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Overwintering of Columbia Spotted Frogs in Northeastern Oregon

Abstract

We studied behavior and locations of overwintering Columbia spotted frogs in northeastern Oregon. We monitored 66 radio-tagged frogs as they moved to overwintering sites during 1997-2000. Frogs used a diversity of overwintering sites, but all sites had an aquatic component including ice-covered ponds (44%), partially-frozen ponds (29%), lotic habitats (23%), and temporary backwaters and seeps (4%). The distance between the original point of frog capture in August-September and the overwintering site varied from 15 to 1200 m. Individuals in ponds were active all winter and remained in shallow water within 1 m of the shore. Frogs overwintering in ponds selected microhabitats with significantly higher water temperatures and dissolved oxygen concentrations compared to other locations in the ponds. Movements during the overwintering period appeared to be linked to water temperatures and dissolved oxygen concentrations.

Introduction

Knowledge of overwintering sites is one of the major gaps in our understanding of ranid frog ecology. Authors have speculated about overwintering habitats (Nussbaum et al. 1983), but precise overwintering locations are known for few species. Temperate marsh- and pond-dwelling ranid frogs often overwinter underwater, although some of the same species have been observed overwintering terrestrially at lower elevations. Overwintering sites have been described for the common frog (*Rana temporaria*) (Smith 1951, Koskela and Pasanen 1974), pickerel frog (*R. palustris*) (Logier 1952, Johnson 1987), leopard frog (*R. pipiens*) (Cunjak 1986, Rand 1950, Emery et al. 1972), green frog (*R. clamitans*) (Pope 1944, Pinder et al. 1992, Lamoureux and Madison 1999), and bullfrog (*R. catesbeiana*) (Stinner et al. 1994).

Oxygen depletion can kill or physiologically stress frogs overwintering in ice-covered ponds (Bradford 1983). Recent field studies have shown that overwintering frogs remain active under ice (Friet 1993; Stinner et al. 1994), and that localized depletion of dissolved oxygen may trigger movement. However, movements also could represent avoidance of low temperatures. For frogs submerged under ice, movement between layers of naturally occurring temperature and oxygen gradients may be necessary for survival (Tatter-

sall and Boutilier 1997). Terrestrial overwintering may minimize the risk of oxygen depletion but may increase risk of desiccation, freezing, or predation.

Ranid frogs may aggregate in large numbers at overwintering sites (Breckenridge 1944), so disturbing unrecognized overwintering sites may compromise entire populations. Recent indications that amphibians have declined on a global scale (Wake 1991) have increased the need for a more comprehensive understanding of overwintering patterns. To date, there have been no thorough studies of overwintering sites of Columbia spotted frogs (*R. luteiventris*). Our objectives were to identify overwintering sites and to determine temperatures and dissolved oxygen levels associated with these sites of Columbia spotted frogs in northeastern Oregon.

Methods

We monitored overwintering activity in radio-tagged Columbia spotted frogs from September 1997 until March 2000. We radio-tagged 10 frogs (6 females, 4 males) in 1997, 42 frogs (27 females, 15 males) in 1998, and 48 frogs (28 females, 20 males) in 1999. Frogs were captured in three habitat types: (1) Grande Ronde River, (2) ponds located in the upper Grande Ronde River watershed, Union County, Oregon, and (3) Crawfish Lake, a 125,600 m² lake (10 m deep) in the North Fork John Day River watershed of Grant County at 2040 m in elevation. The ponds in the

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Grande Ronde River watershed were 95–4132 m² in size and within 200 m of the river (within the floodplain), except Rainbow pond, which was a large (28,526 m²) and isolated pond on a ridge 3600 m from the river. The ponds were 0.9–3 m deep, and 915–1800 m in elevation. Winter air temperatures in these study areas were usually below freezing from December through February, with extremes of -30°C in December 1998. All ponds were permanent and in forested habitats.

Frogs were captured with dip nets along the river and pond shores in August and September of each year. Frogs were sexed and weighed to the nearest 0.2 g, and those weighing ≥ 22 g were fitted with a radio transmitter. Transmitters (model BD-2G, Holohil Systems Inc., Ontario, Canada) weighed 1.8 g, lasted 6 months, and had a range of 200–300 m. Each transmitter was glued to a flat 6-mm wide satin ribbon harness that was fitted around the waist of each frog (Bull 2000). Frogs were checked monthly for abrasions and harness fit when accessible.

Frogs were monitored once each week, from capture until the transmitter failed, the frog slipped out of the harness or was killed, or the signal could not be detected. We attempted to confirm the frog's location visually; if the frog was under ice, we estimated the location to within 0.3 m of the frog. Each time a frog was located, we recorded the date, aquatic habitat type, distance from the previous location, snow depth, and the percent of water surface area covered with ice. Overwintering sites were classified as ice-covered ponds, partially-frozen ponds, temporary backwaters, seeps, and lotic habitats (creeks and rivers). Distance traveled to the overwintering site was the linear distance from the original point of capture to the overwintering site. Water depth and distance from shore were recorded at each overwintering site. Frogs that could not be located with ground tracking were searched for with a fixed-wing airplane within a 5-km radius of the last known location of the frog within 2–6 wk after the frog was missing.

Water temperature and dissolved oxygen were determined in 1998 and 1999; in 1997, we identified overwintering sites only. Water temperature and dissolved oxygen (DO) were measured with a portable YSI meter (Model 55) and were recorded as close to each frog as possible (typically within 0.3 m) once ice formed on a pond.

Water temperature and DO were also recorded at one fixed location in each ice-covered and partially-frozen pond each week as long as frogs were monitored in that pond in 1998 and 1999. We selected sites for the fixed locations on the opposite end of the pond from the frogs' locations and at the same distance from the shore that the frogs were located. Readings were taken approximately 10 cm above the pond bottom for both frog and fixed locations. Readings at fixed locations were intended to represent a sample of water temperature and DO in each pond, but were not recorded at seeps, temporary backwaters, and under banks. Seeps and backwaters were too small to get readings away from the frog, and banks were inaccessible. Readings at fixed locations in lotic habitats were not collected after an interval of 2 wk because water flow resulted in few differences between fixed and frog locations. A 10-cm diameter ice auger was used to reach water for water temperature and DO readings when ice was present.

Values of DO and water temperature measured at fixed points and at frog locations in ice-covered and partially-frozen ponds were compared using Wilcoxon matched-pairs signed ranks tests (Snedecor and Cochran 1980). Due to the question of independence of multiple locations on the same frog, the mean water temperature and DO for each frog and for each fixed location in one pond during the time period they were monitored were used in the analysis. If more than one frog was monitored at a pond, only data for the frog that was monitored the longest were used; we only monitored the same data at one fixed location in each pond. We used Wilcoxon matched-pairs signed ranks tests to compare DO and water temperature recorded at one frog in Rainbow pond and Crawfish Lake in 1999 when frogs in both ponds were monitored (data paired by date). Distances that each frog traveled between successive visits were compared at Rainbow pond and Crawfish Lake before and after the surface froze and between sites using t-tests after transforming the data (base-10 log transformation) to achieve normality. The level of significance was set at $P = 0.05$.

Results

From 1997 to 1999, 68 frogs were radio-tagged in ponds and 32 frogs tagged along rivers. Eight, 23, and 35 frogs were tracked to overwintering sites in 1997, 1998, and 1999; the remainder of

the frogs died, slipped transmitters, or had transmitters fail. Of the 66 frogs monitored to overwintering sites, 29 overwintered in ice-covered ponds, 19 in partially-frozen ponds, 15 in lotic habitats, 2 in temporary backwaters, and 1 in a seep (Figure 1). Seven of 46 frogs originally captured in ponds and 9 of 20 frogs originally captured in the river, moved a mean distance of 275 ± 4.3 m to a different site to overwinter between 21 September and 13 October. The other 50 frogs overwintered in the original capture site.

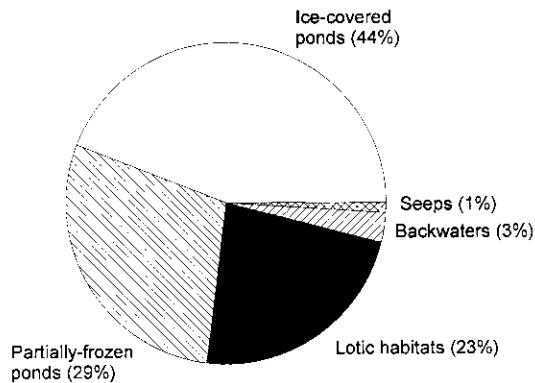


Figure 1. Proportional use of overwintering sites of Columbia spotted frogs, 1997-2000.

Ice-Covered Ponds

Twenty-nine frogs overwintered in seven ice-covered ponds (Figure 1). Mean area of these ponds equaled $22,275 \pm 56.4$ m², and mean depth equaled 2.4 ± 0.6 m. Surfaces froze for all ponds by late November or early December each year and thawed between March and May. Once the pond surface froze, DO declined over the winter (Table 1). For frogs that overwintered under the ice, DO levels were significantly higher ($Z = -2.53$, $P = 0.012$) at frog locations than at fixed points, but water temperatures did not differ statistically (Table 1).

Because of their large sizes, only Rainbow and Crawfish offered opportunities for extensive frog movements. Frogs under ice at Rainbow moved throughout the winter: 90% of locations of 14 frogs were within 1 m of shore and in water < 1m deep. Distances traveled by frogs before and after the pond's surface froze were significantly different in 1997 ($t = -2.10$, 97 df, $P = 0.039$) and in 1999 ($t = 2.25$, 29 df, $P < 0.001$) but did not differ statistically in 1998 (Figure 2). After ice covered the surface of the pond, 71% of the locations of 14 frogs were found on the north shore, which lacked

TABLE 1. Mean (\pm SE) measurements of dissolved oxygen (mg/l) and water temperature ($^{\circ}$ C) at frog locations and at fixed points in ice-covered ponds, partially-frozen ponds, and lotic habitats used for overwintering by Columbia spotted frogs in north-eastern Oregon, 1999-2000.

Variable/ month	Ice-covered ponds	Partially-frozen ponds	Lotic habitats
Dissolved oxygen			
December			
Frogs	7.2 ± 0.6	4.6 ± 0.5	11.9 ± 0.4
Fixed	1.6 ± 0.6	4.0 ± 0.4	
January			
Frogs	7.0 ± 0.5	4.4 ± 0.4	11.4 ± 0.3
Fixed	2.1 ± 0.4	2.5 ± 0.4	
February			
Frogs	5.8 ± 0.7	4.7 ± 0.8	10.9 ± 0.6
Fixed	1.0 ± 0.2	2.1 ± 0.5	
Water temperature			
December			
Frogs	0.6 ± 0.1	3.7 ± 0.3	0.4 ± 0.1
Fixed	0.4 ± 0.1	1.3 ± 0.2	
January			
Frogs	0.3 ± 0.1	2.4 ± 0.3	0.4 ± 0.0
Fixed	0.2 ± 0.0	0.6 ± 0.1	
February			
Frogs	0.5 ± 0.1	2.6 ± 0.3	0.8 ± 0.1
Fixed	0.5 ± 0.1	0.6 ± 0.3	
No. of frogs at each habitat	8	8	10

emergent or submergent vegetation. In contrast, before ice formed, 97% of the locations of these 14 frogs were found on the west, east, and south shores where emergent vegetation grew.

In contrast, frogs at Crawfish Lake moved significantly shorter distances than frogs at Rainbow pond ($t = -5.64$, 71 df, $P < 0.001$) after the surface froze in 1999 (Figure 2). DO did not differ significantly between the ponds, although water temperature was significantly higher at Rainbow pond ($Z = -2.20$, $P = 0.028$). Frogs in Crawfish Lake moved to a specific overwintering location by mid-October, where they remained hidden under logs in water < 30 cm and within 50 cm of the shore for the winter. Distances traveled by frogs after ice formed were significantly less than before ice formed ($t = -5.64$, 97 df, $P < 0.001$; Figure 2).

Hollow chambers occurred under banks along the edge of two ice-covered ponds, and all 12 radio-tagged frogs in these ponds overwintered in

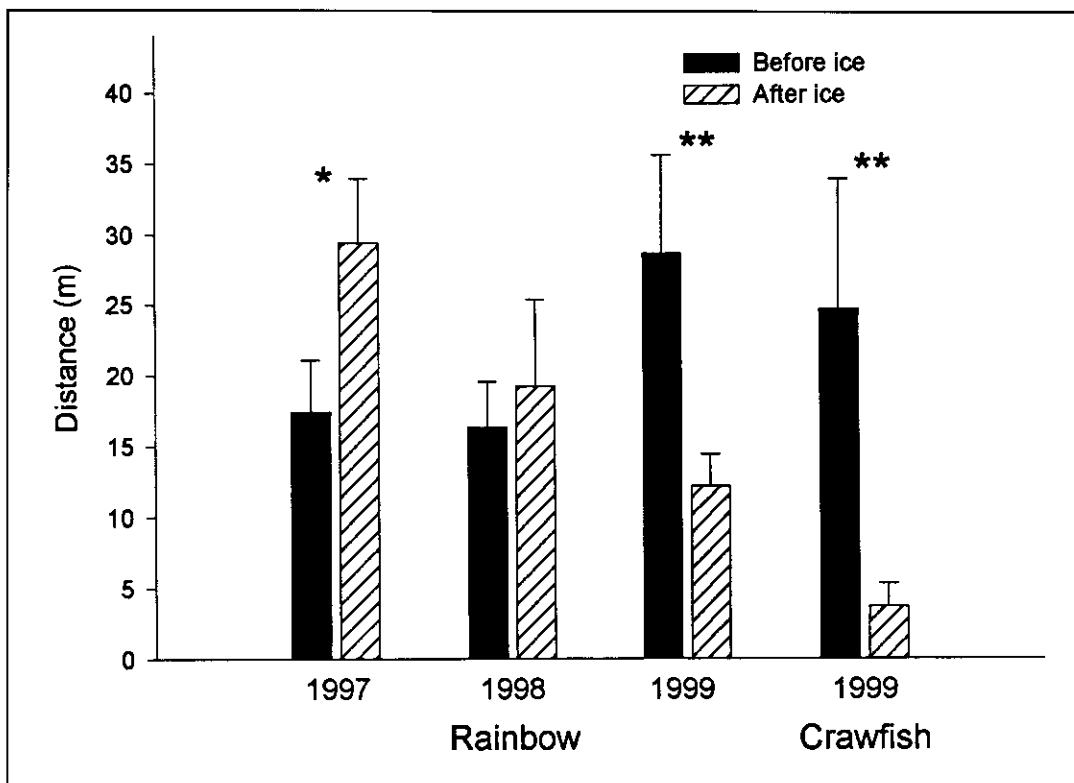


Figure 2. Mean distances (SE shown by lines) traveled by radio-tagged Columbia spotted frogs between consecutive locations before and after ice formed at Rainbow pond during three winters (1997-1998, 1998-1999, and 1999-2000) and at Crawfish Lake during one winter (1999-2000); *: $P < 0.05$, **: $P < 0.001$.

those chambers. Banks had access points through entrance tunnels 10-20 cm in diameter and at or below the water surface. Frogs first entered bank sites between 7-8 October 1997, 12-26 October 1998, and 15-23 November 1999. In 1997 and 1999, frogs remained in the banks for the entire winter. In 1998, when the water level was 25 cm higher, frogs moved between the bank sites and the pond during the winter. This higher water level resulted in the entrances to the five bank sites being submerged, thus accessible to the frogs under the ice. Five of the six frogs monitored in 1998 used more than one bank site in the winter. All frogs overwintered in situations with an air pocket over water in the situations where we could examine the chamber under the bank.

Partially-frozen Ponds

Nineteen frogs overwintered in seven ponds with partially-frozen surfaces that typically had small

areas (0.5-10 m²) of open water surrounded by ice all winter. These ponds had a mean surface area of 793 ± 28.0 m² and a mean depth of 1.2 ± 0.4 m. The majority (95-99%) of pond surfaces froze in November and thawed in March. Open water resulted from an upwelling of warmer water from springs in these otherwise frozen ponds. Frogs occurred in these areas of warmer water at > 90% of the locations after most of the surface of the ponds froze. Water was significantly warmer and DO significantly higher at frog locations than at fixed locations ($Z = -2.37$, $P = 0.018$; $Z = -2.37$, $P = 0.018$) (Table 1).

All 19 frogs were in the warmer water at the overwintering sites between 7 September and 9 November each year. Frogs stayed in the ice-free area all winter and usually traveled < 6 m from the previous location each week. Water depth at the overwinter sites ranged from 10-80 cm; distance from shore ranged from 20-600 cm.

Lotic Habitats

Twelve frogs overwintered in the Grande Ronde River and three in creeks flowing in and out of Crawfish Lake. The 12 frogs in the river overwintered under banks ($n = 9$), in a pool 1.2 m deep ($n = 1$), along the river edge ($n = 1$), and hidden in the submerged grass on the outside of a bank ($n = 1$). DO levels were high in the river throughout the winter compared to ponds (Table 1). The river surface was typically frozen between late December and mid-February, although water flowed under the ice all winter. Of the nine frogs overwintering under banks, six were under an overhanging ledge, two were between the original bank and a piece of sod that had collapsed into the river, one was in a 6-cm diameter hole that went back into the bank, and one was under a log in the bank. An air-water interface occurred at each site. Water depth at bank sites ranged from 8 to 90 cm. Frogs that overwintered under banks moved < 5 m between consecutive visits, while two of the three frogs not protected by banks moved 470 and 500 m downstream in December and January.

The flow of the two creeks where three frogs overwintered kept the water surface from freezing all winter. One site remained open to the air, and the second site was under 1.7 m of snow. All three frogs remained under logs in 25-40 cm of water and were 30-100 cm from shore while at these sites. DO levels remained high (8.5-10.0 mg/l) at both creeks all winter.

Temporary Backwaters and Seeps

Two frogs overwintered in backwaters (2 and 10 m² in size) off the main river where some flow existed during winter but none during late summer. One frog remained under a log in one backwater 18 cm deep, and the other frog was under a bank 57% of the time that it was located and in the open water (25 cm deep) during the remainder. Both frogs moved < 2 m between consecutive locations within the backwaters.

One frog moved 125 m from Rainbow pond to a seep on 11 October 1999 where it overwintered. The seep occurred under the root wad of a fall tree in a forested stand of Engelmann spruce (*Picea engelmannii*) with grass and moss ground cover and small pools of standing water. The water under the root wad never froze during the winter,

although the DO dropped below 1.0 mg/l during February within 0.5 m of the frog.

Discussion

Columbia spotted frogs in northeastern Oregon overwinter in an environment with relatively harsh conditions, where freezing of the frogs is a risk. Strategies for overwintering survival include cold-induced reductions in activity levels and metabolic rates (Boutilier et al. 1997), and avoidance of freezing and anoxic conditions. Additional risks in some aquatic environments include predation and scouring. To avoid these risks, Columbia spotted frogs overwintered under banks and in ice-covered ponds, and maintained considerable mobility in water below 3°C.

In ice-covered ponds, scouring is not present and the risk of predation (except by fish) and freezing is low, but DO may be a determinant of survival. Anaerobic metabolism is adequate for anurans to survive brief anoxic periods; they must move to areas of high oxygen content for long-term survival (Penny 1987). High mortality was observed in mountain yellow-legged frogs (*R. muscosa*) overwintering in ice-covered lakes at high elevation due to oxygen depletion (Bradford 1983). Winterkill of frogs is frequent when snow-covered ponds result in an oxygen deficient environment (Pinder et al. 1992).

In partially-frozen ponds, warm water upwellings keep a portion of the surface ice-free. This would allow light to reach the pond's primary producers, thus increasing DO levels. Frogs may prefer higher temperatures because they enhance locomotory function and maintain conditions that allow air-breathing.

Under conditions in which sufficient DO is available (i.e., normoxic), submerged frogs prefer to remain as warm as possible (Tattersall and Boutilier 1997, 1999). This behavior might explain the significantly higher water temperatures at frog locations compared to fixed locations that we observed. The ability to remain active throughout the winter allows the frogs to take advantage of favorable areas in thermally and chemically stratified bodies of water (Tattersall and Boutilier 1997, 1999).

Although some aquatic plants can continue photosynthesis under ice and snow, the seasonal dieback of aquatic plants often results in elevated detrital decomposition and a net reduction in

oxygen (Marchand 1996). Rose and Crumpton (1996) found that sites within emergent stands of macrophytes in ponds had extremely low DO concentrations and were almost continuously anoxic; the highest DO levels were in open water. In our study, movements of frogs and their preferences for the north shore after ice formed at Rainbow may represent a response to higher levels of DO because aquatic vegetation was absent on the north shore.

Alternatively, lack of movement by frogs at Crawfish Lake after ice formed (with DO levels equivalent to those at Rainbow pond) may have been a response to predation risk by eastern brook trout (*Salvelinus fontinalis*). Emery et al. (1972) found frogs in splake (*Salvelinus fontinalis* X *S. namaycush*) and rainbow trout (*Oncorhynchus mykiss*) stomachs in ponds in the winter. In contrast, frogs at Rainbow, which lacked both fish as predators and logs as cover, were not located in specific overwintering sites.

Frog preference for shallow water near the shore in ice-covered ponds could be a response to higher levels of DO that occur at the ice-water interface (Boutilier et al. 1997) or a means of avoiding predatory fish at Crawfish Lake. In addition, lakes may be markedly hypoxic at depths of 2-4 m (Boutilier et al. 1997).

Unfrozen water and an air pocket were present in the bank sites that we could access. Bank sites

may allow frogs to overwinter in ponds where DO levels in open water fall below 2.0 mg/l for extended periods.

In lotic habitats, where DO levels and freezing are less likely, unpredictability of flow and predators may present more substantial risks to overwintering frogs. Frogs under banks along rivers avoid both scouring and predation.

Different overwintering strategies in Columbia spotted frogs appear to result from tradeoffs among factors that may compromise survival at different sites. Our data, which focused on the potential risks posed by oxygen limitation and freezing, indicate that selected sites generally minimized the risks of both. Oxygen limitation may be a prominent risk factor at high elevation sites because these typically are capped by ice. Additional information is still needed on the submerged DO levels that this species can tolerate during the winter, the exact nature of bank sites, and the extent that predation plays in the selection of overwintering sites.

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