United States Department of Agriculture

Forest Service

Pacific Northwest Research Station

General Technical Report
PNW-GTR-640
July 2005

Ecology of the Columbia Spotted Frog in Northeastern Oregon

Evelyn L. Bull

Author

Evelyn L. Bull is a research wildlife biologist, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850.

Cover photo

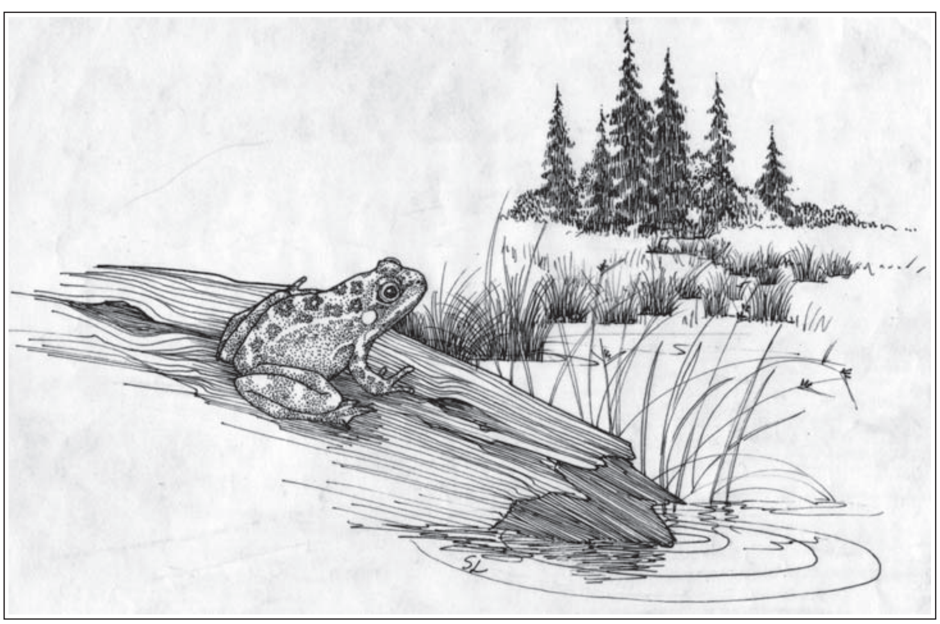
Columbia spotted frogs at an oviposition site with an egg mass present (lower center of photo). All photos by Evelyn Bull.

Abstract

Bull, Evelyn L. 2005. Ecology of the Columbia spotted frog in northeastern Oregon. Gen. Tech. Rep. PNW-GTR-640. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 46 p.

The Columbia spotted frog (*Rana luteiventris*) is one of several amphibians in the Western United States experiencing population declines. The breeding, post-breeding, and overwintering habitat and ecology of this species were investigated in 10 study sites in northeastern Oregon from 1997 through 2004. A variety of habitats with permanent water were used as breeding sites and as postbreeding habitat during the summer. Ice-covered ponds, warm springs, rivers, and seeps in forested habitats were used for overwintering. Diet consisted of a wide variety of mollusks and arthropods with beetles, ants, wasps, and flies composing more than 50 percent. Population size was as high as 135 females at one site, and ratios of males to females ranged from 1.0 to 2.8. The oldest male and female were 9.7 and 8.7 years old, respectively, based on skeletochronology. Males reached sexual maturity at 1 year 9 months after metamorphosis and most females at 2 years 9 months after metamorphosis. One female laid eggs in up to 3 consecutive years. Size (snout-vent length) was not a good indicator of age in frogs older than 2 years. Long-term monitoring is necessary to determine the effects of a variety of disturbance factors and chytrid fungus that could influence spotted frog populations in northeastern Oregon.

Keywords: Columbia spotted frog, *Rana luteiventris*, northeastern Oregon, amphibian ecology.



Susan Lindstedt

Contents

Introduction

The Columbia spotted frog (*Rana luteiventris*) is one of several amphibians in the Western United States experiencing population declines (Reaser and Pilliod 2005, Wente et al., in press) and is classified as imperiled and vulnerable to extirpation and extinction (S2 and S3) in Oregon by NatureServe (2005). Amphibians are good indicators of overall health in forest and rangeland ecosystems because of their dependence on water for reproduction, their unshelled eggs, and their permeable skin, all of which make them particularly sensitive to water-soluble environmental toxins. The rapidity and magnitude of population declines observed in some amphibians in the Western United States (Corn 2000) emphasize the need for baseline ecological data on distribution, abundance, habitat use, demographics, and an assessment of possible threats to populations and the need to monitor populations. Increasing incidence and intensity of fires and other disturbance agents (floods, drought, introduction of fish, habitat alteration, livestock grazing, noxious weed control) in northeastern Oregon may threaten these animals and the integrity of their aquatic habitats.

The information contained in this paper, unless otherwise referenced, was obtained during the course of six studies conducted from 1997 through 2004 in northeastern Oregon. Research was carried out in Union, Baker, Wallowa, Umatilla, and Grant Counties on the Wallowa-Whitman, Umatilla, and Malheur National Forests and on private land (fig. 1). For the purpose of this paper, northeastern Oregon encompasses the Blue, Elkhorn, and Wallowa Mountains. Sites were surveyed for Columbia spotted frogs at elevations that ranged from 720 to 2972 m, and therefore, climatic conditions were variable. Snow (>2 m deep) and freezing temperatures typically occurred at the high-elevation sites from October through May or June. At the low-elevation sites, ponds were typically frozen from November through mid-March, and snow depths varied from zero to 0.5 m. High river flows typically occurred anytime between April and May, and ice flows could occur from January through March. Summer temperatures seldom exceeded 27 °C at the high-elevation sites and 35 °C at the low-elevation sites. Winter temperatures were typically below freezing and as low as -30 °C. Average annual precipitation ranged from 31 to 43 cm in La Grande and from 27 to 62 cm in Wallowa from 1997 through 2004 (Oregon Climate Service, n.d.). The majority of the study sites were in coniferous forest ecosystems with a range of gently sloping terrain to steeply walled canyons.

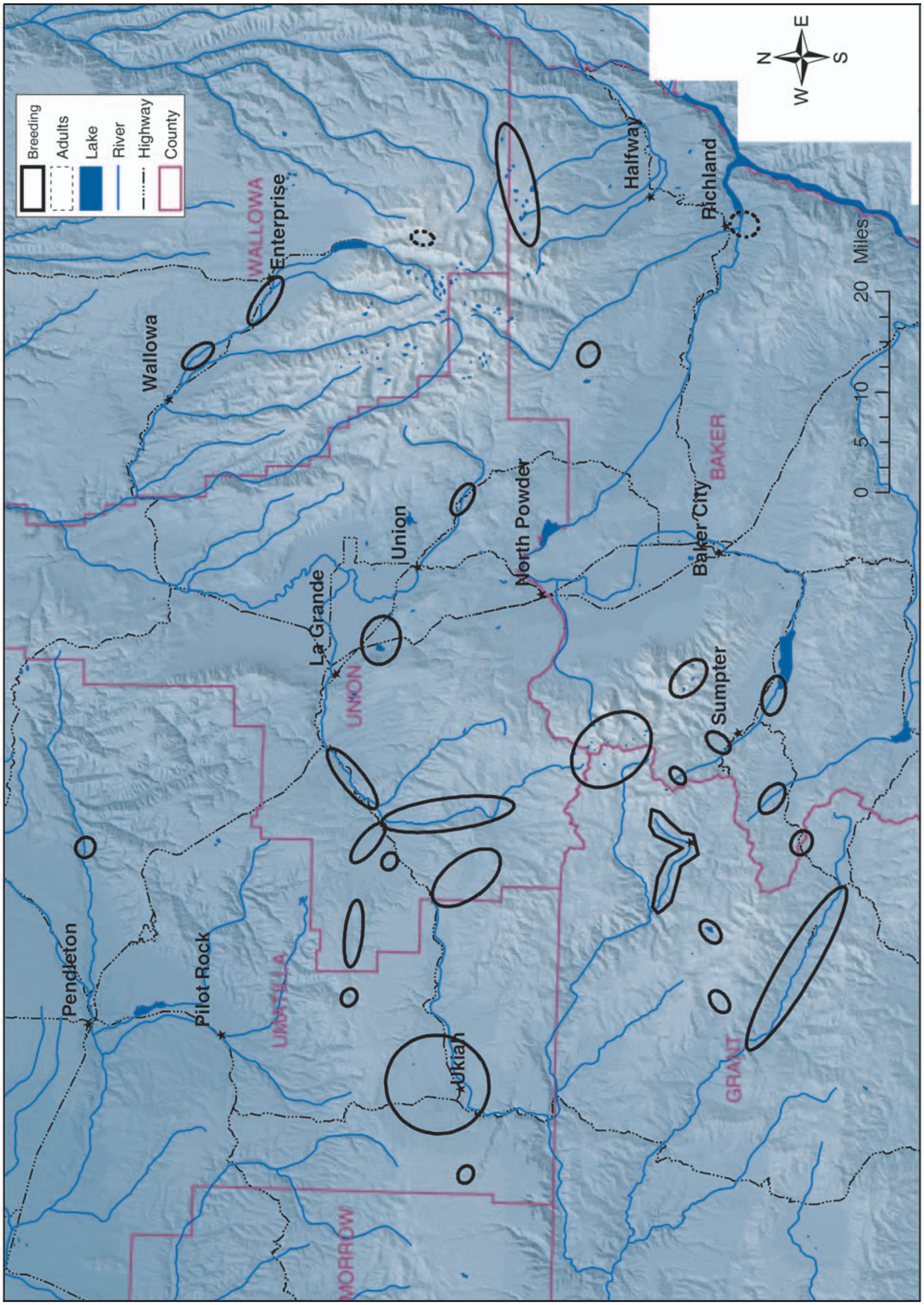


Figure 1—Columbia spotted frog study sites in northeastern Oregon.

Distribution and Genetic Diversity

Overall distribution of the Columbia spotted frog ranges from extreme southeastern Alaska south through British Columbia and Alberta, western Montana and Wyoming, northern and central Idaho, northeastern Oregon, and eastern Washington, with isolated populations in northern Utah, southeastern Oregon, and southwestern Idaho (Reaser and Pilliod 2005). During this study, I found Columbia spotted frogs throughout northeastern Oregon in the following major watersheds: Grande Ronde River, Eagle Creek, John Day River, Powder River, Malheur River, and Wallowa River. Frogs occurred at elevations as low as 720 m in the Powder River drainage near Richland and as high as 2250 m at Roger Lake in the Wallowa Mountains and 2220 m at Dutch Flat Lake in the Elkhorn Mountains.

Green et al. (1996) used genetic differences to differentiate the Columbia spotted frog from the Oregon spotted frog (*R. pretiosa*). The Oregon spotted frog occurs from southern British Columbia to southern Oregon and to the west of the range of the Columbia spotted frog. In addition, Green et al. (1996) identified four primary genetic subunits in the current species complex: Provo River, Great Basin, Tule Valley, and northern populations. Frogs in northeastern Oregon constitute a portion of the Great Basin populations.

Because of these geographic differences and concerns about genetic flow, levels of genetic diversity and gene flow were assessed among six local populations in this study with microsatellite DNA testing (Blouin 2001). These six populations appeared to be part of a healthy metapopulation and showed no evidence of recent servere population declines. The nearest populations were the most genetically similar with a rate of gene flow among populations of around four migrants per generation.

Distinguishing Characteristics

Coloration and Size

The dorsal base color of adult Columbia spotted frogs in northeastern Oregon may be brown, reddish brown, olive green, or tan with irregular-shaped black spots with light centers based on captures of over 2,000 frogs (fig. 2A). The ventral surface of the frogs is cream colored with a yellow, orange, salmon-colored, or gray pigment on the hind legs, lower abdomen, or upper abdomen to the throat (figs. 2B and C). A well-defined white or yellowish stripe runs from the tip of the snout laterally underneath the eye to just above the front limb. The hind legs are fairly short relative to the body length, and there is extensive webbing between the toes on the hind feet. The eyes are upturned.

Figure 2—Color variation on the dorsal (A) and ventral surface (B and C) of Columbia spotted frogs in northeastern Oregon.

Males in this area may grow to 80 mm snout-to-vent length (SVL) and weigh as much as 47 g as an adult. Females may grow to 100 mm SVL and weigh as much as 103 g when gravid. Eggs make up 26 to 38 percent (mean = 31.4 percent, n = 7) of the female's body weight just prior to egg laying, based on body weight immediately after egg deposition. In Idaho, Engle (2001) reported that reproductive females lost 25 to 35 percent of body mass during egg deposition.

Hatchlings are about 7 to 9 mm in total length and are a uniform dark brown with external gills. Larvae (tadpoles) are dark brown to black dorsally, silver or cream colored ventrally with flecks of metallic gold, and lack external gills. The tail fin extends onto about the posterior one-third of the body length (Leonard and Bull 2005). Larvae may reach 45 to 80 mm total length at high-elevation sites and up to 100 mm at low-elevation sites.

Vocalizations

The call is a quiet series of rapid clucking notes and is typically given only during the short breeding season. The call may be given both above and below the surface of the water and is normally heard during diurnal hours. Reaser and Pilliod (2005) also report that captured adults may give a "deep clicking" release call, and captured juveniles and adults may emit a piercing, high-pitched scream.

Breeding

Breeding biology of Columbia spotted frogs was determined from observations at 152 breeding sites in Union, Baker, Wallowa, Grant, and Umatilla Counties by using methods described in Bull and Hayes (2000) and Bull and Marx (2002). In addition, intensive monitoring of breeding ponds in 10 study sites (table 1) occurred each spring from 1997 through 2004 to obtain information on timing of egg laying, time to hatch, and larval development. Radio telemetry was used to monitor activity of individual frogs.

Phenology

Breeding was observed as early as March at the warmest sites and the lowest elevations (922 m) and as late as June at the highest elevation site (2220 m). Males were observed at oviposition sites 1 to 12 days before eggs were deposited. Pairs in amplexus (mating behavior in amphibians) were observed 1 to 9 days before eggs were deposited. One radio-tagged female was in amplexus at her overwintering site in a small pool (<50 cm across) 125 m from the breeding pond on 21 April, and eggs were first detected at the pond on 3 May.

Table 1—Ponds used to study the Columbia spotted frog in northeastern Oregon, 1998-2004

				Factors studied				
Watershed/ study site	**Number of ponds**	**Pond size**	**Eleva-tion**	**Breed-ing**	**Post-age**	**Winter breeding**	**Habits**	**Diet**
		m²	*m*					
Wallowa River watershed								
Wallowa	8	100- 10 000	935	x	x			
Grande Ronde watershed								
Gun	1	887	924	x	x		x	x
Starkey	1	41 000	1001	x	x	x	x	x
Cow Camp	1	1000	1001	x	x		x	x
Whitehorse	1	30 000	1188	x	x		x	
Cooper	1	630	1240	x		x		
Tailings	8	86-264	1380	x	x	x	x	x
Rainbow	1	29 000	1810	x	x	x	x	x
North Fork John Day watershed								
Crawfish Lake	1	126 000	2040	x	x		x	
Powder River watershed								
Anthony Lakes	6	4000-40 000	2130	x		x		

Note: One of the seven lakes at Anthony Lakes drains into the Grande Ronde watershed.

Breeding phenology was remarkably consistent at sites in Wallowa County that were fed by warm springs. At one site, eggs were initially deposited at one of these ponds between 22 and 31 March each year from 1997 through 2004. Eggs were deposited at another site during a 12-day period.

The timing of egg laying was largely a function of water temperature at the oviposition site (Bull and Shepherd 2003), but other factors likely triggered movement of frogs to the oviposition site. Potential contributing factors could be photoperiod or water temperature at overwintering sites. Mean daily water temperature on the day eggs were deposited ranged from 7.6 to 16.0 °C with an average of 9.6 °C at 16 ponds. Maximum water temperature on the day eggs were deposited ranged from 9.8 to 20.2 °C and averaged 15.5 °C. These temperatures were above the minimum embryonic thermal temperature (6 °C) reported for Columbia spotted frogs by Johnson (1965). The minimum water temperature the night following egg deposition ranged from 2.5 to 12.9 °C and averaged 5.6 °C, although embryos are able to withstand cold temperatures (1 °C) for several hours (Licht 1971, Sype 1975). Eggs were typically deposited in the morning and early afternoon, which provided warmer temperatures for the newly fertilized eggs and allowed embryos to undergo several hours of rapid development before being exposed to cold overnight temperatures. Eggs were not deposited on cold days when the maximum water temperature was below 9.4 °C.

Eggs

Eggs are deposited in single globular masses that range from about 8 to 18 cm in diameter. Several females will lay egg masses in one location, some of which are at historical oviposition sites. In one study site, the same oviposition sites have been used at least three decades. Communal egg laying may be advantageous because water temperatures within a cluster of ranid egg masses may be higher than the surrounding water (Herreid and Kinney 1967, Licht 1971, Sype 1975). I did not count numbers of eggs, but egg masses in Montana contain 308 to 2,403 eggs per mass (Maxell 2000). Each ovum is black on the animal pole, which faces up, and light colored on the yolk-laden vegetal pole facing down. Each ovum is about 2 mm in diameter (Johnson 1965) with the surrounding jelly coat measuring about 10 to 12 mm in diameter. Total number of egg masses was correlated (Pearson's correlation coefficient) with water surface area of the breeding pond ($R = 0.49$, $P < 0.01$, $n = 144$).

Hatching

Hatching occurred 12 to 21 days after deposition at breeding ponds. Mean and maximum daily water temperatures were significantly correlated with number of days to hatching (Bull and Shepherd 2003). Water temperature (at hourly recordings) did not drop below 1 °C at night during this period. Larvae stayed within the gelatinous mass for up to a week.

Larval Development

One to 2 weeks after hatching, larvae are agile swimmers. Larvae remained in habitats with abundant aquatic or emergent vegetation or coarse woody debris, which provided rich food supplies (algae, etc.) and protection from predators. Metamorphosis occurred between July at the lower elevations and September at the higher elevations, with timing also being influenced by weather and water temperature. Recently metamorphosed frogs were found the first week in August in the river up to 300 m from breeding ponds at the low-elevation sites and were found in September in seeps and temporary pools in a subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forest 200 to 300 m from Rainbow Pond. In the Bighorn Crags in Idaho, Pilliod et al. (2002) observed mass movements of recently metamorphosed frogs from a breeding pond to overwintering sites in September and October.

At one pond along the Grande Ronde River, metamorphs and recently metamorphosed frogs were netted and marked once each week from August through early October 2000. Only tadpoles were found the first week in August in this pond. A total of 277 metamorphs were marked (toe clipped) in August, and 84 were recaptured on subsequent visits. The peak number of 92 recently metamorphosed frogs occurred on 30 August when no tadpoles were found, so metamorphosis was essentially completed by the end of August at this particular pond. The number of recently metamorphosed frogs in the pond steadily decreased from late August until early October when only eight were netted. Some of the recently metamorphosed frogs had traveled to the river 50 m away where they were recaptured, and others were probably preyed upon by the abundant garter snakes (*Thamnophis* spp.) in the pond.

Habitat

Habitat use of Columbia spotted frogs was determined by locating 152 breeding sites in Union, Baker, Wallowa, Grant, and Umatilla Counties from 1997 through 2004 by using methods described in Bull and Hayes (2000) and Bull and Marx (2002). Habitat conditions during the postbreeding and overwintering periods were determined by monitoring radio-tagged frogs at multiple sites (table 1) by using methods described in Bull and Hayes (2001) and Bull and Hayes (2002), respectively.

Breeding

A wide range of water bodies serve as breeding sites for Columbia spotted frogs, although most have permanent water or retain water through metamorphosis of larvae (figs. 3 and 4). Breeding has been observed in ponds, lakes, reservoirs, oxbows in rivers and creeks, and quarries. Ponds created for livestock watering, for irrigation and settlement ponds, and by mine tailings and beavers (*Castor canadensis*) have all been used for breeding by Columbia spotted frogs in northeastern Oregon. Egg masses were found in the middle of slowly flowing creeks in only three situations. Irrigation reservoirs that exhibited a large drop in water depth in the summer rarely contained spotted frog eggs or adults, presumably because of the loss of aquatic habitat. Disturbance factors that resulted in open aquatic habitat were common at breeding sites (fig. 4).

Eggs were typically deposited in shallow, near-shore regions of water bodies with low emergent vegetation. Water depth at oviposition sites averaged 10.6 cm (SD = 5.1). Eggs were deposited an average of 117.5 cm (SD = 138.4) from the

A

B

Figure 3—Columbia spotted frogs occur in a variety of landscapes ranging from lower elevation riparian habitats dominated by grasses (A) to isolated high-elevation lakes surrounded by coniferous forests (B) in northeastern Oregon.

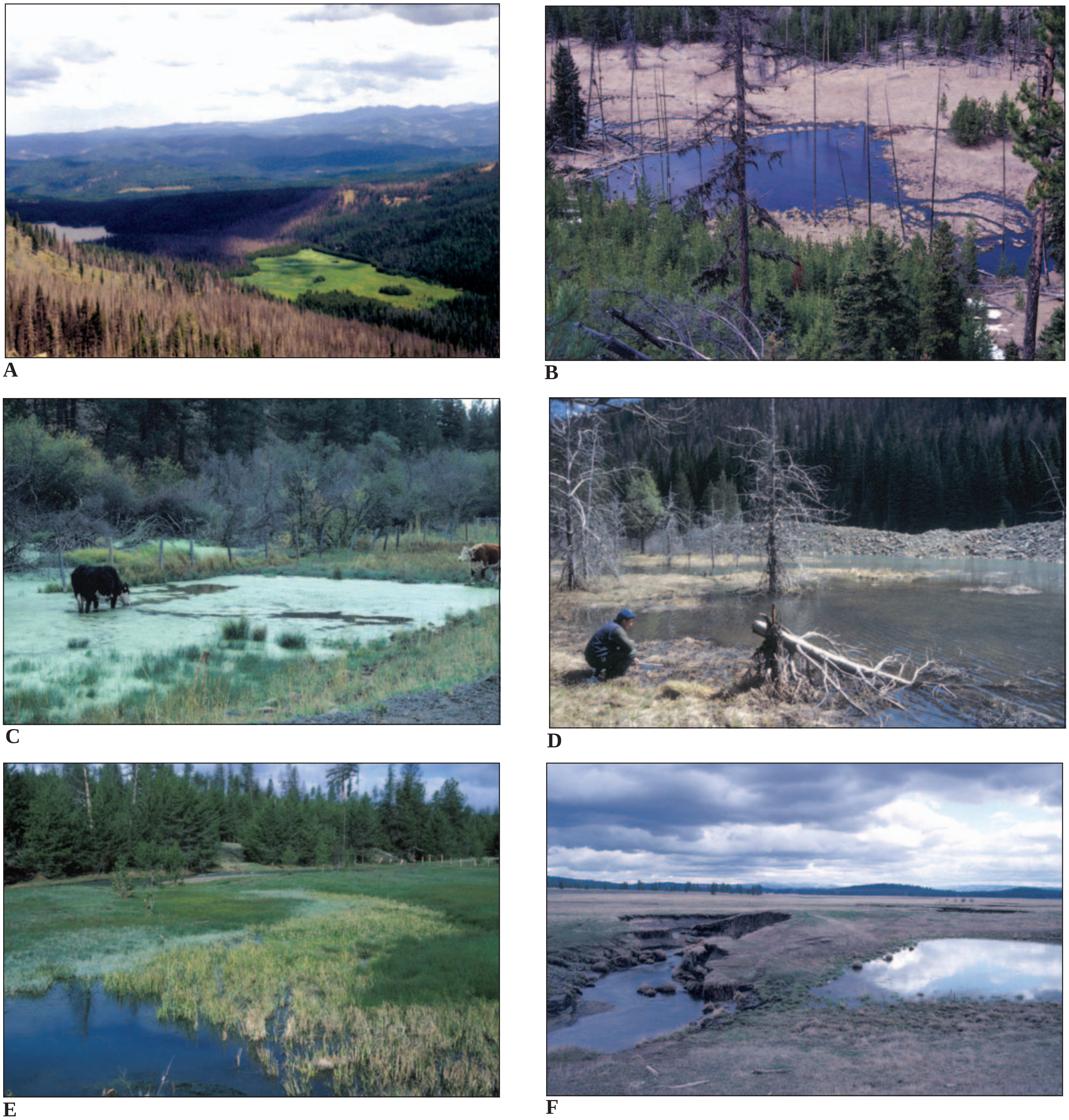


Figure 4—Breeding ponds of the Columbia spotted frog in northeastern Oregon range from abandoned reservoirs (A), beaver ponds (B), isolated ponds not adjacent to rivers (C), mine tailing ponds (D), oxbows along creeks and rivers (E), to holding basins created for watering livestock (F).

shore. The best indicators of abundance of spotted frog egg masses at high-elevation lakes (above 1800 m) were lake size and elevation (negative effects, -), and the amount of shore on the north side with shallow water and emergent plants (positive effects, +) (Bull and Marx 2002). The best indicators of abundance for larvae of spotted frogs at high-elevation lakes were the amount of north shore with shallow water and emergent plants (+), the amount of area with emergent vegetation (-), pH (-), and the amount of coarse woody debris within 3 m of the oviposition site (-) (Bull and Marx 2002). Shallow water on the north shore provided warm water for rapid embryonic and larval development. Typically, open water first appeared on the north shore as lake ice began to melt, and egg laying often commenced with ice still covering a portion of the pond or lake. At lakes above 1800 m, sedges (*Carex* spp.) were the predominant vegetation at oviposition sites. Breeding ponds at elevations below 1800 m were dominated by duckweed (*Lemna minor* L.), pondweed (*Potamogeton* sp.), and buttercup (*Ranunculus* sp.). Emergent and aquatic vegetation, benthic sediment, and coarse woody debris were all used by larvae as cover from predators.

In small ponds less than 300 m^2, eggs were typically deposited at one location in the pond. In larger ponds, egg masses were typically deposited in two to six locations or oviposition sites. Usually egg masses were deposited in the same locations from year to year, although there was variation with some oviposition sites being used more extensively in some years. The location of oviposition sites also changed in years when the historical oviposition site was above water or under deep water owing to fluctuations in the water level.

Postbreeding

Habitat used after breeding differs because some radio-tagged adult frogs (1) remained in the breeding pond for the entire summer, (2) left the breeding pond shortly after breeding, or (3) left the breeding pond in midsummer (Bull and Hayes 2001). Radio-tagged frogs that left the breeding ponds were typically in areas associated with other ponds or rivers in proximity (like the Tailings and Wallowa sites). Frogs in ponds that were isolated (>1000 m) from other bodies of water (like Rainbow Pond) remained there for the entire year, perhaps because the opportunity to move to other aquatic sites was limited or not available.

The behavior of radio-tagged frogs during the summer differed at different elevations. Radio-tagged frogs at sites in the Grande Ronde watershed at 1800 m or less were typically visible on the water surface or shore when located in summer and were actively foraging. At Anthony Lakes at 2130 m elevation, radio-tagged male frogs were typically not seen on the water or land surface but were buried more than 5 cm in mud under the water in July and August when located; females were typically in the water away from the shore. The behavior at Anthony Lakes was not consistent with that observed at other sites in this study or at high-elevation sites in Idaho (Pilliod et al. 2002).

Each fall and spring, juvenile frogs were found at locations where adults were found in addition to smaller aquatic sites like seeps and ephemeral ponds. Juvenile frogs used habitats similar to those of adults in Idaho (Pilliod et al. 2002), whereas Cuellar (1994) found juveniles in small grassy ponds and sloughs but adults usually in large ponds.

Overwintering

Of 66 frogs monitored in the fall and winter from 1997 through 1999, 44 percent overwintered in ice-covered ponds, 29 percent in partially frozen ponds, 23 percent in lotic (flowing water) habitats, 3 percent in backwaters, and 1 percent in seeps (Bull and Hayes 2002). Frogs in ice-covered ponds remained active under the ice during winter and were found at sites with levels of dissolved oxygen significantly higher than levels at fixed points in the ponds. Frogs in partially frozen ponds were found in warmer portions of the pond water at more than 90 percent of the locations. The open water where frogs were found resulted from an upwelling of warmer water from springs. Frogs were seen on the water surface at the springs in February during sunny days when air temperature was about 10 °C and the rest of the pond was frozen. Frogs in lotic habitats remained under banks, under logs, in deep pools, or under ice at the edge of the river. Frogs in backwaters and seeps overwintered under logs or banks. Overwintering sites under banks typically contained an air-water interface, as determined by excavating some sites the next spring.

At Crawfish Lake, three of five radio-tagged frogs left the lake and overwintered in the creeks flowing into and out of it. Frog migration into the creeks resulted in frogs being in water with a higher dissolved oxygen rate and having access to the water surface for part of the winter. Pilliod et al. (2002) found this species using inlets and outlets at lakes for overwintering in Idaho as well.

Movements

Movements of 43 radio-tagged frogs were recorded at six ponds in the Grande Ronde watershed in 1998 (n = 22), one breeding pond along the Wallowa River in 2002 (n = 6), and at four lakes at Anthony Lakes in 2001 (n = 15) during the breeding and postbreeding periods. Sixty-six radio-tagged frogs were tracked to their overwintering sites in the winters of 1997, 1998, and 1999. I located frogs every 1 to 3 weeks and used a global positioning system to record their location and the distance from their previously recorded location. Additional movements of frogs were determined from recaptures of frogs with passive integrated transponders (PIT-tags) inserted under the skin on the dorsal surface of frogs >40 mm SVL (as described by Prentice et al. 1990). Frogs were captured with dip nets in all breeding ponds each spring for 1 to 5 days during oviposition. The first study was initiated in 1997, and additional breeding ponds were located each year. Frogs were also captured during the first 2 weeks in August from 1999 through 2003. The primary emphasis on capturing frogs was during the breeding season because many mature frogs leave the ponds after breeding (Bull and Hayes 2001). In August, the breeding ponds were searched as well as stretches of river and ponds within 500 m of breeding sites, as previous studies demonstrated that Columbia spotted frogs moved that far from breeding ponds to rivers or other ponds during the summer (Bull and Hayes 2001).

Captured frogs were sexed, measured (SVL), and weighed (g). Precision of measurements was 3 to 5 mm for SVL and 2 g for weight because measurements taken by different people result in slightly different readings. The maturity of individuals was estimated based on the presence of dark nuptial pads on the thumb in males (Augert and Joly 1993) and on distended abdomens in gravid females. I believe breeding in these study sites occurred prior to frog foraging (and thus the distended abdomens were from eggs rather than ingested prey) because (1) insect activity was low owing to cold temperatures, and (2) we found no contents in the stomachs when we attempted to collect diet samples.

Breeding and Site Fidelity

The majority of frogs returned to the same breeding pond each year. I recaptured 54 to 60 percent of the males and 34 to 50 percent of the females at the same breeding pond in a subsequent year at three of the study sites (Crawfish Lake, Rainbow, Tailings) (table 2). These rates of recapture are similar to the 66 percent of males and 56 percent of females recaptured at the same breeding sites in the Bighorn Crags in Idaho (Pilliod et al. 2002).

Although the majority of frogs returned to the same oviposition site each year, I found some frogs used a different pond in areas where multiple breeding sites occurred. In the Tailings study site there are eight breeding ponds along a 1.2-km stretch of the Grande Ronde River. Twenty-eight percent of 133 PIT-tagged males and 11 percent of 28 females used more than one breeding pond in subsequent years, and five of these males used three breeding sites. The distance between

Table 2—Recapture of PIT-tagged Columbia spotted frogs in six study sites in northeastern Oregon, 1998-2004

			Years after tagging that frog was last captured						
Site	**Number of tagged frogs**	**Years monitored**	**1**	**2**	**3**	**4**	**5**	**6**	**Total frogs recaptured**
			Percentage of tagged frogs recaptured						
Wallowa		2000-2003							
Males	207		5	1					6
Females	52		0	0					0
Gun		1999-2004							
Males	120		32	4	5	2	1		44
Females	71		17	1					18
Starkey		1998-2004							
Males	405		18	7	1	1			27
Females	226		8	3	<1				11
Tailings		1998-2004							
Males	244		22	16	13	5	2	<1	58
Females	133		23	9	2	1			35
Rainbow		1998-2004							
Males	490		18	16	11	6	3	<1	54
Females	232		21	9	4	<1			34
Crawfish		1999-2004							
Males	62		23	18	16	3			60
Females	12		25	25					50

PIT = passive integrated transponders.

breeding sites used by individual males ranged from 80 to 1200 m and averaged 390 m. Three females used breeding sites 80, 140, and 180 m apart in different years.

Frogs either never left the breeding site, returned to the breeding site in August and September, returned in spring just prior to egg laying, or moved part of the way back to the breeding site in fall. One female traveled 0.9 km up the Grande Ronde River in September to overwinter in the river 300 m downslope from a breeding pond. One female traveled 2.3 km down the Grande Ronde River in September. A gravid female in the Grande Ronde River traveled 500 m downstream in January toward a breeding site where eggs were deposited in April. Gravid females were found traveling to two breeding sites along creeks 15 to 150 m away from the overwintering site several days after egg laying had started. Females traveled longer distances from the breeding ponds to summer habitat and overwintering sites than males, which was also reported in the Bighorn Crags in Idaho where a male traveled 424 m and a female traveled 1033 m from a breeding site (Pilliod et al. 2002). Annual movements to and from breeding sites ranged from 40 to 550 m in south-central Montana (Hollenbeck 1974).

Radio-tagged male frogs at Crawfish Lake and Rainbow Pond moved 150 to 200 m from overwintering sites to breeding sites up to 20 days before egg laying occurred. One male that overwintered in a pond 150 m from Rainbow Pond traveled in runoff water under snow and through a culvert to return to the ice-covered Rainbow Pond and arrived 2 weeks prior to egg laying. A male that overwintered in a creek flowing into Crawfish Lake returned to the oviposition site under the ice 10 days prior to egg laying.

Rainbow was the only completely isolated pond in this study with the nearest riparian habit 0.8 km away. A 93 mm (SVL) female and a 56 mm male were originally captured at Rainbow Pond and were recaptured 2 and 3 years later in one of the Tailings ponds 4 km away. Funk et al. (2005a) suggested that gene flow in the Columbia spotted frog was restricted by ridges and elevation, and that populations generally included more than a single pond except for very isolated ponds.

Postbreeding

Of 22 radio-tagged frogs monitored for more than 28 days at six ponds in the Grande Ronde watershed, 11 remained in the breeding pond for the summer and 11 moved 60 to 560 m to other ponds or the river. All marked frogs spent the summer in Rainbow Pond, which is isolated from other permanent water bodies. Along the Wallowa River, all six radio-tagged frogs left the breeding pond and moved <180 m to small creeks or other permanent ponds. At Anthony Lakes, 14 of 15 frogs remained in the same breeding ponds for the summer, typically traveling <200 m between consecutive locations at 2- to 3-week intervals. Only one female traveled as far as 350 m in July down a creek bed to a second lake where she remained until September when the transmitter was removed. Frogs seldom left large bodies of water (>1 ha) during the summer, perhaps because food resources were more available, and predators were less concentrated than in the small ponds along the Grande Ronde River. In northwestern Montana, high juvenile dispersal rates over long distances with large elevation gains were supported by evidence of high gene flow (Funk et al. 2005b).

Overwintering

Frogs moved to overwintering sites between late August and mid-October. Of 28 frogs (both males and females) radio tagged in ponds in August and early September, 27 overwintered in the same ponds. Of 24 frogs (7 males and 17 females) radio tagged in the river, 9 (females) moved to a pond and 15 (7 males and 8 females) overwintered in the river. The maximum distance traveled to an overwintering site was 2.3 km.

Rainbow Pond is a large pond where all radio-tagged frogs remained for the summer. For overwintering, 5 of 26 radio-tagged frogs moved to sites outside of Rainbow Pond: 1 of 5 frogs moved in 1997, 2 of 6 frogs in 1999, and 2 of 15 frogs in 2000. Movements away from Rainbow Pond included a male moving 150 m downslope to a small permanent pond (8 m diameter); a male moving about 400 m along an old mining ditch with water and overwintering under an adjacent bank; and two females and one male moving about 125 m over land to a spruce bog that contained seeps where the frogs overwintered. All frog movements away from Rainbow Pond in the different years were between mid-September and mid-October, and rain typically preceded movements.

Food Habits

Diet was determined from 296 diet samples collected from frogs every 2 weeks from June through mid-October 2002 in ponds and rivers at four study sites (table 1); for details about methods, see Bull (2003). A diet sample was obtained by flushing the stomach of a frog with a catheter attached to a 65-cc syring inserted through the mouth and esophagus of the frog (Legler and Sullivan 1979, Whitaker et al. 1983). Food fragments were identified to order or family and categorized into five size classes (1 to 4.5, 5 to 9.5, 10 to 14.5, 15 to 19.5, 20 to 24.5, and ≥25 mm in length). During the same period that frog diet samples were collected, available aerial invertebrates were sampled with sticky traps, and available aquatic invertebrates were sampled with dip nets at both pond and river habitats at the study sites.

Diet

The Columbia spotted frog is a generalist taking a wide variety of prey within the size range that it can catch and ingest. Larger invertebrates were consumed by frogs in a higher percentage than was found in samples of available invertebrates captured at the study sites. This finding suggests that frogs selected larger prey, which would maximize caloric return for capture effort. In addition to mollusks and arthropods, prey items of Columbia spotted frogs included nine orders of insects, although only three orders represented ≥10 percent of the diet: beetles (21 percent), ants/wasps (21 percent), and flies (10 percent) (table 3). Prey items were primarily in the smaller size classes: 40 percent were 1 to 4.5 mm, 29 percent were 5 to 9.5 mm, 21 percent were 10 to 14.5 mm, and 10 percent were ≥15 mm. However, more than 60 percent of the available prey was 1 to 4.5 mm in size. Composition of diet differed between habitats (ponds and rivers; table 3) and among frog

Table 3—Prey items identified to order or family that were found in diet samples of Columbia spotted frogs captured in ponds and rivers in northeastern Oregon, 2002

Phylum/class/order/family	Pond	River	Total
Mollusca (mollusks)	9	—	9
Gastropoda (snails)	15	9	24
Arthropoda (arthropods)			
Crustacea (crustaceans)	—	6	6
Amphipoda (scuds)	49	1	50
Arachnida (arachnids)	—	1	1
Acari (mites and ticks)	14	—	14
Araneae (spiders)	51	63	114
Insecta (insects)			
Ephemeroptera (mayflies)	22	3	25
Odonata (dragonflies and damselflies)	42	2	44
Orthoptera (grasshoppers)	9	16	25
Plecoptera (stoneflies)	1	10	11
Hemiptera (true bugs)	5	20	27
Corixidae (water boatmen)	8	7	15
Gerridae (water striders)	15	26	41
Notonectidae (backswimmers)	9	1	10
Homoptera (aphids, scales, hoppers)	1	1	2
Aphididae (aphids)	36	29	65
Coleoptera (beetles)	96	85	181
Carabidae (ground beetles)	18	43	61
Curculionidae (snout beetles)	3	12	15
Elateridae (click beetles)	3	2	5
Hydrophilidae (water scavenger beetles)	—	15	15
Trichoptera (caddisflies)	11	6	17
Lepidoptera (butterflies and moths)	33	23	56
Diptera (flies)	68	66	134
Hymenoptera (ants, bees, wasps)	9	9	18
Formicidae (ants)	99	52	151
Vespidae (wasps)	71	29	100
Unknown and other	35	24	63
Total			1,299

Note: Prey items composing ≤1 percent of the diet are not listed. Invertebrates identified to family are not included in the totals for the order.

— = none found.

size classes (<56, 56-70, >70 mm) but not by sex. A higher proportion of stoneflies, water striders, and beetles occurred in diet samples from rivers, and a higher proportion of scuds, mayflies, dragonflies, damselflies, and ants/wasps occurred in diet samples from ponds. Composition of diet differed among study sites and changed over the summer with an increase in true bugs and ants/wasps and a decrease in spiders and beetles (fig. 5). Two recently metamorphosed Columbia spotted frogs were found in the stomachs of female Columbia spotted frogs indicating that cannibalism occurs in this species, which was also reported in this species by Pilliod (1999). Columbia spotted frogs were observed feeding on toadlets at Lilypad Lake (Pearl 2000) and on a Pacific treefrog (*Pseudacris regilla*) metamorph in this study.

Diet samples contained a mean of 4.4 prey items (SD = 4.04) with a range of no identifiable prey to 28 prey items per sample. Number of prey items did not differ by sex of frog, water type, month, or study site, although frogs >70 mm SVL ate more prey items (mean = 5.1 items) than frogs 56 to 70 mm SVL (mean = 3.8 items). Male frogs captured along rivers contained diet samples with a greater biomass than males captured at ponds, which may be a primary reason that some frogs inhabit rivers.

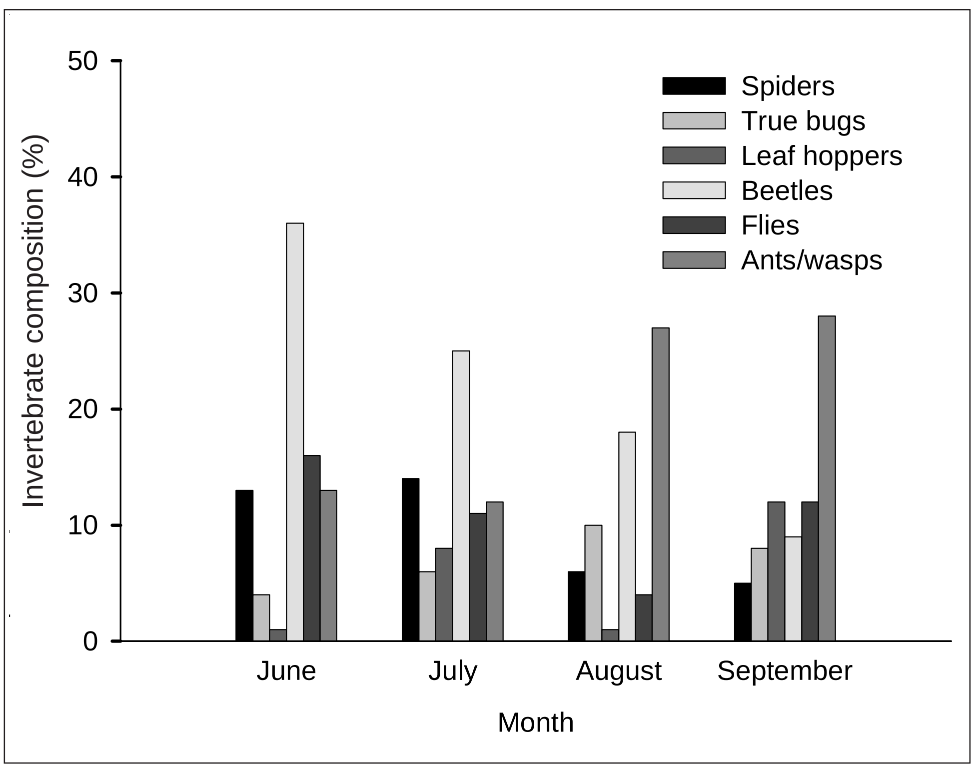


Figure 5—Proportion of 1,299 prey items in six orders found in Columbia spotted frog diet in 2002 in northeastern Oregon. Only orders with >50 prey items are displayed.

Frogs foraged actively from June through September with some foraging into October. Assuming the digestion rate was the same, biomass of diet samples was higher in September than in July, which suggests that frogs maximized their foraging late in the season, presumably for overwintering and egg production. Females also appeared to maximize prey intake to produce eggs annually; females >55 mm SVL had larger diet samples than males of the same size. In contrast, females ≤55 mm SVL consumed less prey than males of the same size. These smaller females are not likely to be reproductive the following year (Turner 1960) and may not need additional energy for egg production.

Demography and Populations

Parameters such as female fecundity, age at maturity, longevity, and growth are major components of a species' life history and influence a population's dynamics and structure (Engle 2001, Patla 1997, Turner 1960). Knowledge of these population parameters is important in determining a population's or species' ability to withstand environmental disturbances and recolonize sites. Population parameters of Columbia spotted frogs were determined in eight study sites containing a total of 22 breeding ponds based on PIT-tag data and skeletochronology.

For age determination, I collected a phalange from frogs of each sex in each of three SVL size classes (<50 mm, 50 to 70 mm, and >70 mm) (three to five frogs for most classes) at all the study areas except Crawfish in spring 1999. Age was determined by skeletochronology (Matson's Lab, Milltown, MT 59851); the lines of arrested growth (LAG) in transverse sections taken from the mid-diaphysis phalanges were counted in individual frogs (Guarino et al. 1995, Leclair and Castanet 1987, Ryser 1988). A number of potential error sources limit the accuracy of skeletochronology in all species, including the resorption of bone layers and numerous other characteristics that diminish the visual distinctness of LAG. Bone deposition characteristics cause LAG distinctness to vary not only among species but also among different populations of the same species. Skeletochronology error can be minimized by using population-specific, standardized analysis models that are continually evaluated by using specimens from individuals of known age or with known sampling time intervals. Some degree of error is inherent in the method; however, the use of standardized analysis models enables a constant error rate, allowing the detection of significant changes in population age structure (Matson 2005).

The first of July was used as the standardized "birthday" for Columbia spotted frogs because it was the earliest known date of metamorphosis in these populations. No recently metamorphosed frogs were detected in any of the ponds prior to this date, but they were frequently seen in late July and August in most of the study sites. Using this "birthday," I classified tadpoles that had transformed the previous summer by months of age until 1 July of the following year, at which time the age would be 1 year.

Sexual Maturity and Aging

Sexual maturity was typically reached at 1 year and 9 months in males and at 2 years and 9 months in females, based on age determination from skeletochronology in 253 frogs. Thirteen of 14 males that were 1 year and 9 months, were at oviposition sites during the breeding season and were assumed to be sexually mature. Of four females aged at 1 year and 9 months, one was gravid and in amplexus at a lower elevation site, and the other three females were not gravid at the time of capture. Six females that were 2 years and 9 months were all gravid and occurred at Gun and Starkey, which are low-elevation sites. Outside northeastern Oregon, the closely related *R. pretiosa* matures at 2 to 3 years at low-elevation sites in British Columbia, and Columbia spotted frogs reach sexual maturity at 4 to 6 years at high-elevation sites in Wyoming (Licht 1975). In central Nevada, male Columbia spotted frogs reach sexual maturity after 1 or 2 winters and females 1 or 2 years later (Reaser 2000).

Size at sexual maturity was variable. The smallest gravid females (with distended abdomens) in amplexus were 59 and 61 mm SVL at the Wallowa site. The smallest males at oviposition sites were 47 and 49 mm SVL at Wallowa; these males were in amplexus with females, which indicated that sexual maturity had been reached.

The SVL differed significantly among the age classes of males ($F = 35.44$, 4 df, $P < 0.001$), with 1-year old frogs differing from all other ages (ages 2 to 5 years), and 2-year-old frogs differing from ages 3 to 5 (fig. 6). SVL differed significantly among the age classes of females ($F = 61.53$, 4 df, $P < 0.001$), with 1-year old frogs differing from ages 2 to 5 years old, and 2-year-old frogs differing from ages 3 to 5 years old. Older male and female frogs did not differ in SVL (fig. 6). Although from a statistical standpoint there were significant differences between 1- and 2-year-old males and females, the high degree of overlap in older frogs suggests that size is not a good indication of age in Columbia spotted frogs. These findings agree with Halliday and Verrell (1988) who concluded that age and body size in amphibians are generally positively correlated but that considerable variability occurs in body size within a given age class. Gibbons and McCarthy (1984), Gittins et al. (1982), and Guarino et al. (1995) found that identification of

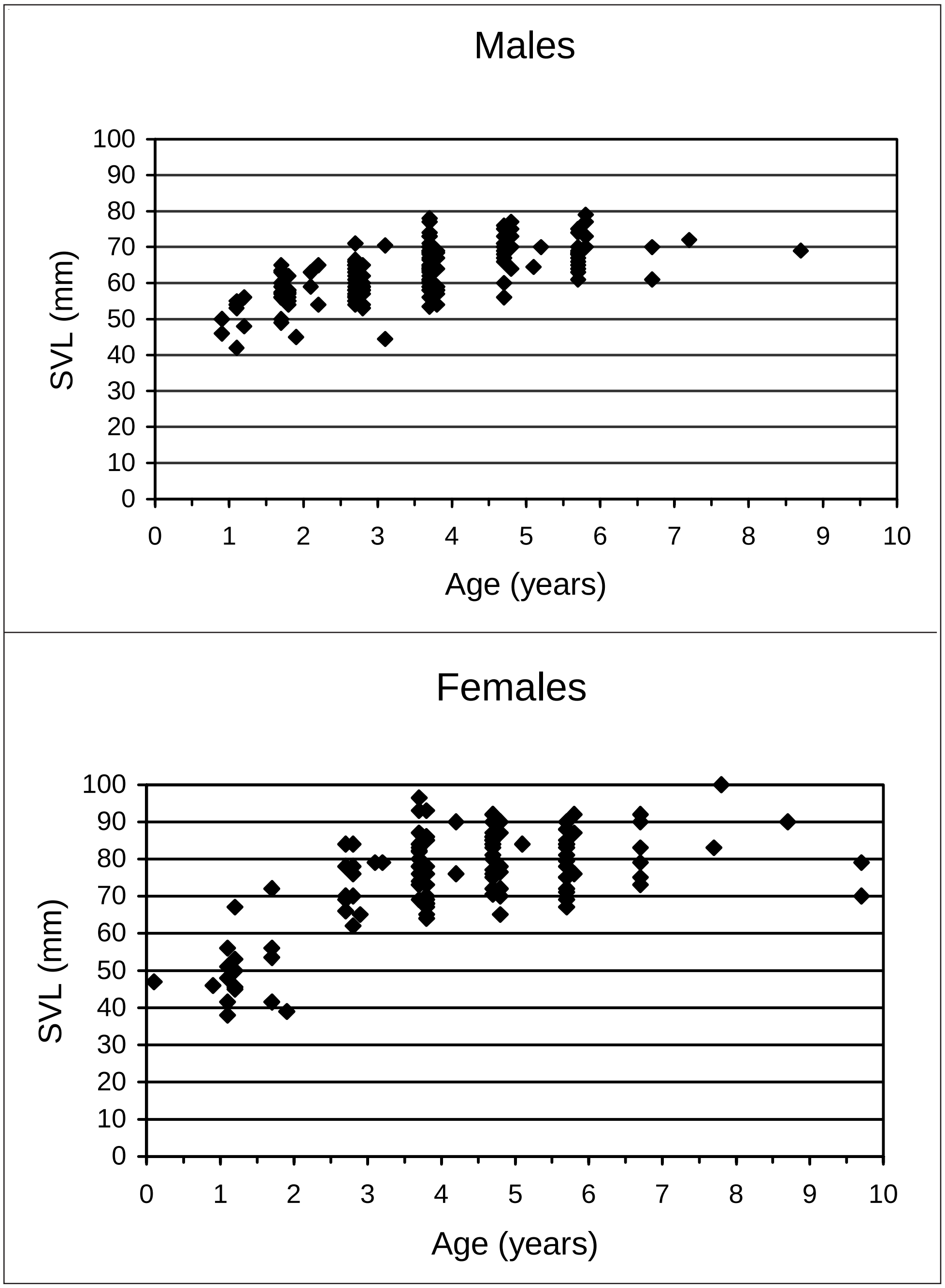


Figure 6—Estimated age and mean snout-vent length (SVL) of male and female Columbia spotted frogs in northeastern Oregon.

age groups in amphibians was impossible except for the early age classes. Understanding the lack of relationship between age and size is important, as some past studies (Turner 1958, 1960) have estimated adult age based on size. More reliable methods of aging include recapture of marked individuals and skeletochronology.

Sexual dimorphism occurred in frogs 2 years or older. Significant size differences between sexes occurred in frogs 2 years of age (t = -3.73, 47 df, P = 0.001), 3 years (t = -9.28, 59 df, P < 0.001), 4 years (t = -7.31, 38 df, P < 0.001), and 5 years (t = -6.17, 32 df, P < 0.001). Small sample size precluded analysis of frogs older than 5 years. Sexual size dimorphism in an adult frog population implies either a difference between the sexes in growth rate, age at first reproduction, or in age- or sex-specific mortality affecting longevity (Leclair and Laurin 1996). The observations in this study show a clear sexual size dimorphism from 2 years through 5 years indicating females were larger than males at age 2 years. Leclair and Laurin (1996) suggested that the higher growth rate of ranid females may be because males invest more time and energy into courting and chorusing or that females may have inherently different growth patterns than males. Given the dramatic differences in body size in the populations I studied, females appeared to be inherently larger than males (fig. 6) as reported by Turner (1960).

Growth Rate

Growth of individual frogs was determined within a growing season by calculating the amount of increase in length per day between recaptures. The growth per day was averaged within size classes of 10-mm intervals for males and females whose length at their initial capture was 40 to 49 mm, 50 to 59, 60 to 69, etc. Growth rates were calculated at each study site where sample size allowed. Annual growth was calculated as either the growth between breeding seasons in consecutive years or as the growth between consecutive Augusts. Growth of frogs recaptured within 2 weeks or during winter was not calculated because there was typically no increase during these periods.

Maximum growth within a season and between consecutive years occurred in males 40 to 49 mm SVL and in females 40 to 59 mm SVL (tables 4 and 5). Females had higher growth rates than males in all size classes. Generally, growth rates declined as the size class approached maximum. The largest male and female measured were 80 and 100 mm, respectively. Considerable variability occurred in growth rates among the study sites (tables 4 and 5). Growth rates in male Columbia spotted frogs were similar to those reported by Hollenbeck (1974) in Montana for frogs 40 to 49 mm (0.216 mm/day) and 60 to 69 mm (0.37 mm/day). The males 50 to 59 mm had a higher growth rate in Montana (0.190 mm/day)

Table 4—Growth (SD, N) of male Columbia spotted frogs in northeastern Oregon

	Growth interval			
Size class/site	**Within same year**	**1 year**	**2 years**	**3 years**
	mm/day	*mm/1 year*	*mm/2 years*	*mm/3 years*
40-49 mm				
Tailings	—	8 (1.41, 2)	15 (–,1)	—
Rainbow	0.152 (0.0959, 3)	14.3 (3.54, 6)	18 (–,1)	—
50-59 mm				
Wallowa	—	-1.4 (3.33, 6)	—	—
Gun	—	10 (–,1)	—	—
Starkey	0.018 (0.0194, 7)	5.5 (2.55, 10)	5.5 (1.23, 5)	—
Tailings	0.038 (0.0161, 5)	4.6 (2.05, 8)	7.5 (2.78, 5)	—
Rainbow	0.119 (0.0663, 19)	10.8 (3.39, 15)	11.1 (3.70, 5)	—
60-69 mm				
Wallowa	—	-0.5 (4.95, 2)	—	—
Gun	0.016 (0.0230, 13)	2.8 (2.14, 19)	2.8 (0.29, 3)	—
Starkey	0.001 (0.0131, 17)	2.0 (1.74, 34)	2.3 (2.09, 9)	2.3 (1.77, 2)
Tailings	0.014 (0.0194, 15)	1.8 (1.92, 38)	2.7 (1.75, 11)	—
Rainbow	0.042 (0.0294, 69)	4.1 (2.22, 91)	5.8 (2.81, 34)	6.1 (3.12, 8)
Crawfish	—	3.3 (2.68, 6)	—	—
70-79 mm				
Gun	0.001 (0.0166, 8)	-0.3 (2.43, 7)	0.7 (2.06, 4)	—
Starkey	0.008 (1)	0 (–,1)	—	—
Tailings	—	—	1 (–,1)	—
Rainbow	0.010 (0.0230, 36)	0.8 (1.64, 27)	2.1 (2.11, 13)	1.8 (2.36, 5)
Crawfish	—	-0.7 (1.07, 13)	—	—

Note: Intervals of growth include measurements taken within the same year and between consecutive breeding seasons or consecutive Augusts. The size class is the class the frog belonged to at the beginning of the measurement period. N represents the number of frogs measured in each size class and time interval at each site. Dashes indicate insufficient sample size to perform calculations.

Table 5—Growth (SD, N) of female Columbia spotted frogs in northeastern Oregon

	Growth interval			
Size class/site	**Within same year**	**1 year**	**2 years**	**3 years**
	mm/day	*mm/1 year*	*mm/2 years*	*mm/3 years*
40-49 mm				
Starkey	—	19 (–,1)	28 (–,1)	—
Rainbow	0.106 (0.0697, 3)	21.1 (2.78, 4)	—	—
50-59 mm				
Gun	0.342 (0.2418, 3)	—	—	—
Starkey	0.0492 (–,1)	13.5 (2.12, 2)	—	—
Rainbow	0.176 (0.0789, 3)	16.3 (6.66, 3)	34 (–,1)	—
60-69 mm				
Gun	0.158 (–,1)	18.5 (–,1)	—	—
Starkey	0.059 (–,1)	12.3 (6.21, 3)	—	—
Tailings	0.038 (0.0202, 3)	3.8 (2.57, 3)	9 (–, 1)	—
Rainbow	0.198 (0.1116, 5)	12.9 (3.53, 7)	15 (4.24, 2)	—
70-79 mm				
Gun	0.028 (–,1)	—	—	—
Starkey	0.093 (0.0779, 5)	3.5 (3.11, 4)	—	—
Tailings	0.028 (0.0295, 13)	1.1 (2.67, 14)	4 (0, 2)	—
Rainbow	0.107 (0.0452, 12)	9.7 (4.74, 11)	14 (–,1)	21 (–,1)
80-89 mm				
Gun	0.022 (0.0084, 4)	-1.7 (3.46, 3)	—	—
Starkey	0.024 (0.0341, 4)	0.5 (–,1)	1 (–,1)	—
Tailings	0.009 (–,1)	2.17 (7.42, 3)	—	—
Rainbow	0.049 (0.0382, 13)	4.5 (3.30, 12)	5 (5.29, 4)	
Crawfish	—	1 (–,1)	—	—
90-99 mm				
Gun	0.005 (0.0064, 2)	—	—	—
Rainbow	0.012 (0.0159, 3)	-0.3 (0.58, 3)	2 (–,1)	-2 (–,1)

Note: Intervals of growth include measurements taken within the same year and between consecutive breeding seasons or consecutive Augusts. The size class is the class the frog belonged to at the beginning of the measurement period. N represents the number of frogs measured in each size class and time interval at each site. Dashes indicate insufficient sample size to perform calculations.

than in northeastern Oregon (0.018-0.119 mm/day, table 4). The growth rates of females 50 to 80 mm SVL were higher in northeastern Oregon than in Montana. In Montana, Hollenbeck found few females larger than 80 mm and few males larger than 69 mm. Growth rates for females may be lower in Montana as females do not grow as large as they do in northeastern Oregon. In western Utah, adult females averaged 60.5 mm SVL and males 51.6 mm (Cuellar 1994), which are smaller than adult frogs in northeastern Oregon.

The loss of length in some frogs captured in two consecutive breeding seasons was detected more commonly with males than females and in the larger size classes (tables 4 and 5). This observation of apparent shrinkage could relate to the difficulty of measuring an animal as active and pliable as a frog (Turner 1960) or to the loss of pliability over the winter.

Just as the growth rates differed by site, the maximum and mean body size attained at some study sites differed (fig. 7). In general, the three largest ponds and lakes that were the most isolated from a river (Rainbow, Crawfish, Gun) contained the largest males and females. The study site closest to the river with multiple breeding sites (Wallowa) contained the smallest males and females. Skeletochronology revealed that the smaller frogs are not necessarily younger frogs at some of the sites. The ages of adult males >50 mm and adult females >60 mm across seven study sites were significantly different ($F = 15.27$, 6 df, $P < 0.01$). The 41 frogs aged at Tailings were significantly older (mean = 5 years, SD = 1.83) than any of the other sites, even though these frogs were smaller. The 75 frogs at Rainbow were significantly older (mean = 4.3 years, SD = 1.60) than the 51 frogs aged at Wallowa (mean = 3.3 years, SD = 0.84) and the 13 frogs aged at Whitehorse (mean = 3.2 years, SD = 1.26). Mean ages were 3.9 years (SD = 1.74, N = 26) at Cow Camp, 3.9 years (SD = 0.94, N = 40) at Gun, and 3.5 years (SD = 1.06, N = 44) at Starkey. Some of the factors that could influence the size difference in frogs at the various study sites include food supply, foraging behavior modification in response to predators, water temperature, ambient air temperature, or genetic differences.

Frogs at Wallowa, Tailings, and Starkey were primarily associated with river or creek habitat, and the water temperatures were an average of 5.6 °C cooler than ponds (Bull and Hayes 2001), which may have retarded growth. In contrast, males captured in rivers had diet samples with greater biomasses than males captured in ponds. Large prey items such as dragonflies, yellowjackets (wasps), and butterflies were more abundant at Rainbow Pond than at river habitats (Bull 2003), which could result in greater growth at this pond. Isolated ponds may have fewer predators than river habitats have, resulting in frogs in ponds spending more time foraging than frogs in rivers.

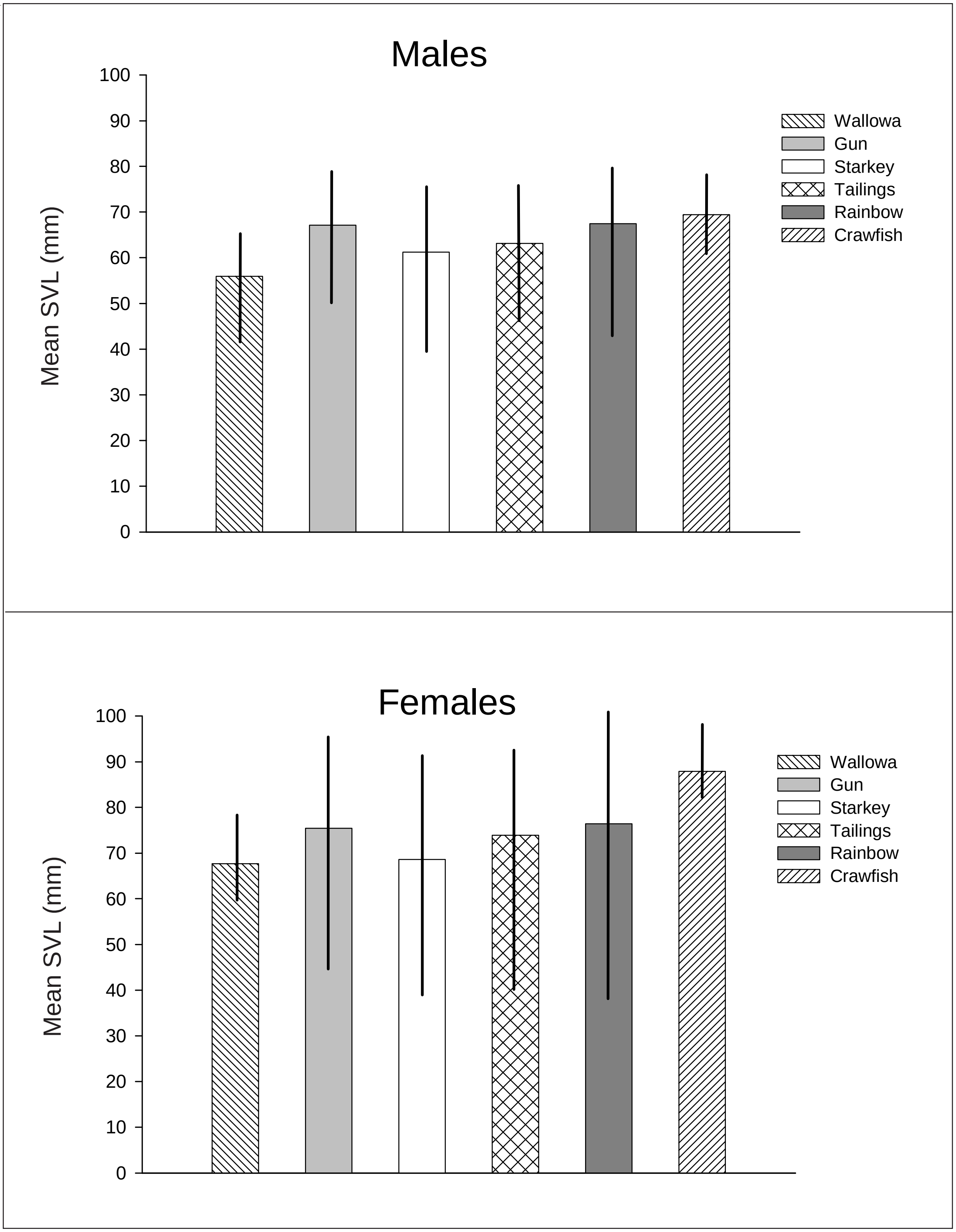


Figure 7—Mean snout-vent length (SVL) of male and female Columbia spotted frogs at six breeding sites in northeastern Oregon. Range is indicated by the bars.

Female Fecundity

Forty of 46 adult females captured during the breeding season in 2 consecutive years were gravid and in amplexus in both years at four of the study areas (Gun, Tailings, Rainbow, Crawfish); one female at Rainbow was gravid and in amplexus in 3 consecutive years. Adult females were not captured in consecutive years at the other study sites. The females captured in consecutive springs that were not gravid both years may already have deposited their eggs at the time of capture.

The annual production of eggs by at least some of the females in this study was in contrast to Turner's (1962) observation that *R. p. pretiosa* (later reclassified as *R. luteiventris*) did not breed each year in Yellowstone National Park. The higher elevation and longer, harder winters at Yellowstone National Park likely played a role in egg production. In British Columbia, *R. pretiosa* breeds every year at low-elevation sites (Licht 1975).

Lifespan

A total of 2,254 frogs were PIT-tagged from 1998 through 2004. Based on the recapture of PIT-tagged frogs and assuming that frogs were 2 years old when first captured, the two oldest males were 9 years and the oldest female was 7 years and were found at Rainbow Pond and Tailings Ponds. Based on skeletochronology, the oldest male was 9.7 years at Tailings and the oldest female was 8.7 years at Starkey.

Based on mark-recapture methods, the oldest male and female Columbia spotted frogs in Yellowstone National Park were believed to live 9 years and 10 to 12 years, respectively (Turner 1962), and the oldest female in central Idaho was 10 years (Pilliod 2005). Based on skeletochronology, the oldest female was 12 years in central Idaho (Pilliod 2005), 9 years in southwestern Idaho (Engle and Munger 1998), and 7 years in central Nevada (Reaser 2000). The oldest male was 3 years in central Nevada (Reaser 2000).

Population Size

Population size of gravid females, based on numbers of egg masses, was monitored from 4 to 8 years at 16 breeding ponds (table 6). The number of egg masses (i.e., gravid females) differed in some years by site. For example, the number of egg masses at one Wallowa breeding pond more than doubled in 2000 but only in that year. In 2000, the number of egg masses at Rainbow pond also increased and continued to increase until 2004 when the number declined.

Table 6—Number of egg masses located at 16 Columbia spotted frog breeding ponds in northeastern Oregon, 1997-2004

Site	Number of ponds	Year 1997	1998	1999	2000	2001	2002	2003	2004
Wallowa	1	28	17	27	62	28	23	15	15
Gun	1		12	20	24	16	17	13	7
Starkey	1	27	40	54	76	78	40	25	40
Cow Camp	1				11	12	8	12	9
Whitehorse	1					10	13	6	6
Cooper	1		8	5	7	2	3	0	0
Tailings	7				43	45	45	40	52
Rainbow	1	35	25	29	53	66	79	70	56
Crawfish	1				10	7	6		9
Anthony Lakes	1				38	42	47	70	82

Note: Numbers represent the total number of egg masses at each pond, except at Tailings, where the numbers represent the sum of all masses at seven ponds.

The largest number of egg masses (135) and thus gravid females occurred in a large wet meadow (20 ha) created by an abandoned reservoir 1 km above Olive Lake. The second highest concentration, 100 egg masses, occurred in Olive Lake. The number of egg masses ranged from 1 to 135 across 152 breeding sites.

There was a predominance of males at most of the study sites. Apparent fluctuation in numbers of males captured at the study sites may have been a result of different weather conditions each year, although some of the fluctuations are so large that I feel confident that they reflect a change in the population numbers (fig. 8). The sex ratio of males to females during the breeding season ranged from 1.0 to 2.8 at six study sites.

Climate may be a factor influencing the variation observed in the abundance of egg masses and adults detected during the breeding season (table 6). The number of egg masses and frogs detected at the Wallowa study site in 2000 was at least twice the number in any other year (table 6). Evaluating the maximum and minimum mean monthly air temperatures recorded at the breeding pond between 1995 and 2003 (Hohmann 2005) showed that the minimum mean monthly temperatures in July, August, and September of 1998 were higher than in any other year (fig. 9A). The July 1998 maximum mean monthly temperature was higher than that of any other year between 1996 and 2003 (fig. 9B). Because male and some female Columbia spotted frogs at low-elevation sites are sexually mature at 1 year and 9 months, it is feasible that the frogs breeding in 2000 were recruited in 1998. High numbers of egg masses were also detected at Rainbow and Starkey Ponds in 2000.

A 10-fold increase in number of recently metamorphosed frogs was also detected at Rainbow Pond in August 2003 compared to any other year since 1999

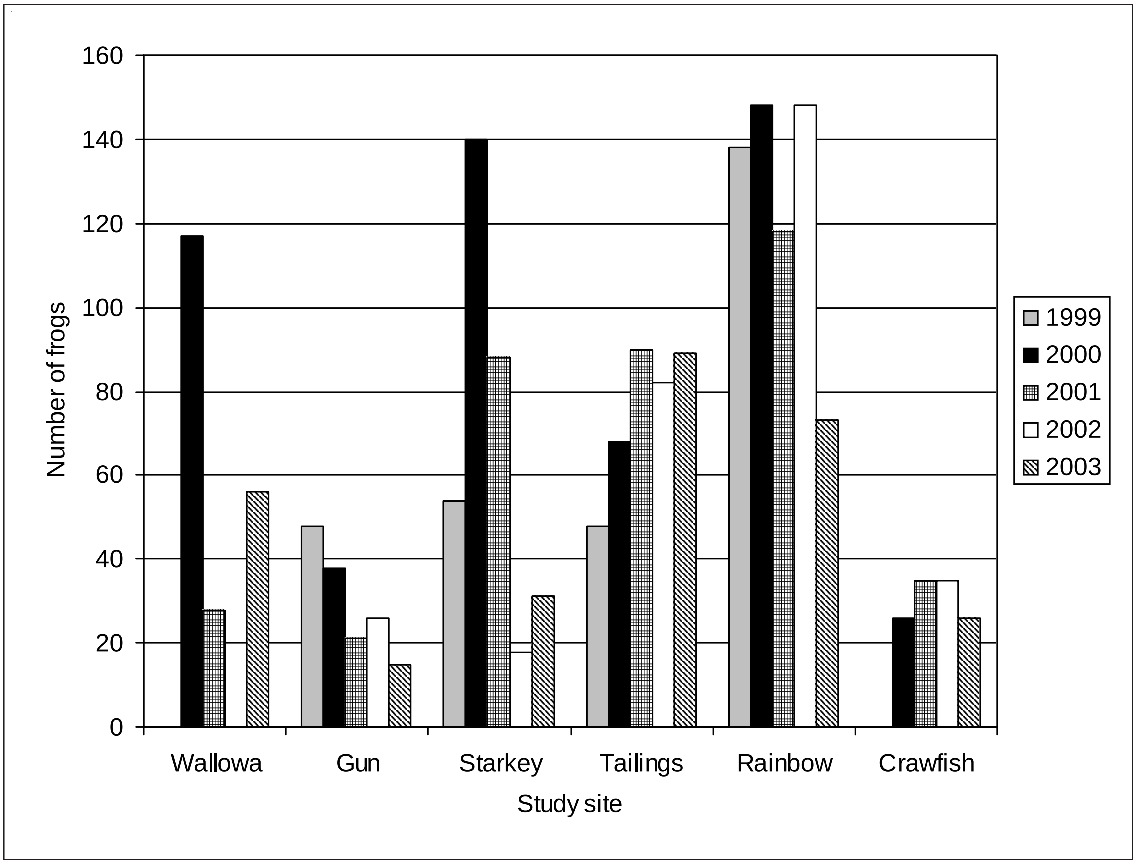
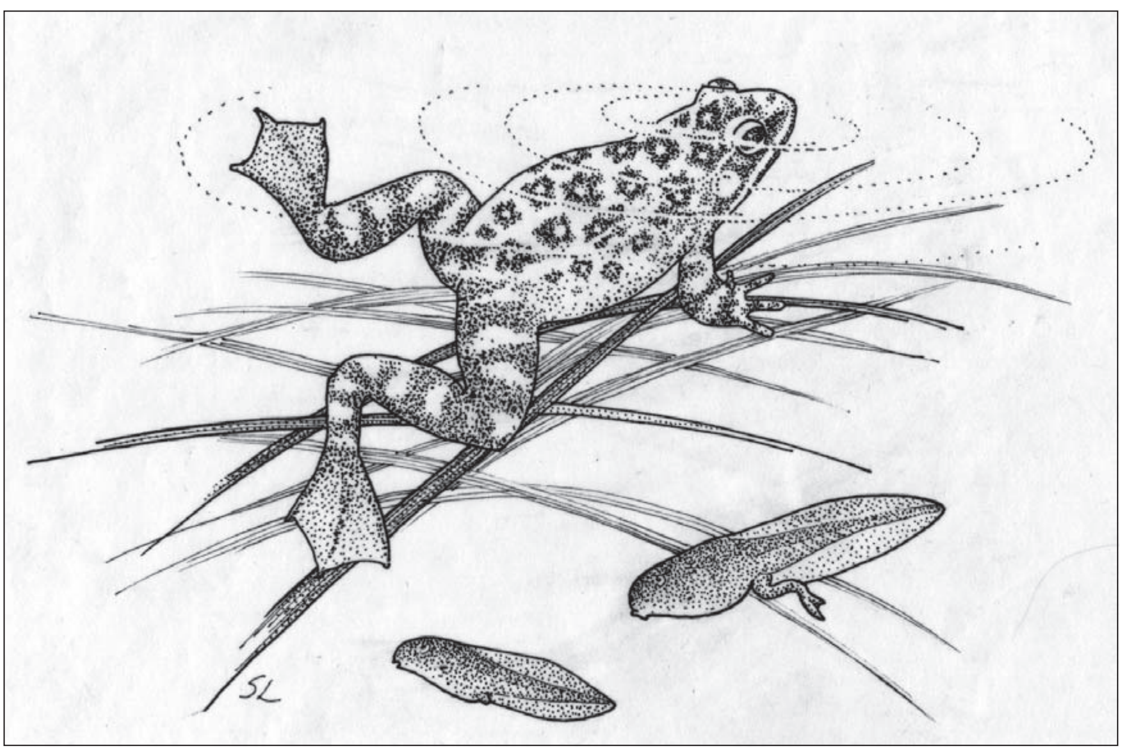
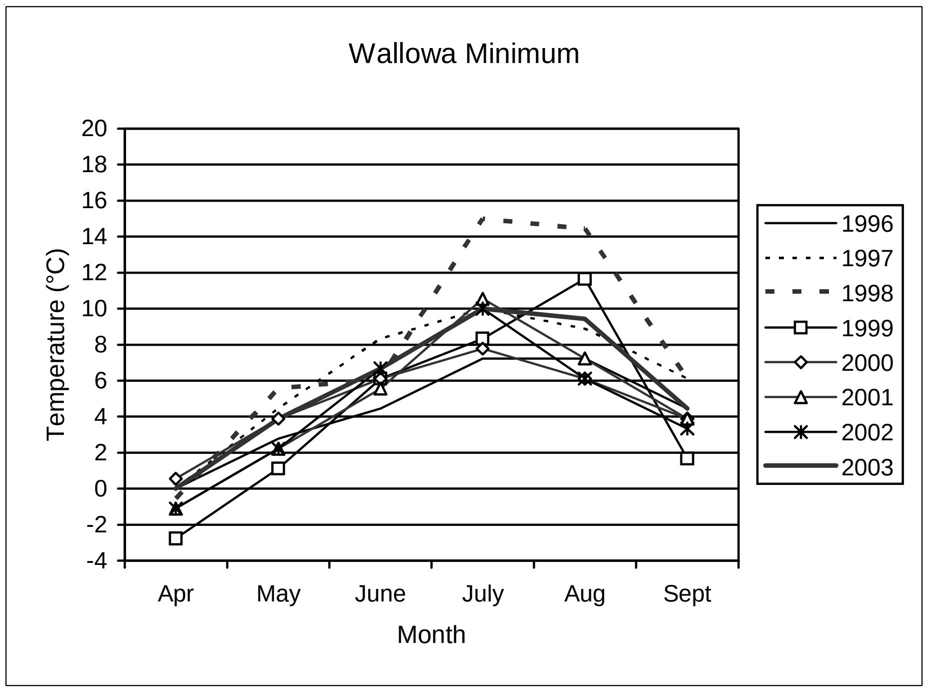


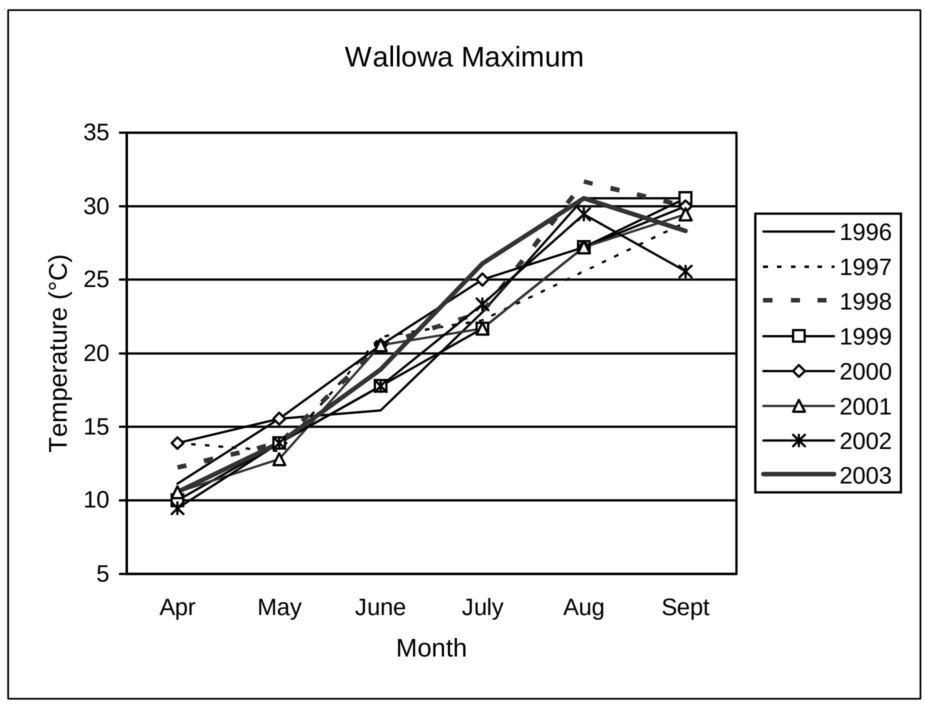
Figure 8–Number of male Columbia spotted frogs captured at six breeding sites in northeastern Oregon from 1999 through 2003.



Susan Lindstedt



A



B

Figure 9—Mean minimum and maximum monthly air temperatures at the breeding pond in Wallowa, Oregon, between 1996 and 2003. Source: Hohmann 2005.

(2,000 to 4,000 frogs in 2003 compared to <200 in other years). The minimum and maximum mean monthly air temperatures in La Grande (the nearest weather station) were the highest or nearly the highest in June, July, and August 2003 compared to other years (fig. 10A and 10B). Although La Grande is 900 m lower in elevation than Rainbow Pond, the temperature pattern should be the same at both sites.

Observations at these two study sites suggest that warmer than average air temperatures from June through August increase the recruitment rate at some breeding ponds and may explain increases in breeding population sizes 2 or more years later. Warmer temperatures increase the food supply for and development of larvae, result in earlier metamorphosis, and enable recently metamorphosed frogs to put on more growth prior to overwintering. This growth probably increases their survival rate over the winter. Warmer than average temperatures may be detrimental at some breeding sites owing to evaporation of pond water before metamorphosis occurs and a possible loss of habitat used outside the breeding season.

Causes of Mortality

Between 1997 and 2001, 193 adult frogs were radio-tagged and monitored every 1 to 2 weeks. For 3 to 6 months from the time of radio-tagging, 58 percent survived, 18 percent had the transmitter come off or had been killed, 7 percent had the transmitter quit, 6 percent were missing or had been killed, 5 percent were killed by predators, 4 percent were dead with no evidence of predation, 1 percent were run over by a vehicle, and 1 percent died from entanglement in vegetation. The frogs that were missing could have been carried off by a predator or had their transmitter damaged by a predator. In situations where only the transmitter was recovered, the frog may have been consumed by a predator.

I detected evidence of predation of 11 radio-tagged frogs by birds (n = 5), mink (*Mustela vison*) or northern river otters (*Lutra canadensis*) (n = 2), and garter snakes (n = 4). Three radio-tagged frogs were found with only the skeleton remaining after the tissue had been picked from the bones suggesting avian predation, probably by a corvid. I suspect raven (*Corvus corax*) predation of gravid females occurred at one oviposition site at Rainbow each year as indicated by unlaid eggs from gravid females on the ground, whitewash, and ravens on the shore. Over the course of 8 years, numerous adults were found with severed limbs, punctures in their skin, and scars on their dorsal surface.

Six radio-tagged frogs were found dead in the open water (n = 2) or under the ice (n = 4) from November through February with no evidence of predation. Each April or May when the ice melted, 1 to 17 dead adults and up to 35 juveniles (<1

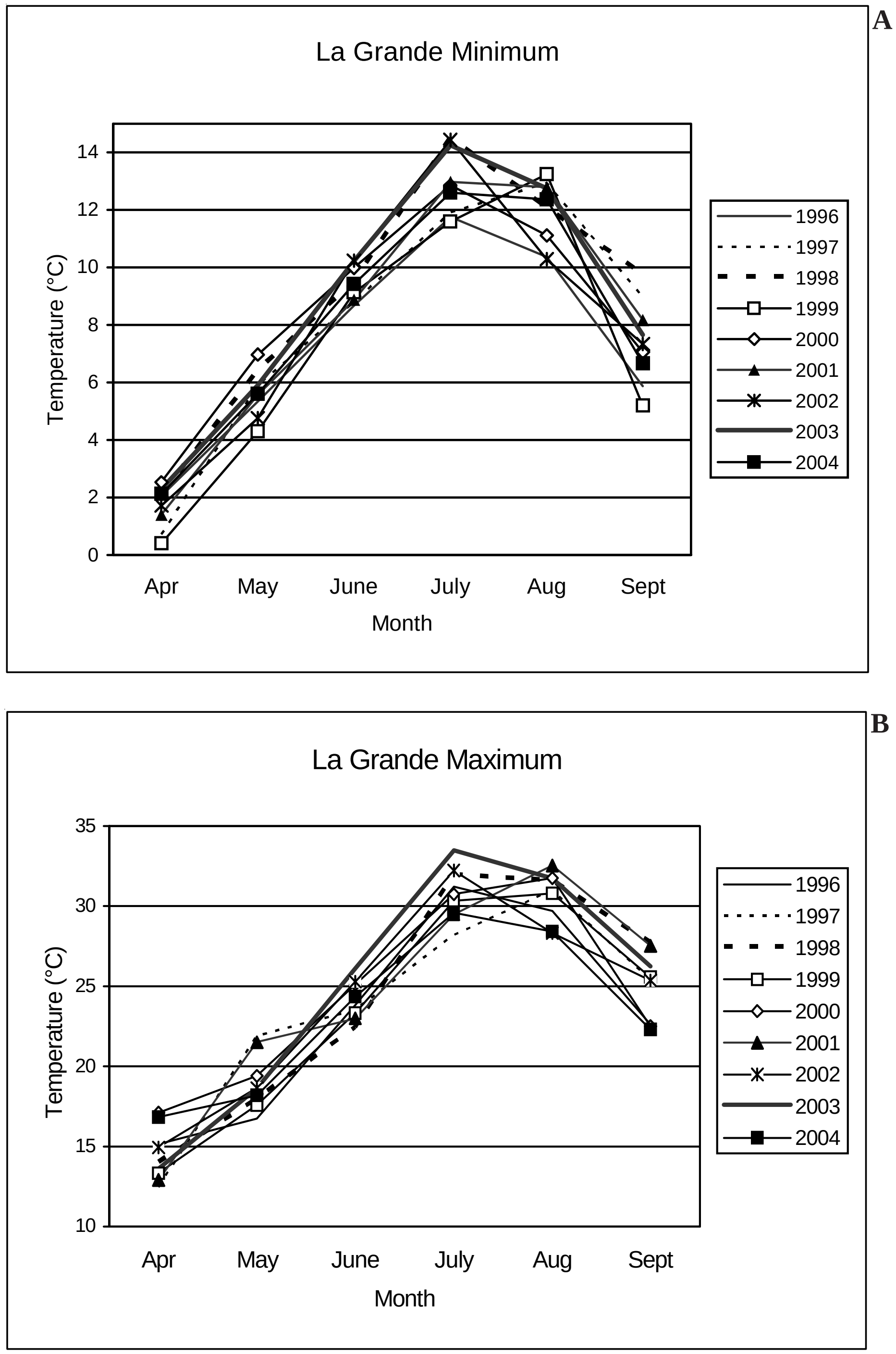


Figure 10—Mean minimum and maximum monthly air temperatures in La Grande, Oregon, between 1996 and 2004. Source: Oregon Climate Service n.d.

year old) were detected on the bottom of Rainbow Pond. Based on PIT-tags and skeletochronology, the ages of 12 of these adults were 3 to 6 years or older, so they were mature adults. All the dead females contained eggs. Based on the degree of decomposition, the mortality appeared to occur in late winter, although frogs that died in early winter would be decomposed by spring when the ice melted. Low levels of dissolved oxygen may have contributed to the mortality, although chytrid fungus may have been a factor. Fourteen of twenty live frogs tested positive for chytrid fungus at Rainbow Pond in 2005.

Scouring from ice flows also could cause mortality of frogs overwintering in the river. One radio-tagged frog with a recently broken hind leg was found 550 m downstream from the overwintering site immediately following an ice flow in the river. The bank that the frog had been under was washed away by the ice flow.

Garter snakes, giant water bugs (Belostomatidae), and kingfishers (*Ceryle alcyon*) were observed preying on larvae. During metamorphosis, larvae were particularly vulnerable to predation when they remained in the shallow, warmer water or on the water surface. Numbers of recently metamorphosed frogs were positively correlated with garter snakes based on numbers at 127 breeding sites in July and August (Bull and Hayes 2000). It appeared that garter snakes moved into the breeding ponds at the time of metamorphosis as food supply increased. Metamorphosing anurans were more vulnerable to predation by snakes owing to mobility lower than that of fully metamorphosed individuals or larvae (Arnold and Wasserburg 1978).

Numbers of recently metamorphosed frogs were inversely correlated with the presence of fishes where all the sites were below 1860 m in elevation (Bull and Hayes 2000). Long-nosed dace (*Rhinichthys cataractae* Valenciennes) and rainbow trout (*Oncorhynchus mykiss* Walbaum) may prey on spotted frog larvae (Hayes and Jennings 1986) and were present at some of these breeding sites. In contrast, the numbers of larvae at high-elevation lakes (over 1800 m in elevation) with and without fish (eastern brook trout [*Salvelinus fontinalis*] and rainbow trout) were not statistically different (Bull and Marx 2002); however, the mean number of larvae captured in sweeps with a dip net covering an area of 1 m^2 area was 4.0 (SD = 10.1) at 11 lakes without fish compared to 2.6 (SD = 4.6) at 11 lakes with fish. Other studies on *Rana luteiventris* have found negative correlations with fish presence at high elevations (Munger et al. 1997, Murphy 2002, Pilliod and Peterson 2001, Wyrick 2004).

The primary causes of mortality in eggs are desiccation, freezing, and flooding. Embryos at the lower elevation ponds are at greatest risk of mortality from desiccation and flooding because of high water fluctuations that result from a lack of precipitation or heavy rains prior to hatching. Embryos at the high-elevation lakes are at greatest risk of mortality from freezing (Licht 1975). In most years, mortality of embryos on the upper surface of the egg masses occurred at some of the breeding ponds.

Predation of embryos occurs, although it has less influence on embryo survival than water level and temperature. Leeches consumed all the embryos at one breeding pond for 3 consecutive years, and no egg masses have been detected at this site in 3 years. Hovingh (1993) reported leeches (*Haemopis marmorata*) on Columbia spotted frog egg masses in Utah. Numbers of egg masses at high-elevation lakes with and without fish (eastern brook trout and rainbow trout) were not statistically different, although the average number of egg masses at 11 lakes without fish was 14.4 (SD = 30.7) compared to an average of 9.8 (SD = 23.7) at 11 lakes with fish (Bull and Marx 2002).

Diseases and Parasites

About 20 percent of the frogs at Rainbow Pond and 10 percent at Crawfish Lake have a fungal brush-border on the eyelids, poor integrity of the skin of the feet resulting in spontaneous bleeding when handled, and flaccid skin; these conditions are detected only in spring. Low levels of dissolved oxygen under the ice may have stressed the frogs and allowed fungal establishment.

Columbia spotted frogs with multiple hind limbs were found at the Starkey study site. It is believed that these frogs were infected at the larval stage with a nematode parasite (*Ribeiroia*) of the snail genus (Johnson et al. 1999). Johnson et al. (1999) suggested that accelerated eutrophication of water as a result of organic pollution may cause numbers of the planorbid snail (an intermediate host of *Ribeiroia*) to increase, which could increase the rate of parasite infection and deformities in frogs. The Starkey site is heavily grazed with livestock and contains the highest level of organic pollution of any of the study sites investigated in this study, which may be the cause of these deformities. It is not clear what impact these deformities have on a population’s viability.

Conservation and Management

The following factors have potentially contributed to the decline of amphibian species in the Western United States: (1) habitat alteration and loss (timber harvest, grazing, fire), (2) introduction of exotic species (fish, bullfrogs), (3) environmental pollutants, (4) climate change, (5) pathogens, (6) increased ambient UV-B radiation, and (7) resource extraction. Only some of these factors are likely to affect

Columbia spotted frogs in northeastern Oregon and will be discussed below. Few chemical pollutants are known to be used in the range of the Columbia spotted frog in northeastern Oregon.

Habitat Alteration

Habitat alteration may be beneficial or detrimental to Columbia spotted frogs depending on the resulting conditions. Human activities that have been beneficial to Columbia spotted frogs include permanent ponds created to provide water for livestock or wildlife, irrigation, settling ponds used in mining, and ponds created for aesthetic purposes. Beavers reintroduced in the Owyhee Mountains may have resulted in an increase in Columbia spotted frog numbers (Munger et al. 1997, Reaser and Pilliod 2005). Loss of beavers results in the loss of open, lentic habitat in riparian zones and can lead to declining water tables (Reaser 1997). Wetlands created along the Provo River in Utah contained Columbia spotted frog egg masses within 1 year of their creation (Ammon et al. 2003, Reaser and Pilliod 2005).

Draining of wetlands used by Columbia spotted frogs is detrimental owing to the elimination of breeding, postbreeding, and overwintering habitat. In Yellowstone National Park, the pumping of a headwater spring eliminated a breeding site and changed the hydrology of the area and likely resulted in a decrease in Columbia spotted frog numbers (Patla and Peterson 1999).

Timber harvesting—

Timber harvesting is unlikely to have a large impact on Columbia spotted frogs in most situations because of the unharvested buffer strips typically retained in riparian areas to protect the sensitivity of the area (USDA USDI 1995). However, the creation of roads, which often accompanies timber harvest activities, adjacent to breeding sites could result in mortality of frogs moving to and from breeding sites as observed in this study. Patla and Peterson (1999) hypothesize that the direct mortality and impediment to movement associated with road construction in Yellowstone National Park are related to the decline of one Columbia spotted frog population.

Grazing—

Although grazing did not significantly affect Columbia spotted frog reproduction during the periods and at the levels investigated in northeastern Oregon (Bull and Hayes 2000), overgrazing could negatively affect reproduction if egg masses or recently metamorphosed frogs are directly trampled or if banks are collapsed along ponds or rivers that serve as overwintering sites. In some situations, certain levels of grazing may benefit spotted frog habitat by removing vegetation, creating openings, and increasing solar radiation; such changes could increase water temperatures and provide areas for amphibians to bask and forage (Bull and Hayes 2000). About 60 percent of one pond in this study (Starkey; fig. 4C) was fenced to exclude cattle; all five oviposition sites at this site occurred in the grazed portion of the pond, although the cattle were not present until 2 months after egg laying at this pond. Oviposition sites in this pond had shallow water and low ground vegetation and no overhead canopy as a result of grazing the summer prior to egg laying. Four breeding ponds in Wallowa were fenced to exclude cattle in 2003. In spring 2004, the vegetation had created dense mats reducing the amount of shallow water at the oviposition sites, and egg masses occurred at three of the four sites. In spring 2005, egg masses occurred at two of the four ponds. Protection from grazing reduced the open surface water used for egg laying at these oviposition sites.

A number of the indirect effects of livestock grazing may be detrimental to amphibians. Reaser (2000) believed the presence of cattle was one of the most important human-caused factors that negatively affected the distribution of Columbia spotted frogs in central Nevada. Fecal contamination may cause eutrophication of water and an increase in planorbid snail numbers, number of nematode parasites, and the rate of parasite infection that causes limb deformities in amphibians (Johnson et al. 1999). Grazing may negatively affect movements of recently metamorphosed frogs by removing vegetation and compacting the soil, which could decrease hiding cover and increase their rate of desiccation when traveling (Engle 2001).

Fire—

Direct mortality of Columbia spotted frogs from fire is probably minimal owing to the highly aquatic nature of this species (Pilliod et al. 2003). However, the mortality of trees and removal of coarse woody debris immediately adjacent to the wetlands could affect this species by altering habitat used for dispersal or the microclimate at the breeding sites. Removing the canopy adjacent to the breeding sites may be beneficial by increasing solar radiation, warming the water, speeding the development and transformation of larvae, and increasing their chances of overwintering survival (Maxell 2000).

Some activities used to control fires may be detrimental to this species when water is removed from breeding or overwintering sites. Water was removed from

Rainbow Pond to help control a wildfire in September 2001, but the water quantity removed was limited to a 0.5-m reduction in water depth to ensure that adequate overwintering habitat remained in the 3-m-deep pond.

Introduction of Exotic Species

Fish—
At low elevations, long-nosed dace (native) preyed on larvae of Columbia spotted frogs and significantly reduced their abundance. The introduction of salmonids to high-elevation lakes has likely influenced populations of Columbia spotted frogs. Although trout are known to prey on Columbia spotted frogs, these frogs still occurred along with trout in lakes that contained abundant emergent vegetation and shallow water providing cover for larvae (Bull and Marx 2002). In contrast, the abundance of all life stages of Columbia spotted frogs was significantly lower in lakes with fish than without in the Bighorn Crags in Idaho (Pilliod and Peterson 2001).

Bullfrogs–
Bullfrogs (*R. catesbeiana*) have been implicated in localized declines of many amphibian species (Bury and Whelan 1984, Pearl et al. 2004) and have likely affected the distribution of the Columbia spotted frog in the Grande Ronde Valley. Presently Columbia spotted frogs still occur in the Grande Ronde Valley (Mahrt 2005) but in fewer areas than reported in the 1950s by Ferguson (1954). Bullfrogs occupy the majority of permanent water bodies in the valley at present; they are not known to occur outside the Grande Ronde Valley in the forested ecosystems and did not occur in the study sites used in this study.

Weeds–
The effects of noxious weeds on amphibians are largely unknown. Aquatic and terrestrial weeds may form dense stands that could exclude native amphibians (Maxell 2000). Most noxious weeds that occur in northeastern Oregon (Rice 2003) are unlikely to affect populations of Columbia spotted frogs owing to the distribution and habitat requirements of these frogs. Data on the toxicity of herbicides to amphibians is limited, but several commonly used herbicides present stressors to eastern amphibians (Relyea 2005). Bautista (n.d.) presents a review of the literature and concludes that amphibians are less sensitive, or about as sensitive as fish to some herbicides.

Climate Change

Certain climatic conditions influence populations of Columbia spotted frogs in northeastern Oregon. During the breeding season, excessive fluctuations in moisture can result in flooding and the loss of egg masses, or desiccation of egg masses and larvae when water levels drop. Embryos that are frozen in ice on the pond surface may die. Summers with above-average temperatures may be detrimental to populations in ephemeral ponds where larvae do not transform before the drying of the water body, but may be beneficial in permanent ponds because transformation occurs earlier allowing recently metamorphosed frogs more growth prior to winter.

Pathogens

The chytrid fungus has been associated with amphibian declines in the Western United States (Daszak et al. 1999, Fellers et al. 2001, Muths et al. 2003). Chytrid fungus is known to occur in two of the watersheds used in this study (U.S. Geological Survey, National Wildlife Health Center 2004), and frogs tested positive for chytrid fungus in the four breeding sites that were sampled in 2005. Chytrid fungus may be related to mortality observed during winter at a number of the study sites.

It is not known if water molds (*Saprolegnia* spp.), which are common pathogens of fish from hatcheries, have influenced Columbia spotted frogs in northeastern Oregon. Certainly some frog populations in this study are in contact with fish that have been released from fish hatcheries. Mold growth on eggs has been detected in some breeding ponds with 2 to 80 percent of the eggs affected.

Human Activity

Columbia spotted frogs are protected in the state of Oregon, although some recreational activities in riparian areas may result in disturbance to frogs, egg masses, or habitat in northeastern Oregon. Some activities, such as shooting Columbia spotted frogs and riding all-terrain vehicles through breeding sites, still persist (Bull, personal observation). Predators of anurans may be more abundant at recreational facilities or around human developments (Olson 1989).

Conclusions

The Columbia spotted frog is widely distributed throughout northeastern Oregon where permanent ponds and rivers or creeks occur, with the exception of the Grande Ronde Valley. Although populations are generally not large, numerous small populations occur, particularly when connected by flowing water. Where pond and river habitats occur in proximity, frogs exhibit movements of up to 2.3 km. This species successfully reproduces in a large variety of breeding sites that maintain a fairly consistent water level and lack of waterflow throughout the year. Overwintering sites include ice-covered ponds, warm springs, rivers, and seeps in forested habitats.

This species occurs in areas with a long history of summer livestock grazing in northeastern Oregon, as well as in areas without grazing. Columbia spotted frogs coexist with trout species and long-nosed dace where suitable habitat exists to provide cover or restrict access from these predators.

From 1997 through 2004, frog populations fluctuated, with the highest numbers of breeding females detected in 2000 and 2001. Since that time, declines in numbers of egg masses have been detected at 7 of the 10 sites. Although populations of Columbia spotted frogs were monitored for 8 years at these sites, a longer period is necessary to assess the overall health of these populations, the influence of disturbance factors and climate, and what population change constitutes a decline versus a normal fluctuation. Valuable information about a population's structure could be gained from genetic analyses. More immediately, the prevalence and effects of chytrid fungus on populations of Columbia spotted frogs need to be determined to evaluate the future prospects of this species.

Acknowledgments

Laurie Allen, Jennifer Boyd, Abe Clark, Thad Heater, Janet Hohmann, and Barb Wales assisted with field work. Jay Shepherd conducted the statistical analyses. The skeletochronology was done by Matson's Laboratory, L.L.C. (Milltown, MT). Several breeding ponds were on private property owned by Janet Hohmann, Nyoda Scott, Doug McDaniel, and Nevada First. The Pacific Northwest Research Station and U.S. Fish and Wildlife Service provided funding. Bryce Maxell, Christopher Pearl, David Pilliod, Jay Shepherd, and Matt Snook reviewed an earlier draft of this manuscript. Amphibians were handled under Oregon Permit numbers 100-97, 026-98, 005-99,015-00, 013-01, 057-02, 047-03, and 021-04.

English Equivalents

When you know:	Multiply by:	To find:
Millimeters (mm)	0.039	Inches
Centimeters (cm)	.394	Inches
Cubic centimeters (cc)	.0338	Ounces
Meters (m)	3.28	Feet
Kilometers (km)	.62	Miles
Hectares (ha)	2.4	Acres
Square meters (m^2)	10.7	Square feet
Grams (g)	.0353	Ounces
Degrees Celsius	1.8C + 32	Degrees Fahrenheit

References

Ammon, E.M.; Gorley, C.R.; Wilson, K.W.; Ross, D.A.; Peterson, C.R. 2003. Advances in habitat restoration for the Columbia spotted frog (*Rana luteiventris*): a case study from the Provo River population. In: Proceedings: California riparian systems: processes and floodplains management, ecology and restoration. Sacramento, CA: Riparian Habitat Joint Venture and Western Section of The Wildlife Society: 348-356.

Arnold, S.J.; Wassersug, R.J. 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. Ecology. 59: 1014-1022.

Augert, D.; Joly, P. 1993. Plasticity of age at maturity between two neighbouring populations of the common frog (*Rana temporaria* L.). Canadian Journal of Zoology. 71: 26-33.

Bautista, S.L. [N.d.]. Summary of herbicide effects to wildlife. Manuscript in preparation. On file with: S. Bautista, USDA Forest Service, Pacific Northwest Region, P.O. Box 3623, Portand, OR 97208-3623.

Blouin, M. 2001. Microsatellite DNA testing of Columbia spotted frog toe samples. Unpublished report. On file with: USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850.

Bull, E.L. 2003. Diet and prey availability of Columbia spotted frogs in northeastern Oregon. Northwest Science. 77: 349-356.

Bull, E.L.; Hayes, M.P. 2000. Livestock effects on reproduction of the Columbia spotted frog. Journal of Range Management. 53: 291-294.

Bull, E.L.; Hayes, M.P. 2001. Post-breeding season movements of Columbia spotted frogs (*Rana luteiventris*) in northeastern Oregon. Western North American Naturalist. 61: 119-123.

Bull, E.L.; Hayes, M.P. 2002. Overwintering of Columbia spotted frogs in northeastern Oregon. Northwest Science. 76: 141-147.

Bull, E.L.; Marx, D.B. 2002. Influence of fish and habitat on amphibian communities in high elevation lakes in northeastern Oregon. Northwest Science. 76: 240-248.

Bull, E.L.; Shepherd, J.F. 2003. Water temperature at oviposition sites of *Rana luteiventris* in northeastern Oregon. Western North American Naturalist. 63: 108-113.

Bury, R.B.; Whelan, J.A. 1984. Ecology and management of the bullfrog. Resource Publication 155. [Place of publication unknown]. U.S. Fish and Wildlife Service. 23 p.

Corn, S. 2000. Amphibian declines: review of some current hypotheses. In: Sparling, D.W.; Bishop, C.A.; Linder, G., eds. Exotoxicology of amphibians and reptiles. Pensacola, FL: Society of Environmental Toxicology and Chemistry: 663-696.

Cuellar, O. 1994. Ecological observation on *Rana pretiosa* in western Utah. Alytes. 12: 109-121.

Daszak, P.; Berger, L.; Cunningham, A.A.; Hyatt, A.D.; Green, D.E.; Speare, R. 1999. Emerging infectious diseases and amphibian population declines. Emerging Infectious Diseases. 5: 735-748.

Engle, J.C. 2001. Population biology and natural history of Columbia spotted frogs (*Rana luteiventris*) in the Owyhee uplands of southwest Idaho: implications for monitoring and management. Boise, ID: Boise State University. 37 p. M.S. thesis.

Engle, J.C.; Munger, J.C. 1998. Population structure of spotted frogs in the Owyhee Mountains. Tech. Bull. 98-20. Boise, ID: Idaho Bureau of Land Management. 10 p.

Fellers, G.M.; Green, D.E.; Longcore, J.E. 2001. Oral chytridiomycosis in the mountain yellow-legged frog (*Rana muscosa*). Copeia. 2001: 945-953.

Ferguson, D.E. 1954. An annotated list of the amphibians and reptiles of Union County, Oregon. Herpetologica. 10: 149-152.

Funk, W.C.; Blouin, M.S.; Corn, P.S.; Maxell, B.A.; Pilliod, D.S.; Amish, S.; Allendorf, F.W. 2005a. Population structure of Columbia spotted frogs (*Rana luteiventris*) is strongly affected by the landscape. Molecular Ecology. 14: 483-496.

Funk, W.C.; Greene, A.E.; Corn, P.S.; Allendorf, F.W. 2005b. High dispersal in a frog species suggests that it is vulnerable to habitat fragmentation. Biology Letters (Royal Society of London). 1: 13-16.

Gibbons, M.M.; McCarthy, T.K. 1984. Growth, maturation and survival of frogs *Rana temporaria* L. Holarctic Ecology. 7: 419-427.

Gittins, S.P.; Steeds, J.E.; Williams, R. 1982. Population age-structure of the common toad (*Bufo bufo*) at a lake in mid-Wales determined from annual growth rings in the phalanges. British Journal of Herpetology. 6: 249-252.

Green, D.M.; Sharbel, T.F.; Kearsley, J.; Kaiser, H. 1996. Postglacial range fluctuation, genetic subdivision and speciation in the Western North American spotted frog complex, *Rana pretiosa*. Evolution. 50: 374-390.

Guarino, F.M.; Angelini, F.; Cammarota, M. 1995. A skeletochronological analysis of three syntopic amphibian species from southern Italy. Amphibia-Reptilia. 16: 297-302.

Halliday, T.R.; Verrell, P.A. 1988. Body size and age in amphibians and reptiles. Journal of Herpetology. 22: 253-265.

Hayes, M.P.; Jennings, M.R. 1986. Decline of ranid frog species in western North America: are bullfrogs (*Rana catesbeiana*) responsible? Journal of Herpetology. 20: 490-509.

Herreid, C.F.; Kinney, S. 1967. Temperature and development of the wood frog, *Rana sylvatica*, in Alaska. Ecology. 48: 579-590.

Hohmann, J.E. 2005. Unpublished data. On file with: Janet Hohmann, biologist, 69796 Jim Town Road, Wallowa, OR 97885.

Hollenbeck, R.R. 1974. Growth rates and movements within a population of *Rana pretiosa pretiosa* Baird and Girard in south central Montana. Bozeman, MT: Montana State University. 65 p. M.S. thesis.

Hovingh, P. 1993. Aquatic habitats, life history observations, and zoogeographic considerations of the spotted frog (*Rana pretiosa*) in Tule Valley, Utah. Great Basin Naturalist. 53: 168-179.

Johnson, O.W. 1965. Early development, embryonic temperature tolerance and rate of development in *Rana pretiosa luteiventris* Thompson. Corvallis, OR: Oregon State University. 74 p. Ph.D. dissertation.

Johnson, P.T.J.; Lunde, K.B.; Ritchie, E.G.; Launer, A.E. 1999. The effect of trematode infection on amphibian limb development and survivorship. Science. 284: 802-804.

Leclair, R., Jr.; Castanet, J. 1987. A skeletochronological assessment of age and growth in the frog *Rana pipiens* Schreber (Amphibia, Anura) from southwestern Quebec. Copeia. 1987: 361-369.

Leclair, R., Jr.; Laurin, G. 1996. Growth and body size in populations of mink frogs *Rana septentrionalis* from two latitudes. Ecography. 19: 296-304.

Legler, J.M.; Sullivan, L.J. 1979. The application of stomach flushing to lizards and anurans. Herpetologica. 35: 107-110.

Leonard, W.P.; Bull, E.L. 2005. Columbia spotted frogs, *Rana luteiventris*. In: Jones, L.L.C.; Leonard, W.P.; Olson, D.H., eds. Amphibians of the Pacific Northwest. Seattle, WA: Seattle Audubon Society: 212-215.

Licht, L.E. 1971. Breeding habits and embryonic thermal requirements of the frogs, *Rana aurora aurora* and *Rana pretiosa pretiosa*, in the Pacific Northwest. Ecology. 52: 116-124.

Licht, L.E. 1975. Comparative life history features of the western spotted frog, *Rana pretiosa*, from low- and high-elevation populations. Canadian Journal of Zoology. 53: 1254-1257.

Mahrt, L. 2005. Personal communication. Ecologist, Biology Department, Eastern Oregon University, La Grande, OR 97850.

Matson, G.J. 2005. Personal communication. Owner. Matson's Laboratory, P.O. Box 308, Milltown, MT 59851.

Maxell, B.A. 2000. Management of Montana's amphibians: a review of factors that may present a risk to population viability and accounts on the identification, distribution, taxonomy, habitat use, natural history and the status and conservation of individual species. Unpublished report. On file with: USDA Forest Service, Northern Regional Office, 200 East Broadway, Missoula, MT 59807.

Munger, J.C.; Barnett, B.R.; Ames, A. 1997. 1996 Sawtooth Wilderness amphibian survey. A challenge cost share agreement between the Sawtooth National Forest, U.S. Department of Agriculture, Forest Service, and Boise State University. Boise, ID: Boise State University. 10 p.

Murphy, P.D. 2002. The effects of different species of introduced salmonids on amphibians in headwater lakes of north-central Idaho. Pocatello, ID: Idaho State University. M.S. thesis.

Muths, E; Corn, P.S.; Pessier, A.P.; Green, D.E. 2003. Evidence for disease related amphibian decline in Colorado. Biological Conservation. 110: 357-365.

NatureServe. 2005. NatureServe Explorer: an online encyclopedia of life [Web application]. Version 4.3. Arlington, VA: NatureServe. http://www.natureserve.org/explorer. (March 28, 2005).

Olson, D.H. 1989. Predation on breeding western toads (*Bufo boreas*). Copeia. 1989: 391-397.

Oregon Climate Service. [N.d]. http//www.ocs.oregonstate.edu/index.html. (March 15, 2005).

Patla, D.A. 1997. Changes in a population of spotted frogs in Yellowstone National Park between 1953 and 1995: the effects of habitat modification. Pocatello, ID: Idaho State University. 215 p. M.S. thesis.

Patla, D.A.; Peterson, C.R. 1999. Are amphibians declining in Yellowstone National Park? Yellowstone Science. 1999 (Winter): 2-11.

Pearl, C.A. 2000. *Bufo boreas* (western toad) predation. Herpetological Review. 31: 233-234.

Pearl, C.A., Adams, M.J.; Bury, R.B.; McCreary, B. 2004. Asymmetrical effects of introduced bullfrogs (*Rana catesbeiana*) on native ranid frogs in Oregon, USA. Copeia. 2004: 11-20.

Pilliod, D.S. 1999. *Rana luteiventris* cannibalism. Herpetological Review. 32: 93.

Pilliod, D.S. 2005. Personal communication. Ecologist, Biological Sciences Department, Cal Poly, San Luis Obispo, CA 93410.

Pilliod, D.S.; Bury, R.B.; Hyde, E.J.; Pearl, C.A.; Corn, P.S. 2003. Fire and amphibians in North America. Forest Ecology and Management. 178: 163-181.

Pilliod, D.S.; Peterson, C.R. 2001. Local and landscape effects of introduced trout on amphibians in historically fishless watersheds. Ecosystems. 2001: 322-333.

Pilliod, D.S.; Peterson, C.R.; Ritson, P.I. 2002. Seasonal migration of Columbia spotted frogs (*Rana luteiventris*) among complementary resources in a high mountain basin. Canadian Journal of Zoology. 80: 1849-1862.

Prentice, E.F.; Flagg, T.A.; McCutcheon, C.S. 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. American Fisheries Society Symposium. 7: 317-322.

Reaser, J.K. 1997. Amphibian declines: conservation science and adaptive management. Stanford, CA: Stanford University. 148 p. Ph.D. dissertation.

Reaser, J.K. 2000. Demographic analyses of the Columbia spotted frog (*Rana luteiventris*): case study in spatio-temporal variation. Canadian Journal of Zoology. 78: 1158-1167.

Reaser, J.K.; Pilliod, D.S. 2005. Columbia spotted frog (*Rana luteiventris*). In: Lannoo, M.J., ed. Status and conservation of United States amphibians. Berkeley, CA: University of California Press: 559-563.

Relyea, R.A. 2005. The impact of insecticides and herbicides on the biodiversity and productivity of aquatic communities. Ecological Applications. 15(2): 618-627.

Rice, P.M. 2003. INVADERS Database System. http//invader.dbs.umt.edu. (June 19, 2003).

Ryser, J. 1988. Determination of growth and maturation in the common frog, *Rana temporaria*, by skeletochronology. Journal of Zoology, London. 216: 673-685.

Sype, W.E. 1975. Breeding habits, embryonic thermal requirements and embryonic and larval development of the Cascade frog, *Rana cascadae* Slater. Corvallis, OR: Oregon State University. 113 p. Ph.D. dissertation.

Turner, F.B. 1958. Life-history of the western spotted frogs in Yellowstone National Park. Herpetologica. 14: 96-100.

Turner, F.B. 1960. Population structure and dynamics of the western spotted frog, *Rana pretiosa* Baird & Girard, in Yellowstone National Park, Wyoming. Ecological Monographs. 30: 251-278.

Turner, F.B. 1962. The demography of frogs and toads. Quarterly Review of Biology. 37: 303-314.

U.S. Department of Agriculture, Forest Service; U.S. Department of the Interior, Bureau of Land Management [USDA USDI]. 1995. Environmental assessment: decision notice and finding of no significant impact. Interim strategies for managing fish-producing watersheds in eastern Oregon and Washington, Idaho, western Montana and portions of Nevada. (Inland Native Fish Strategy INFISH). [Place of publication unknown]: [Irregular pagination].

U.S. Geological Survey, National Wildlife Health Center. 2004. Diagnostic Service Case Report No. 19112. Madison, WI. 3 p.

Wente, W.; Adams, M.J.; Pearl, C.A. [In press]. Evidence of decline for *Bufo boreas* and *Rana luteiventris* in and around the northern Great Basin, western USA. Alytes. 22.

Whitaker, J.O., Jr.; Cross, S.P.; Skovlin, J.M.; Maser, C. 1983. Food habits of the spotted frog (*Rana pretiosa*) from managed sites in Grant County, Oregon. Northwest Science. 57: 147-154.

Wyrick, A.C. 2004. Demography of the Columbia spotted frog (*Rana luteiventris*) in the presence or absence of fish in the Absaroka-Beartooth Wilderness, Montana. Missoula, MT: University of Montana. 118 p. Ph.D. dissertation.

Pacific Northwest Research Station

Web site	http://www.fs.fed.us/pnw
Telephone	(503) 808-2592
Publication requests	(503) 808-2138
FAX	(503) 808-2130
E-mail	pnw_pnwpubs@fs.fed.us
Mailing address	Publications Distribution Pacific Northwest Research Station P.O. Box 3890 Portland, OR 97208-3890

This page has been left blank intentionally.
Document continues on next page.

U.S. Department of Agriculture
Pacific Northwest Research Station
333 S.W. First Avenue
P.O. Box 3890
Portland, OR 97208-3890