidence for nonvocal cues being es-

pecially important for long distance orientation by *aurora* to breeding sites. Unless the frogs all overwinter in the lake (there is evidence against this), they would have to reach the lake from the woods without use of any vocal cues from the lake itself. However, once on arrival at the water, the males could join the "chorus" and females could find a mate.

There is the possibility that once *aurora* emerge from hibernation, they immediately move to (or stay in) water. Females may then be able to find the breeding sites by following the vocal cues given underwater by calling males. At low water temperatures, the mating call may travel considerable distance and be heard for several hundred feet away. Such behavior, underwater orientation from long distances, would be unique among ranids, but it has not been investigated carefully enough to discount the possibility. Nonetheless, there remains the fact that most males had already arrived and remained at the LCR breeding sites for a full week before any calls were given. Thus males almost certainly rely on nonvocal cues for orientation, and females should be expected to possess the same ability.

There is no doubt that the male mating call is very efficient for short distance attraction. As will be discussed, not a single interspecific cross occurred during either year at the LCR, which strongly suggests that female *aurora* are able to successfully discriminate between the calls of *aurora* and *pretiosa* which were often heard at the same time and place.

If female *aurora* find their way to the breeding sites without use of mating calls to guide them, as is suspected, they may arrive in various stages of physiological readiness and receptivity. Females begin migrations from variable distances away from breeding sites, and some may arrive before they are receptive. A female arriving before she is ready to oviposit would have to remain in the vicinity of males which are quick to clasp any animal likely to be a female. If a preovulating female is clasped too soon, she must be able to secure her release so as to not remain in amplexus for long durations, for amplexic pairs are probably more vulnerable to predation. The elaborate release behavior of unreceptive female *aurora* (Licht 1969) may have evolved because female *aurora* are likely to reach breeding sites before receptive and are

prone to premature amplexus. Females of other species of *Rana* which do not show such elaborate release behavior may not need it if they are responding to male calls from long distances and are most likely to arrive and be clasped when ready.

There is also the fact that male *aurora* show tenacious clasping behavior before they are vocal, and thus may encounter females en route to breeding sites and away from water. (The males of no other North American *Rana* are known to be receptive before vocal (Bogert 1960). However, males of *R. temporaria* in Europe are (Savage 1935).) At such an early time, prolonged amplexus is clearly disadvantageous. On 25 February, 1968, I caught a male *aurora* in amplexus with a female *pretiosa* about 30 ft from water. There had been no *aurora* mating calls previously. The pair remained in amplexus for 3 days in the laboratory, although the female *pretiosa* gave release calls and abdominal vibrations. As described (Licht 1969), female *aurora* initially attempt to gain release with such behavior, but it is insufficient and instead they resort to more elaborate techniques.

Unreceptive female *aurora* cannot gain their release as quickly when in deep water as when in water only a few inches. However, a female *aurora* which has not ovulated and is not receptive may not likely enter deep water where normal pairing and spawning occur. Presumably only a receptive female seeking a male would venture into the deeper water where males call, and she would not seek her release when clasped. Her release behavior is most efficient in a solid substrate or shallow water, in precisely those places where an eager male may attempt amplexus as the female is moving to breeding sites, or remaining nearby until ovulation occurs. The amplexic pair of *aurora* in Stanley Park described by Licht (1969) was apparently a case of premature clasping of a female by an eager male.

Female *aurora* may be clasped only shortly before they ovulate, and a means of stimulating them to ovulate and to hasten, or even maintain their receptivity after ovulation, would be advantageous. The single note emitted by amplexic males (Fig. 3), may be a means for such stimulation. It is repeated almost every second directly into the female's ear; in addition,

the male pulls backwards very slightly on the female's back as he emits each note. Moreover, the note is little more than a burst of energy in the frequency range which characterizes the area of dominant frequencies in the *aurora* mating call (compare Figs. 2 and 3). Electrophysiological studies (Frishkopf and Goldstein 1963) show a close correspondence between the sensitivity of the inner ear of the bullfrog (*Rana catesbeiana*), and the dominant frequencies in the bullfrog mating call. This suggests that the ear of *aurora* may be attuned to the region of 750–1500 Hz, the area of most energy in the single note and mating call.

Savage (1935) noted that amplexic male *temporaria* emit a single note about once every second, just as *aurora* do. However, no other North American *Rana* is known to vocalize in such a fashion. It may be because the sound is so low in volume, it has been overlooked, and it may be more common to the behavior of other *Rana* as well.

The second type of call given by clasping males is very much like a male release call. The amplexic call is given more rapidly and more often whenever a female struggles to gain her release from the male (see Table I in Licht 1969). It may be that any sort of movement, such as that from a struggling unreceptive female, or even a swimming receptive one, is proper stimulus to evoke these calls from the clasping male. Because they are similar to release calls, they may be 'interpreted' as such by other nearby males, which are normally quick to clasp with almost any suitable form near them. Nearby males may not approach another male giving a release call, or something very much alike, and would thus stay clear of the amplexic pair. More work is needed on the function of these calls.

There is much similarity between the breeding behavior of *aurora* and that of *R. temporaria* in England, as described by Savage (1935). He found that *temporaria* males assemble and congregate at breeding sites in silence, just as does *aurora*. Male *temporaria* are receptive before vocal, and amplexic males also emit a single note of low volume almost every second. Savage concluded that voice plays a minor role in aggregating both sexes in *temporaria*, but instead they rely on olfactory cues based on specific

smells from breeding sites. The parallel in aspects of breeding in these two species is very close, and warrants further study.

Adult *aurora* (and *pretiosa*) begin breeding activities at temperatures around 5–6 °C, yet juveniles and adults during the nonbreeding season are inactive at temperatures below 10 °C (author's unpublished data). Perhaps hormonal levels in breeding adults are sufficiently high to enable them to remain active at relatively low temperatures prevalent during the breeding season.

A final point regarding the breeding behavior of *aurora* is whether the males are, in some sense, territorial. Both *Rana clamitans* (Martof 1953) and *R. catesbeiana* (Emlen 1968) are known to be territorial during the breeding season. Male *aurora* almost always called several feet apart, and even on surfacing for air, usually submerged very near the same place. The possibility that the amplexic call is commonly given even with receptive females, and that this functions as a territorial call, has not been ruled out. The behavior of *aurora* males in a "chorus" is quite different from that of *pretiosa* males, and while it is virtually certain that *pretiosa* males are not territorial, additional evidence is needed to refute or confirm this for *aurora*.

#### *The Behavior of Rana pretiosa*

The breeding behavior of *pretiosa* in the Pacific Northwest does not seem to differ from that of populations in the eastern part of its range. In Wyoming, at 7800 ft, *pretiosa* also lay their eggs clumped along very shallow margins of temporary ponds (Turner 1958). In both Wyoming and the LCR, the mating call is of low volume and consists of a variable number of short bass notes. In Wyoming, *pretiosa* does not breed until May or June, but this is presumably due to the altitude and difference in spring isotherm.

The mating call of *pretiosa* is not heard beyond 80–100 ft from breeding sites. The significance of such a low volume call for use in long distance attraction is uncertain. Several females were found within 75 ft of the breeding sites before calling had initiated. By following the movements of frogs in a mark-recapture program throughout the year, evidence has accumulated indicating that females may move very

near the breeding sites during the fall, before winter hibernation. Several females which normally remain in feeding areas established in the southern end of the field were found to have moved to the northern end by late fall (October), were recaptured near breeding sites in March before calling began, and by May were again caught in the southern end of the field. Females may overwinter near breeding sites, and after emergence would be near enough to the calling males to respond to vocal cues when receptive (males may do the same). This would mean that nonvocal cues were used to initially orient to the vicinity of breeding sites, and these cues may be available for frogs moving in the fall as well as early spring. During both years at the LCR, *pretiosa* spawned in identical sites, less than 1 ft apart, and there may possibly be unique features about these areas. As with *aurora*, the call plays a major role in aiding a female to locate a male nearby, but its role as a cue for long distance attraction must be examined.

Unreceptive female *pretiosa* are able to gain their release by techniques similar to *Rana pipiens* (Noble and Aronson 1942) and *R. sylvatica* (Noble and Farris 1929), but less elaborate than those of *aurora* (Licht 1969). This suggests that female *pretiosa* may not be clasped as often before receptive as *aurora*, and that there is no necessity for unusual release behavior. Since females were found on land within 60 ft of calling males for several days, they apparently stay clear of the males until physiologically ready. It may also be that male *pretiosa* do not clasp as tenaciously or as quickly as male *aurora*, but little information is available on these comparisons.

The behavior exhibited by male *pretiosa*, which may call from the jelly surface of deposited egg masses, and females, which may seek other eggs on which to deposit their own, has not been described for other species of anurans. The adaptive significance of this behavior will be considered in another study.

#### *Comparative Behavior and Reproductive Isolation*

In the LCR study area, both species begin breeding activity on virtually the same day of the year, and as seen in Tables I and II, egg laying may occur simultaneously. Both species breed in the same restricted portions of the pond and

river. The mating call of both can be heard at the same time and place. Adult males of both species are 45–60 mm (snout to vent), and the females are 63–75 mm. One might expect a high percentage of interspecific matings under these circumstances.

During both years, I found only one interspecific pair in amplexus, a male *aurora* and a female *pretiosa*. The *pretiosa* was clasped as she moved to breeding sites. Of all the egg masses studied, only a single egg mass may have resulted from a cross by a *pretiosa* and *aurora*: the eggs were the size of *pretiosa* females. However, even this mass may not have been a hybrid one, for it may have been destroyed in early developmental stages by cold temperatures. I have not yet crossed these species to determine the level of genetic compatibility, but it is unlikely that hybrid embryos will develop normally. Dumas (1966) and Porter (1961) have demonstrated that hybrid crosses of Pacific Northwest *Rana* do not produce viable offspring, and they crossed both *aurora* and *pretiosa* with other species. Moreover, after examining several hundred frogs in the field, I have not found one resembling a hybrid and difficult to identify as either species.

Thus there is no clear evidence for interspecific matings in these species breeding under conditions very susceptible to even chance encounters. Dozens of egg masses of each species have been found within several feet of each other.

Table III summarizes the main similarities and differences in the prebreeding and breeding behavior of the two species.

The following factors seem important for their successful reproductive isolation, although both species of frogs use the northern half of the pond and restricted portions of the river nearby for breeding in the LCR locality.

(1) The mating call of each is distinctive and females are likely to respond to those emitted by conspecific males as found in other anurans (Littlejohn and Michaud 1959).

(2) In the pond and river, *aurora* breeds in water at least 3 ft from shore, and in depths of 12 in. and greater. *Pretiosa* breed at the very edges of the river overflow and pond border in water only a few inches deep.

(3) *Aurora* call underwater, *pretiosa* in air.

(4) *Aurora* call mainly throughout the night, and *pretiosa* in the afternoon and evening, and only on warmer nights.

(5) *Aurora* females may respond to male calls only during the night and early morning, and they spawn only during the night. They spawn in deep water in areas where male *aurora* call. *Pretiosa* females spawn mainly during mid-afternoon hours and in very shallow water in those spots where males have congregated.

(6) The effect of the single note uttered by amplexic male *aurora* on the spawning behavior of the female is unknown. If it is a necessary part of the courtship behavior leading to suc-

TABLE III

Summary of main similarities and differences in the prebreeding and breeding behavior of *R. aurora* and *R. pretiosa* at the Little Campbell River study area

<i>Rana aurora</i>	<i>Rana pretiosa</i>
(1) Emerge from hibernation in February and March	(1) Same
(2) Move to breeding sites when air is minimum of 5–6°C	(2) Same
(3) Use the northern portions of pond and river for breeding	(3) Same
(4) Males vocalize several feet apart	(4) Males vocalize inches apart in small groups
(5) Males vocalize under several feet of water at least 3 ft from shoreline	(5) Males vocalize in air from shallow margins of pond and river
(6) Calls given mainly at night but may occur during the day	(6) Calling occurs during daylight and on nights above 5–6°C
(7) Females spawn during the night	(7) Females spawn during the day, often in full sunshine
(8) Eggs laid several feet apart attached to vegetation in depths of 12 in. or more and 3 ft or more from margins of pond and river	(8) Eggs laid in groups unattached in only a few inches of water at river and pond margins
(9) In 1968 calling began 28 February and spawning ended 13 March; 8 March and 3 April in 1969	(9) Calling began 29 February and spawning ended 10 March in 1968; 9 March and 23 March in 1969

cessful egg laying, a female *aurora* may be inhibited from releasing her eggs if clasped by a silent male *pretiosa*.

These factors work to reduce gamete wastage by restricting interspecific matings. Mayr (1963) has noted that ethological premating isolating mechanisms may be reinforced in the area of sympatry if compared to allopatric populations of each species. Blair (1955) has reported on such a finding in frogs of the genus *Microhyla* in the southwestern United States. However, based on the reports of Storm (1960) for *aurora* in Oregon, and Turner (1958) for *pretiosa* in Wyoming, and the present work on populations of *aurora* in Stanley Park and Marion Lake, there do not seem to be major differences in behavior of these species in allopatric and sympatric populations. Nevertheless, differences may be subtle, and studies are continuing in this direction.

According to Dumas (1966), the western populations of *pretiosa*, such as that at the LCR, are post-Pleistocene reinvasions from the east. Apparently the behavioral adaptations for breeding acquired by *pretiosa* in the main part of its range to the east, preadapted them for successful coexistence with *aurora* in the Pacific Northwest. Although both species respond to the same external stimuli influencing the initiation of breeding activity, they respond with different behavioral patterns. The eggs they deposit are subject to very different external stresses, especially temperature, yet both species have maintained large populations through different tactics. Further studies are continuing to elucidate the 'strategies' of each species.

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