BEAVER REINTRODUCTION CORRELATES WITH SPOTTED FROG POPULATION RESTORATION AND TERRESTRIAL MOVEMENT PATTERNS OF NEWLY METAMORPHOSED COLUMBIA SPOTTED FROGS IN THE OWYHEE UPLANDS OF SOUTHWESTERN IDAHO

by

Hallie Anne Lingo

A thesis
submitted in partial fulfillment
of the requirements for the degree of
Master of Science in Biology
Boise State University

December 2013

BOISE STATE UNIVERSITY GRADUATE COLLEGE

DEFENSE COMMITTEE AND FINAL READING APPROVALS

of the thesis submitted by

Hallie Anne Lingo

Thesis Title: Beaver Reintroduction Correlates With Spotted Frog Population Restoration and Terrestrial Movement Patterns of Newly Metamorphosed Columbia Spotted Frogs in the Owyhee Uplands of Southwestern Idaho

Date of Final Oral Examination: 10 May 2013

The following individuals read and discussed the thesis submitted by student Hallie Anne Lingo, and they evaluated her presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

James C. Munger, Ph.D.	Chair, Supervisory Committee
Ian C. Robertson, Ph.D.	Member, Supervisory Committee
Peter Koetsier, Ph.D.	Member, Supervisory Committee

The final reading approval of the thesis was granted by James C. Munger, Ph.D., Chair of the Supervisory Committee. The thesis was approved for the Graduate College by John R. Pelton, Ph.D., Dean of the Graduate College.

ABSTRACT

This thesis examines topics relevant to Columbia spotted frogs (*Rana luteiventris*) in the Owyhee Uplands of southwestern Idaho. First, I present a detailed discussion of both the ecology and conservation status of spotted frogs. Concerns about declining spotted frog numbers in the southern portions of the species' range were first expressed in the early 1990's. In response, several studies on the behavior and ecology of spotted frog have been conducted by Boise State University. In addition, the Idaho Department of Fish and Game monitors the status of spotted frogs in the Owyhees using an occupancy model developed and implemented in 2007. For the most part, the population comprises small, semi-isolated breeding groups and is genetically structured by the drainages that it occupies. Spotted frogs in the Owyhees are listed as a species of concern under the Endangered Species Act of 1973.

Stoneman Creek in the Owyhees housed a robust population of spotted frogs that relied on habitat provided by a beaver dam, until the beaver were lost from the site in 1992. Following the loss of beaver at Stoneman Creek, the dam began to erode, eventually resulting in the loss of suitable habitat for spotted frogs. By 1998, surveys for spotted frogs along Stoneman Creek indicated a potential loss of the population. In an attempt to restore declining spotted frog habitat along Stoneman Creek, 5 beavers were released at the eroding beaver dam in 2001. At least one beaver settled along the stream and enhanced the eroding beaver dam, thus improving spotted frog habitat. The spotted frog population rapidly rebounded following beaver reintroduction to the stream. I found that spotted frog recruitment within the improved habitat occurred in two ways: through immigration and successful breeding.

I constructed a field experiment designed to look at the permeability of uplands to movements by newly metamorphosed spotted frogs. Because overland movements by frogs pose a high risk of desiccation, it is unclear whether frogs can undergo terrestrial movements to access wetlands for foraging and suitable overwintering habitat for individual survival and whether among-population movements can take place. I found that spotted frog metamorphs do in fact undertake small-scale terrestrial movements. Terrestrial movements occurred mostly overnight. With increasingly dry conditions, the probability of movements occurring became increasingly dependent on dropping temperatures. Dropping temperatures were used in analyses as a correlate for precipitation.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I: AN OVERVIEW OF THE ECOLOGY AND CONSERVATION STATUS OF COLUMBIA SPOTTED FROGS (*Rana luteiventris*) IN FRAGMENTED HABITAT PATCHES IN THE OWYHEE UPLANDS OF SOUTHWESTERN IDAHO

Introduction

Disjunct populations of Columbia spotted frogs (*Rana luteiventris*) live in portions of the high elevation desert of the Great Basin (Turner 1993; Munger et al. 1994; Reaser 2000; Engle 2001a; Columbia Spotted Frog Technical Team [CSFTT] 2003; Reaser and Pilliod 2005; Moser and Patton 2006; Moser 2007; Funk et al. 2008, Lohr and Haak 2009; Funk and Robertson 2011), one of the most arid regions in North America (Sada and Vineyard 2002). Although occasional springs, seeps, and wetlands provide habitat for frogs, these water sources are often ephemeral and can be separated by large expanses of arid uplands and often steep topography (Heaton 1990; Sada and Vinyard 2002). Steep topography has been shown to negatively affect gene flow among spotted frog populations (Funk et al. 2005). Spotted frogs in this region are rarely more than a few meters away from a water source (Engle 2001a; Gourley and Romin 2002; CSFTT 2003). These small, seemingly fragile creatures appear to be isolated in aquatic habitats that are fragmented by harsh climatic and landscape conditions.

Whether a landscape is relatively uniform in elevation and aspect, or exists as a rugged, mountainous terrain, one truth holds: At almost any scale, the earth consists of fragmented habitats (Lord and Norton 1990; Meffe and Carroll 1994). Habitat encompasses the sum of resources required by an individual, population, or species to successfully complete a life cycle (Franklin et al. 2002 and references therein). Fragmented habitat, within the context of the present study, is defined as the condition in which the landscape is not dominated by a single vegetative community, but rather consists of a mosaic of vegetation types and structures, of varying connectivity, and at numerous scales (Lord and Norton 1990; Franklin et al. 2002). Rarely is a large patch of habitat stable for a long period of time. Instead, habitat is always undergoing some form of disturbance that results in varied levels of seral progression and fragmentation (Huston 1979; Romme 1982).

With natural habitat fragmentation, species diversity and richness are maintained across the landscape, because, in an environment of change, no single species becomes so established that it out-competes and suppresses sympatrics (Connell 1979; Huston 1979). In addition, natural disturbance maintains habitat heterogeneity across a landscape, thereby allowing for a greater variety of niches and species (Huston 1979). However, with changing climatic regimes, some disturbances, such as wildfire, are increasing in frequency and intensity with unknown results on amphibian populations (Hossak et al. 2012)

Conversely, human-caused habitat fragmentation sometimes has detrimental effects on species diversity and richness across a landscape. By creating very simple habitats such as monocultural farm fields, plant diversity is lost and many fungal, insect, and other animal species are intentionally eliminated (Pimentel et al. 1992). Small, starkly delineated habitat patches, such as remnant forests following heavy timber harvest, have abrupt edges that directly abut denuded landscapes. Often, these abrupt shifts between habitat types create population sinks where few can survive and the species requiring transition zones are lost, a situation commonly called the edge effect (Gates and Gysel 1978). In habitats separated by artificial barriers, such as heavily trafficked roads, not only is species diversity lessened, but species inhabiting increasingly isolated habitat fragments persist at increasing peril (Meffe and Carroll 1994; Gravel et al. 2012). Furthermore, artificially fragmented landscapes often give rise to small, isolated habitat patches. Small habitat patches and habitat patch isolation are associated with the loss of species richness and an increased risk of extinction (MacArthur and Wilson 1967; Fahrig and Merriam 1985; Wilcox and Murphy 1985; Debinski and Holt 2000; McCoy and Mushinski 2007).

Habitat fragmentation affects species and communities in several ways and at several scales (Wilcox and Murphy 1985; Lord and Norton 1990). As landscapes become increasingly fragmented through human activities, entire habitat types become lost, patches of undisturbed habitat grow smaller, and species inhabiting remnant patches become isolated (Wilcox and Murphy 1985). Wiens (1989) noted that habitat fragmentation affected species in the following ways. First, fragmentation results in the direct loss of habitat area, shifting occupants to increasingly smaller habitat patches. Second, as landscapes grow increasingly fragmented, patches of suitable habitat grow increasingly isolated from like patches. Habitat patch isolation can result in an increased risk of extinction (MacArthur and Wilson 1967).

Aquatic habitats within the Great Basin Region of northern Utah, northern Nevada, southwestern Idaho, and southeastern Oregon are naturally fragmented by arid uplands (Heaton 1990; Sada and Vinyard 2002). The Great Basin became a haven for many species during glacial times of the Pleistocene Epoch, 35,000 to 10,000 years b.p. (Heaton 1990). The landscape features of the great Basin made it a moderate climate between deserts to the south and glaciated mountains to the north, thus creating suitable habitat for species fleeing the surrounding inhospitable regions (Heaton 1990). As temperatures began to rise with the start of the Holocene, the Great Basin grew increasingly arid, and many species began to radiate outward. However, some less mobile species remained in shrinking aquatic habitats, forming relict populations separated by increasingly arid uplands. Now those isolated pockets of water are in demand for uses such as livestock watering and agricultural irrigation (Sada and Vinyard 2002). These factors appear to be further isolating already patchily distributed species. One such species is the Columbia spotted frog.

Amphibians play a variety of important roles in their ecosystems (Dodd and Cade 1998 and references therein). As ectotherms, their energy is focused on reproduction and body mass attainment, rather than on thermoregulation. They produce large numbers of eggs and young that form the prey base for numerous taxa, including mammals, reptiles, fish, invertebrates, and birds. As adults, they are often voracious predators of invertebrates and, sometimes, even small mammals. Their choice of prey is seemingly limited only by their gape size and ability to forage away from aquatic habitats. As such, their loss from some systems can affect the food web as both predators and prey (Blaustein 1994).

In recent times amphibians have been undergoing losses in population numbers, and, in some cases, species are disappearing altogether from areas all over the planet (see references in Hayes and Jennings 1986; Blaustein and Wake 1990 and references therein;

Blaustein 1994; Bury 1999 for a review of references; Shoo et al. 2011). Anthropogenic practices such as urban development, exotic species introductions, and dam construction are implicated in the declines (Jennings and Hayes 1994). In addition, climatic changes are affecting the duration that ponds contain water, hydroperiod, and can support larval amphibians (McMenamin et al. 2008; Shoo et al. 2011; Amburgey et al. 2012). Humans, however, may also negatively affect amphibian survival through more subtle impacts on seemingly pristine environments (Fellers and Drost 1993; Blaustein 1994). For example, fire suppression facilitates seral progression and the encroachment of shrubs and woody plants into wetlands that amphibians depend on (Fellers and Drost 1993). Atmospheric phenomena such as increased ultraviolet radiation, global climate change, and air pollution acidifying water sources affect areas devoid of human habitation, and have also been implicated in amphibian losses worldwide (Wyman, 1990; McMenamin et al. 2008). As many as one third of the amphibian species occupying the United States appear to be imperiled to some extent (Bury 1999). Endemic amphibian species, ie., those whose range is limited and who are habitat specialists, tend to show more frequent losses in numbers (Bury 1999). The Columbia spotted frog shows patterns of endemism in the more southern portions of its range (Ross et al. 1994) and appears to be in decline (Turner 1993).

Suitable patches of frog habitat in the Great Basin are naturally fragmented due to seasonally arid conditions, limited resources, and their ephemeral nature (Engle 2001a; Gourley and Romin 2002; Munger and Lingo 2002; CSFTT 2003). Correspondingly, the Great Basin population of spotted frogs is divided into several subpopulations. In Nevada there are three subpopulations: (1) the Jarbridge-Independence subpopulation;

(2) the Ruby Mountain subpopulation; (3) the Toiyabe Range subpopulation (Green et al. 1996; Reaser 1997; CSFTT 2003). The Great Basin population extends so far north as to include frog populations in northeastern Oregon (Bull 2005; Funk and Robertson 2011). A portion of the Great Basin population known as the Owyhee subpopulation, occurs in southwestern Idaho, the region on which this thesis focuses.

Columbia spotted frogs in the Owyhee uplands of southwestern Idaho were classified as part of the Great Basin population when the species first received federal conservation status (Turner 1993). These southernmost populations of Columbia spotted frogs are disjunct from the rest of the species' range (Ross et al. 1994; Funk and Roberson 2011). In general, the number of frogs found within patches of suitable habitat in the Owyhees is relatively small (Munger et al. 1998; Engle 2001a; Munger and Lingo 2002 and 2003; Blankinship and Munger 2004; Funk and Roberson 2011).

In 1989, reduction in population numbers and some losses of historic populations led to the petitioning of the US Fish and Wildlife service to list Columbia spotted frogs for protection under the Endangered Species Act (ESA) of 1973. In 1993, the US Fish and Wildlife Service classified the Great Basin, West Desert, and Wasatch Front populations of Columbia spotted frogs as candidates for threatened or endangered status under the ESA (Turner 1993). The three populations warranting conservation status occupy the southernmost and arid portion of the species' range.

In 1997, the listing status of spotted frogs in the Great Basin and West Desert populations was further downgraded to prevent listing while conservation and restoration efforts were ongoing. The West Desert population of spotted frogs was withdrawn from federal candidate status altogether in 1998. This change in status followed the reduction of threats to the population along with development of a ten-year conservation agreement outlining ongoing protection and management plans (Utah Department of Wildlife Resources [UDWR] 2006).

By 2001, however, the Great Basin population of frogs received higher priority status because of increased threats to the species' persistence in these portions of its range (CSFTT 2003). Even by 2005, some populations of spotted frogs continued to undergo declines (Wente et al. 2005; Bull 2005 and references therein). A portion of the Great Basin population, the Owyhees subpopulation, received the highest listing rank possible for a subspecies because of the discovery of Chytridiomycosis fungus at a breeding pond (Engle 2001a), a decline in numbers, and imminent threats to some of the larger breeding groups within the population (US Fish and Wildlife Service [USFWS] 2006).

The population trends of the Owyhee subpopulation of spotted frogs had been tracked by a monitoring protocol first initiated in 2000 (Engle 2000). The Idaho Department of Fish and Game revised the population monitoring protocol in 2007 (Moser 2007). The current monitoring plan is based on modeling the occupancy patterns of potential habitat across the landscape (Moser 2007). Because the model requires several years of data to provide accurate information on population trends, it is unclear whether the population of spotted frogs within the Owyhees continues to decline. What does seem apparent, however, is that observations are positively linked to annual precipitation (Munger and Lingo 2003; Lohr and Haak 2009).

The Owyhee Mountains

Over 3.6 million acres of Owyhee County are publicly owned and managed by the Bureau of Land Management. Throughout the upland area, juniper (*Juniperus* *osteosperma*) and mountain mahogany (*Cercocarpus ledifolius*) are the primary trees. Aspen (*Populus tremuliodes*), and birch (*Betula papyrifera*) are occasionally associated with seeps and springs. The rest of the habitat is characterized as sagebrush-steppe with willows (*Salix spp.*) sometimes dominating areas surrounding permanent water.

The mountains reach 2400m in elevation. Although it is common for the Owyhees to receive over 1.5m of snow in the winter, there is often little or no rain throughout the summer months. Rain typically begins to fall in mid-to-late September, marking the start of the major precipitation season in the Owyhees. In the spring, the last vestiges of snowpack, at moderate elevations, are gone by June.

Columbia Spotted Frogs

Taxonomy

Baird and Girard (1853) are credited with first recognizing the spotted frog, *Rana pretiosa*. Later, the taxon was divided into two subspecies based on pigmentation (Thompson 1913). With increased focus on the differences in form as related to range, the more eastern subspecies of spotted frogs became *Rana pretiosa luteiventris*, based on morphological differences, while the subspecies in the western portion of the spotted frogs' range was *Rana pretiosa pretiosa* (Morris and Tanner 1969).

The US Fish and Wildlife Service further subdivided the two subspecies into five separate populations: 1) *The Main Population,* (now considered *Northern*), ranging from Alaska, British Columbia, Alberta, Wyoming, Montana, northern and central Idaho, to eastern Washington and northeastern Oregon, where they are considered abundant (Gomez, 1994); 2) *The Great Basin Population,* occurring in southwestern Idaho, southeastern Oregon, and northern Nevada; 3) *The West Coast Population* is located in western Washington, western Oregon, and northeastern California (range of present-day *Rana pretiosa*); 4) *The Wasatch Front Population,* in Utah and; 5) *The West Desert Population* which is also in Utah (Turner 1993).

Following allozyme and quantitative morphometric analyses, the eastern and western subspecies of spotted frogs were separated at the species level, and the Columbia spotted frog *Rana luteiventris* was first recognized in the eastern portion of the ranid's range (Figure 1). The Oregon spotted frog, *Rana pretiosa*, was designated as the more western species and is limited to northeastern California, western Oregon, and western Washington (Green et al. 1996).

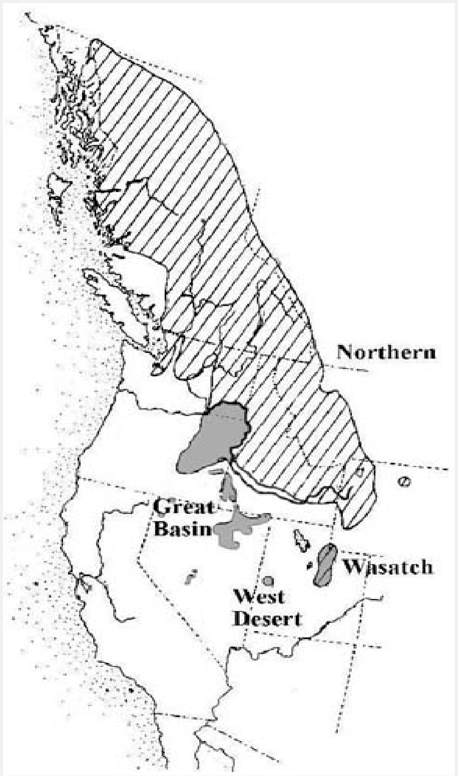


Figure 1. Range of Columbia spotted frogs (Green et al. 1996). Note that the West Coast population is not labeled in the range map. This map resulted from a paper separating the West Coast population into a species distinct from Columbia spotted frogs, The Oregon spotted frog *(Rana pretiosa*). The Columbia spotted frogs in the

southern portion of the species' range have conservation listing status because of declining numbers. The populations to the south are disjunct from the northern population

Genetic analyses of Columbia spotted frogs throughout their range confirm that there are distinct, non-mixing populations of frogs, the most isolated of which are those to the south in Utah and Nevada (Bos and Sites 2001). However, the Owyhees subpopulation of spotted frogs, a portion of the Great Basin population that occurs in southwestern Idaho, were not included in their analyses. It was later found that Owyhees subpopulation does not appear to mix with other portions of the Great Basin population (Funk et al. 2008).

Identification

Although maximum adult size appears to vary across the frog's range and by gender (Bull 2005), adult Columbia spotted frogs in the Owyhees range in snout-vent length from 55 mm to 90mm (Engle 2001a). The maximum age of captured spotted frogs also appears to vary by geographic area (Bull 2005). Efforts to age Owyhees spotted frogs using skeletochronology found the maximum age to be nine years (Engle and Munger 1998).

Columbia spotted frogs have light to dark brown or olive dorsal surfaces with variable spot numbers, patterns, and shapes (Engle 2001a). Spotted frogs differ from leopard frogs, which are closely-related and occasionally sympatric, in several ways. Spotted frogs' dorsal spots do not have a lighter colored halo like that found on the leopard frog (Corkran and Thoms 1996). Also, the webbing on the hind feet of leopard frogs does not extend to the phalange tips as it does on spotted frogs (Corkran and Thoms 1996). The ventral pigmentation of the two species differs in that spotted frogs have a characteristic yellowish wash that is not shared by the mostly white-bellied leopard frog (CSFTT 2003).

A key diagnostic feature of spotted frogs is their cream colored or yellowish jaw stripe, which runs from the snout to just over the front limb (Engle 2001a; Bull 2005). Often all that is seen of frogs is the snout protruding from the water, and in the case of spotted frogs, the jaw stripe is visible (Figure 2). The dorsolateral fold is conspicuous on spotted frogs and is also diagnostic. Columbia spotted frogs have ventral surfaces that are orange, yellow, or white (Figure 3). The yellow color morph is dominant in the Owyhees, but individuals can have the darker orange coloration as well (Engle 2001a). Younger spotted frogs have less distinct coloration, especially on the ventral surface, which is mostly without pigmentation upon emergence and for most of the first year.

Figure 2. Diagnostic pale jaw stripe of spotted frogs. Because spotted frogs often bask by submerging most of their bodies with only their snout out of the water, this is typically the only part of the frog a surveyor will see. Being able to recognize the jaw stripe is helpful in areas where the range of a similar species overlaps that of spotted frogs.

Figure 3. Orange ventral pigmentation typical of an adult spotted frog. The pigmentation generally develops by the second year. If there is a question as to whether a captured frog is a metamorph, subadult, or adult, checking for this pigmentation can be helpful. In subadults, the ventral pigmentation may start as white and shift to yellow or orange as the individual matures. In juveniles, there is no ventral pigmentation.

Columbia spotted frogs are sexually dimorphic in that adult males have swollen and darkened thumb bases, called thumb, or nuptial pads (Figure 4) (Engle 2001a). Adult males over two years old are slightly smaller than females of the same age class (Bull 2005). Adult females are probably inherently larger than males to allow egg mass development (Turner 1962).

Figure 4. Nuptual pads of an adult male spotted frog. The nuptual pads aid males in amplexus. Female and juvenile spotted frogs do not have nuptial pads.

Anurans sympatric with spotted frogs in the Owyhees are easily distinguishable from one another as adults. Western toads, *Bufo boreas,* are more terrestrial than spotted frogs and are accordingly more rugose, and the webbing on their hind feet does not extend to the tip of the toes, unlike in spotted frogs. Toads have raised and obvious granular glands down their dorsal surface, and their key diagnostic feature is the light-colored stripe down the center of their back (Figure 5). Pacific tree frogs, *Hyla regilla,* are brown, tan, or green. Their key diagnostic features are a black eye patch or mask that extends from the tip of the snout to the shoulder and their suction cup-like toe pads that allow them to cling to vertical surfaces (Figure 6) (Corkran and Thoms 1996).

Figure 5. A western toad (*Bufo boreas*). Western toads are found at sites where spotted frogs occur in the Owyhees. However, toads are identifiable by their dorsal stripe, granular skin, and heavy limbs.

Figure 6. The Pacific tree frog (*Hyla regilla*). Tree frogs are identified by their black eye stripe. Tree frogs are widespread throughout the Owyhees and are seen at spotted frog breeding sites in the spring. During the summer months tree frogs are more nocturnal, and it becomes uncommon to see adult tree frogs.

Egg masses also differ among the amphibian species found in the Owyhees. Spotted frog egg masses are free-floating at the surface of the water. Although they are commonly found clustered, single spotted frog egg masses are rounded and roughly the size of a softball (Figures 7 and 8). Long-toed salamanders (*Ambystoma macrodactylum*) frequently breed in the same ponds as spotted frogs in, at least some portions of the spotted frog's range. Their egg masses are visible as numerous embryos within a single jelly mass. Tree frog embryos are each encased in a single egg that is singly laid. Both long-toed salamanders and Pacific tree frogs attach their eggs to submerged vegetation (Figure 9). Western toads deposit eggs in jelly-coated strands that are distinct from the eggs of all other amphibians in the Owyhees (Figure 10).

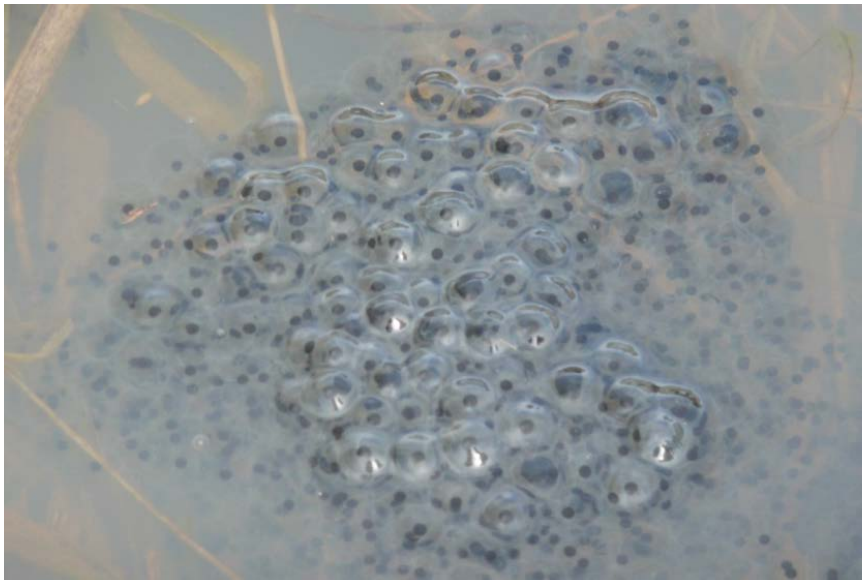


Figure 7. A single spotted frog egg mass. Spotted frog egg masses are roughly the size of a softball and can be found floating on the surface of shallow, standing water. Spotted frogs do not adhere egg masses to submerged vegetation.

Figure 8. Cluster of spotted frog egg masses. It is common to find communal spotted frog breeding sites with several egg masses deposited in the same area.

Figure 9. Long-toed salamander egg masses (red) next to Pacific tree frog egg masses (yellow). In contrast to spotted frogs, both species attach egg masses to submerged vegetation.

Figure 10. Western toad egg strands (Photo by Charles Peterson, Idaho Natural History Museum, Idaho State University). Western toads have the most distinct egg structures of all Owyhees amphibians. Toads may deposit egg strands in standing or slow-moving water.

The larval forms of the Owyhees anurans are also distinguishable from one another. Spotted frog tadpoles have very round silhouettes when viewed from above, and their eyes protrude from the topmost portion of their heads (Engle 2001a). Tree frog tadpoles have eyes that protrude from the sides of their heads, breaking the outline of the tadpole's body. Western toad tadpoles often occur as a large swarm of small, very dark larvae whose tail silhouette, when viewed laterally, is very low (Corkran and Thoms 1996).

Life History

The Columbia spotted frog breeding season begins after the emergence of frogs in April or May, depending on elevation and weather (Morris and Tanner 1969). Late April marks the peak of Columbia spotted frog breeding in the Owyhees (Engle 2001a). Males emerge from hibernation first and aggregate, forming calling groups at breeding ponds.

Within a week, egg masses form in communal clusters in water less than 30 cm deep in ponds, stream backwash areas, and oxbow pools.

Larvae emerge from egg masses within two to three weeks of egg mass deposition (Engle 2001a). Spotted frog larvae, commonly called tadpoles, in the Owyhees require standing or extremely slow-moving water such as ponds or oxbows in streams (Munger et al. 1997). Tadpoles use mud substrate and aquatic vegetation as refugia. Egg masses hatch in early May and tadpoles mature during the warm summer months, eventually emerging as quadrupedal metamorphs as early as mid-July. Metamorphs emerge throughout the late summer months and into October or November, depending on the year's first freezing temperatures. Although unconfirmed, there is evidence that some spotted frogs in the Owyhees may overwinter as tadpoles (Engle 2001a). In other portions of their range, emergence occurs in the same year as deposition (Pilliod and Peterson 2001). Following emergence, metamorphs survive the winter by hibernating and spend the following summer growing into subadults.

The age at which spotted frogs reach sexual maturity varies within the species' range and by gender, so that frogs can take anywhere from one winter to six years to breed (Bull 2005). Engle (2001a) found that within the Owyhees subpopulation, male frogs are generally large enough to breed by their third year and females by their fourth year.

Adult spotted frogs are opportunistic predators of a wide variety of insect food, often including terrestrial species in their diets (Bull 2005). Spotted frogs are cannibalistic, and adult frogs will eat metamorphs (Bull 2005; Engle 2001a; pers. obs.).

Larval Columbia spotted frogs feed on pond substrate and algae attached to submerged portions of aquatic vegetation (Howard and Munger 2003).

Habitat

Key habitat components required by spotted frogs include hibernacula that provide oxygenated water that will not freeze over winter, suitable breeding areas that contain still or slow moving water with emergent vegetation and with shallow areas that persist long enough for larvae to hatch, insect-rich foraging sites protected by vegetation such as those found in wetlands, refugia such as deep water and dense willows or standing water with floating vegetation where frogs are protected from disruption and predation, open, standing water with little or no shade for basking, and adequate travel corridors that allow frogs to move among foraging, breeding, refuge, basking, and overwintering habitats (Reaser 1997; Engle 2001a; Pilliod and Peterson 2001; Munger and Lingo 2002).

Spotted frogs migrate among key habitat components (Patla 1997; Engle 2001a; Pilliod et al. 2002). Thus, corridors for movement among key habitat components are also critical to spotted frog populations. However, it is unknown at this time what constitutes migratory habitat for spotted frogs in the Owyhees.

Summary

Spotted frogs live in semi-isolated sources of standing, or slow-moving water in the Owyhees. The status of the population is currently monitored by the Idaho Department of Fish and Game. The ongoing monitoring efforts are designed to predict the long-term trajectory of the species. In 2009 it was noted that population numbers tended to fluctuate with annual precipitation levels. However, at that time there was not sufficient information upon which to base further conjecture about the status of the Columbia spotted frog population in the Owyhees.

CHAPTER II: BEAVER (*Castor canadensis*) REINTRODUCTION CORRELATES WITH COLUMBIA SPOTTED FROG (*Rana luteiventris*) POPULATION RESTORATION

Introduction

It has been suggested that many pond-dwelling amphibians in the United States had higher population numbers and wider distributions when they were able to make use of beaver (*Castor canadensis*) impoundments, prior to massive losses of beaver in the western United States (Reaser 1997). For example, lost lentic habitat associated with beaver extirpation has been associated with amphibian declines in the Willamette Valley, Oregon (Olson and Leonard 1997). Beaver are habitat-modifying keystone species whose dam-building behavior can provide key habitat for other species (Stoffyn-Egli and Willison 2011), especially in relatively arid regions (McKinstry et al. 2001).

In a number of arid portions of the west, stockponds, built concurrently with beaver losses, may have provided surrogate habitat for frogs (Reaser 1997). However, water impoundments developed for use as irrigation and livestock watering may be less than ideal amphibian habitat. Ponds excavated for livestock use are sometimes isolated from other water sources by arid uplands for all or most of the year, thereby isolating resident frogs and rendering ponds inaccessible to dispersers (Munger and Lingo 2002). In addition, although frogs depend on ponds for breeding, other landscape features also affect frog population numbers (Sjogren 1994; Patla 1997; Pope et al. 2000; Rothermel

2004). For example, degradation of wetland meadows that provide frogs with foraging habitat and damage to springheads where frogs overwinter often occurs at developed water sources. The end result is sometimes termed the ‘negative matrix effect’ and happens when ponds appear to provide frog habitat, yet losses in frog population numbers still occur due to degradation in other landscape features (Sjogren 1994).

Beaver-created wetlands provide habitat that satisfies the entire life history requirements for some amphibian species (Cunningham et al. 2007). The shallow margins with slow moving or still water provide sites for egg mass deposition. The longer hydroperiod associated with beaver activity allows for larval development. The tall grasses of wetlands help protect frogs from desiccation and predation, while also providing habitat for insects that frogs rely on for prey. The availability of required habitat components and the extent to which frogs can travel among required key habitats, habitat complementation, can determine the presence of amphibians in an area (Rothermel 2004).

Despite their presence throughout most of North America (Figure 11), in some areas of the western US, beaver presence is a rare occurrence (Baker and Hill 2003). Beaver in North America were trapped to near extinction from the 1600’s into the early 1900’s (Naiman et al. 1986 and references therein). Before European settlement in North America, the beaver population was estimated at 60-400 million (Seton 1929 *in* Baker and Hill 2003). Present-day population estimates put beaver numbers between 6-12 million (Naiman et al. 1988). Although beaver numbers have improved since the overharvest of the 1800’s, vast areas that were originally flooded by beaver dams are now dry (Naiman et al. 1986).

Figure 11. Current distribution of beaver (*Castor canadensis*) throughout the United States, Mexico, and Canada (Baker and Hill 2003). It is thought that beaver continue to expand their range, especially in some portions of the western United States and into Mexico.

At present, beaver are often viewed as pests (Baker and Hill 2003). They can block irrigation ditches and culverts, and flood roads, pastures, and crops (McKinstry and Anderson 1999; Collen and Gibson 2001). However, despite the negative effects beaver can have on developed land, they are increasingly recognized as a positive part of ecosystem function (DeVries et al. 2012). Landowners in Wyoming reported that beaver activity improved riparian health, raised water tables, and provided a source of standing surface water for livestock (McKinstry and Anderson 1999). Researchers are finding that imitating beaver dam construction within compromised stream corridors improves riparian health and fish habitat (DeVries et al. 2012). With respect to amphibians, beaver activity increases wetland hydroperiod for larval development, the amount of water available for frog breeding habitat, wetted meadows for foraging, and connectivity among suitable habitat patches (Cunningham et al. 2007; Scherer et al. 2012).

Beaver dams inundate areas, allowing beaver access to willows and other food sources without leaving the protection afforded by water (Berry 1923). Moreover, the deep water associated with dams protects the opening to beaver lodges (Collen and Gibson 2001). Dams may be constructed of a variety of materials, including sagebrush, woody plants, aquatic vegetation, plastic, metal, and other debris (Baker and Hill 2003). There is evidence that beaver are selective of their dam construction materials and will use the less palatable stems in construction, intentionally saving food items.

Beaver can build more than 10 dams per km of stream, entirely altering the geomorphology of stream reaches and creating impoundments for runoff that would otherwise scour stream stretches (Naiman et al. 1986). The interconnected ponds and wetlands created by beaver are often very long-lived as beaver maintain dams throughout their lives, and as subsequent generations continue that maintenance (Johnston and Naiman 1990). Beaver dams sometimes increase the wetted surface area of the channel up to several hundredfold (Johnston and Naiman 1990). When beaver establish along a stream corridor, what had been a running stream, confined to its banks, becomes a large area of shallow, standing water and a complex series of interconnected wetlands and channels (Naiman et al. 1986). The interconnection of the active stream channel with the surrounding floodplain promotes riparian growth (DeVries et al. 2012), potentially providing habitat for amphibians (Stoffyn-Egli and Willison 2011).

Because beaver activity has the potential to enhance frog habitat, I conducted a pilot study in which beaver were reintroduced in an area of the Owyhees to see if this had a positive effect on Columbia spotted frogs. Beaver were reintroduced into Stoneman Creek, a stream with a history of beaver activity, and the site of a declining spotted frog population. Although other streams in the Owyhees show evidence of past beaver activity, Stoneman Creek was the only place where reintroduction efforts were focused in this preliminary study. Signs of beaver activity along other streams indicate that there is suitable beaver habitat within some of the watersheds in the Owyhees.

The beaver at Stoneman Creek were killed in 1992 (Colleen Sweeney, Jill Holderman, Pers. Comm.). In 1993, when surveys of spotted frogs began on Stoneman Creek, the beaver dam was still intact (Munger 1994). The stream had several oxbows and a large reservoir that frogs used for breeding, basking, and foraging (Engle 2000). The beaver impoundments resulted in a large wetland complex that appeared to provide optimal frog habitat (Tim Carrigan, Pers. Comm.). However, in the absence of maintenance by beaver, the dam eroded (Figure 12). By 2000, what had been frog breeding habitat behind the dam and in nearby oxbows reverted to flowing stream and arid uplands (Engle 2000). In the years following the loss of beaver on Stoneman Creek, the resident frog population began to decline in numbers (Figure 13).

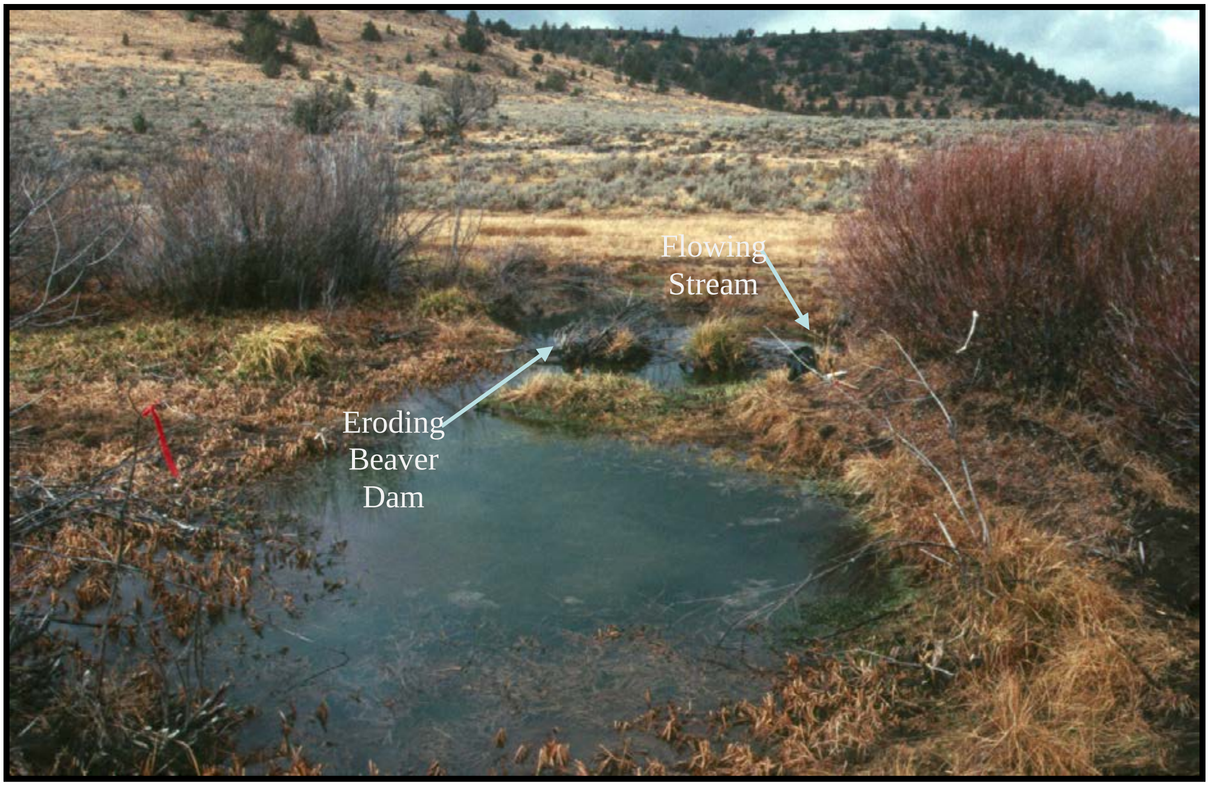


Figure 12. The eroding beaver dam on Stoneman Creek. The flowing portion of Stoneman Creek began to erode the beaver dam by 2000, following the loss of beaver in the early 1990's (Engle 2000). The shallow portion of the impoundment (located in the foreground of the picture) was an egg mass deposition site (Munger and Lingo 2002 and 2003; Blankinship and Munger 2004). Spotted frogs require standing, or slow-moving water for egg mass deposition, so the potential loss of this habitat may have been significant for the resident frogs.

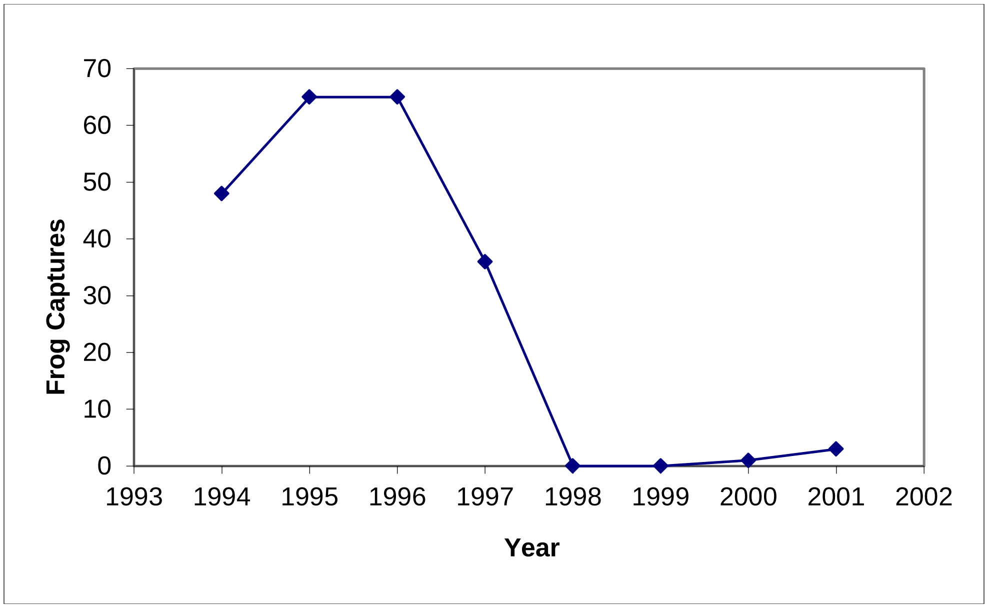


Figure 13. Declining spotted frog captures on Stoneman Creek as the beaver dam eroded, following the loss of beaver in 1992. The data presented were taken from a series of reports where survey timing and intensity varied slightly among years (Munger et al. 1994; Munger et al. 1995; Munger et al. 1997; Engle 2000 and 2001a; Munger and Barnett 2002). Therefore, these numbers should be taken as generalities.

In the summer of 2001, in an effort to restore the spotted frog subpopulation, the remains of the beaver dam were artificially repaired. The idea was that reintroduced beaver would be more likely to remain if provided with preexisting habitat. Following repairs to the dam, five beavers were released with the intention that at least one would establish at the site and maintain the dam, thereby enhancing frog habitat. The intention was to attract spotted frogs back to Stoneman Creek. What was unclear is where the frogs might come from.

In the two years (2002 and 2003) following the beaver reintroduction on Stoneman Creek, I attempted to address the following questions: did the creation of an artificial reservoir facilitate beaver reintroduction? Does beaver reintroduction result in increased standing water, potentially improving spotted frog habitat? Did spotted frog numbers along Stoneman Creek change following the release of beaver? In the event of spotted frog population increases, are they realized via local reproduction, or immigration?

Study Area

Stoneman Creek was a long-established site because of its history of beaver occupancy and repeated annual surveys for spotted frogs (Munger et al. 1994; Munger et al. 1995; Munger et al. 1997; Engle 2000 and 2001a; Munger and Barnett 2002). The portion of the creek where the study took place stretches just over 1 km and is found on the 7.5 minute quad map titled Slack Mountain at the following coordinates: Township 10S range 3W section 7. The beaver dam sits at almost the midpoint of the survey stretch. Stoneman Creek has a 4-6% gradient where beaver reintroductions occurred. The beaver dam is located at approximately 1600m in elevation.

Spotted frogs breed on Stoneman Creek in mid-through late April in most years. The surface of the reservoir froze before the end of October in 2003 and spotted frog activity had ceased for the winter by that time. In most years the spotted frog activity period lasts for six to seven months.

The dense riparian growth along Stoneman Creek is dominated by Geyers willows (*Salix geyeriana*), sedges (*Carex spp.*), and mixed forbs (Figure 14). The xeric slopes above the stream to the south house several naturally-surfacing springs visible because of their stands of aspen (*Populus tremuloides*). The surrounding landscape is characterized by shrub steppe.

Figure 14. The valley housing Stoneman Creek. Note the beaver reservoir to the right in the photograph. The picture was taken from the southern slope of the valley where the upland is dominated by arid shrub steppe. The stream has a 4% gradient in the photographed section.

A series of naturally-surfacing springs form the headwaters of Stoneman Creek. Current Creek flows into Stoneman Creek, and is its only large tributary (Figure 15). From its confluence with Current Creek, Stoneman Creek flows into Deep Creek. Both Current Creek and Deep Creek have records of occupancy by spotted frogs (Engle 2000; Munger and Lingo 2002 and 2003). The surveyed stretch of Stoneman Creek and its confluence with Current Creek are bisected by private property where surveys have never taken place. Similarly, the headwaters of Stoneman Creek are on private land and have never been surveyed. Therefore, the level of connectivity between the Stoneman Creek spotted frog population and the surrounding spotted frog populations is unclear. For Ranid frogs in general, populations need to be separated by more than 5km within a shared watershed to be considered separate (Hammerson 2002). Neither Current Creek nor Deep Creek is that far from Stoneman Creek. Both lie less than 3km away from where surveys take place on Stoneman Creek.

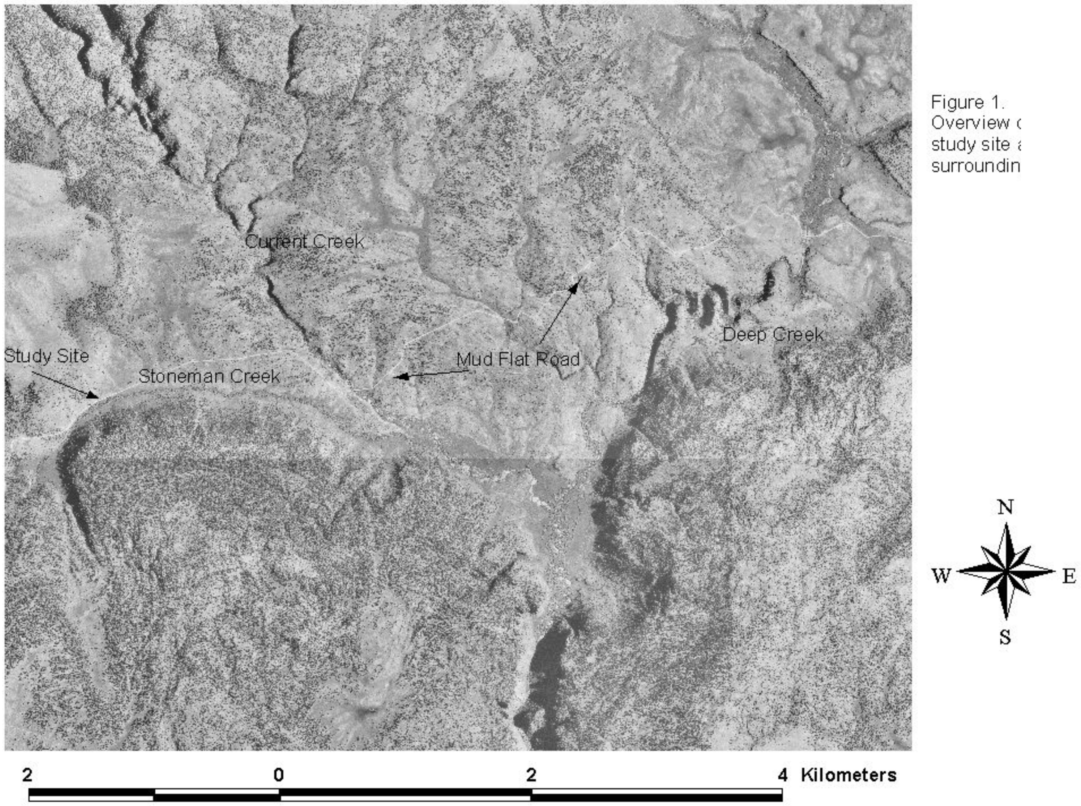


Figure 15. Aerial photograph of Stoneman Creek, its only large tributary, Current Creek, and its confluence with Deep Creek. Current Creek flows into Stoneman Creek approximately 2.7 kilometers from Stoneman Creek's headwaters and 1.9 kilometers from the surveyed stretch of stream. Stoneman Creek flows into Deep Creek roughly 1 kilometer downstream from its confluence with Current Creek. Both Current and Deep Creeks contain spotted frogs, however, whether there is dispersal among the creeks is unknown. Image from the Bureau of Land Management, Boise, Idaho, U.S.A., 2003.

Materials and Methods

Dam Restoration and Beaver Reintroduction

Because the beaver were no longer available to make repairs to the dam, the reservoir above the beaver dam was losing water through a breach caused by erosion (Figure 16). During the summer of 2001, BSU and BLM personnel patched the eroding beaver dam with a standard irrigation dam. A timber was braced horizontally across the breach in the beaver dam. Boards were then leaned against the timber (Figure 17). A 7.6 meter-long piece of 2.3 meter-wide plastic dam material was strung onto a 5-centimeter diameter steel pipe designed to support the top edge of the dam. The edges of the plastic material were imbedded into the stream bank and substrate to hold the dam material in place.

Figure 16. Breach in the beaver dam where the reservoir lost water and the current began to flow. This breach potentially impacted the resident spotted frog population because the reservoir was a site of egg mass deposition and spotted frogs do not usually deposit egg masses in areas of flowing water.

Figure 17. Framework of the irrigation dam built in 2001. The dam was designed to slow the flow of Stoneman Creek in order to provide suitable spotted frog habitat and to encourage settlement by beaver that were released into the reservoir following repairs.

During August and September 2001, one juvenile and four adult beavers were transported to Stoneman Creek and released. One adult beaver was introduced on August 29; one kit and one adult were introduced on 5 September; two more adults were introduced later in September. Gender was not determined on any of the translocated beaver. All individuals were released at the dam site (Figure 18). All had been captured in the Boise area after being reported as nuisance beaver.

Figure 18. Completed irrigation dam and beaver release site in August and September of 2001. The purpose of the irrigation dam was to provide translocated beaver with suitable habitat in order to induce their settlement along Stoneman Creek.

In an attempt to quantify any changes in the impoundment on Stoneman Creek, surveyors walked the margin of the original reservoir in August of 2001 collecting GPS points. The process was repeated following the artificial repairs to the dams in September of 2001, and again, in the year following beaver reintroductions reintroductions, 2002. The GPS points were then plotted onto aerial photographs of Stoneman Creek to illustrate changes in the reservoir over time.

Frog Surveys and Marking

Surveyors attempted to capture all adult spotted frogs along the surveyed stretch of Stoneman Creek in order to determine whether the captured frog had been previously implanted with a PIT (Passive Integrated Transponder) tag (Northwest Marine

Technologies [NMT] 2012) and to implant tags into unmarked frogs. In addition, I attempted to capture and mark as close to all newly-metamorphosed spotted frogs within the beaver reservoir as possible. A goal of surveys was to put captured frogs in as little peril as possible.

We used visual encounter surveys to find both adult and juvenile frogs within the reservoir and along Stoneman Creek (Olson and Leonard 1997). Surveys extended roughly 0.5km upstream and downstream from the beaver dam. Visual encounter surveys consist of slowly walking the margin of a pond, or stream in an attempt to flush hidden frogs and search for those frogs partially submerged in water for capture. Within the reservoir, surveys were limited by water depth and pond substrate. Surveyors were allowed to use their own discretion in determining how deep to wade into the reservoir in the pursuit of a sighted frog. We found that long-handled dipnets with circular baskets were the most effective means of capturing frogs in deep water. In shallower areas, we often caught frogs by hand.

Handling protocol differed between metamorphs and adults. Captured metamorphs were held in livewells during the survey period to avoid the repeated recapture of the same individuals and to expedite the marking process described below. Livewells consisted of 18.9 L buckets with 2.5 cm holes drilled through the walls on all sides. The holes allowed oxygenated water to flow through the livewells and kept the temperature within livewells equal to that of the surrounding habitat. Captured metamorphs within the present study were never held in livewells for over four hours.

Surveys were terminated when one or more of the following three conditions were met: (1) a 20 minute period went by during which time no metamorphs were observed.

(2) All captures were previously-marked metamorphs. (3) Survey duration had reached four hours and frogs in livewells needed to be released. Because young spotted frogs, which are cryptically colored, do not vocalize, survey duration varied with the terrain and vegetative cover at a site within the mentioned time constraints (Blomquist 2000). Surveys for metamorphs in 2002 began in July when metamorphosis was complete and continued into October, at which time the frogs ceased activity for the winter.

Captured adult frogs were weighed in grams and their snout-vent lengths (SVL) were measured in millimeters. Starting in 1997, if the captured individual measured over 40mm in SVL, a PIT tag was implanted through a small incision on the dorsal surface just posterior to the head (Engle 2001a). PIT tags persist for the duration of the frog's life and provide a unique code for each individual. This allowed me to enumerate the number of frogs captured season-long without concerns about recaptures artificially inflating apparent subpopulation numbers. In addition, the presence or absence of a PIT tag was used to determine whether a captured adult frog had originated at Stoneman Creek. Following the implantation of PIT tags and collection of body metrics, adult spotted frogs were immediately released at the capture site.

Visible Injected Elastomer (VIE) dye (NMT, 2012), rather than PIT tags were used to mark metamorphs. The dye was injected subcutaneously into the hind foot of each suitably-aged capture (Nauwelerts et al. 2000; Kendell 2001). The dye was injected with a 0.3cc syringe into the webbing that separated digits on the frog's hind foot (Figure 19).

Figure 19. Depiction of a VIE mark on a metamorph. We inserted the needle at the ankle (blue arrow), the first joint located proximally from the foot's plantar surface, and then moved the needle to the webbing subcutaneously. This approach prevented dye from seeping out of the insertion point before it hardened.

The biocompatible VIE dye consists of a color elastomer and a curing agent. The two components were mixed together in a 10:1 ratio. Following injection the compound hardens into a flexible solid within a few hours. The hardening process can be slowed by refrigerating the mixture in order to maximize the time surveyors may need to mark captured frogs.

We limited our marking efforts to metamorphs that were near the end of the transformation process and had reached Gosner Developmental Stage 46 (Gosner 1960). Metamorphosing frogs were examined for the pointed snout and more pronounced nares of older frogs before marking (Figure 20). When possible, we avoided capturing the younger metamorphs. Because younger metamorphs (pre-Gosner stage 46) do not have the more rugose skin of fully developed frogs, we were concerned that the handling required to mark these individuals would be excessively stressful (Figure 21). Therefore, younger frogs were immediately released.

Figure 20. Spotted frog metamorph that was old enough (Gosner Developmental Stage 46, Gosner 1960) for marking. Note the rugose skin, lack of tail, and pointed snout, all of which indicate a fully-metamorphosed juvenile frog.

Figure 21. Metamorphosing spotted frogs. Neither of the frogs pictured were suitable for marking. The metamorph in front still has tail remnants and is in stage 44-45 of development (Gosner 1960). The metamorph in back is still fully-aquatic and is unsuitable for marking.

Assumptions

In an attempt to determine whether frogs captured along Stoneman Creek in 2003 were adult immigrants, or the result of increased breeding effort on the part of frogs already in residence, I applied three critera to define captured adults. I assumed that any frog fitting all three of the following criteria had grown to maturity elsewhere and then immigrated to the beaver dam area on Stoneman Creek.

(1) The frog measured over 57mm. I used VIE marking on emerging metamorphs in 2002 to establish growth rates. Knowing the growth rate of metamorphs allowed me to establish a size criterion for age. The largest emerging young from 2002 reached an SVL of 57mm when recaptured the following year. My observations on metamorph growth rates indicate that it is highly unlikely that a metamorph would reach an SVL of greater than 57 mm in one year. Therefore, I adopted the generalization that individuals over 57mm were at least 2 years old.

(2) The frog did not have a VIE mark. As described above, I intensively captured and marked metamorphs during emergence in 2002 at the reservoir. Therefore, frogs not bearing VIE marks were assumed to be from a natal site separate from the Stoneman Creek beaver complex.

(3) The captured frog lacked a PIT tag. Since 1997 adult frogs along the stretch of Stoneman Creek, where beaver activity has been noted, have been captured and implanted with PIT tags. The frogs in the beaver impoundment along Stoneman Creek were PIT tagged as part of mark-recapture surveys included in a spotted frog monitoring protocol (Engle 2000). In addition, several

studies on the ecology of spotted frogs have taken place on Stoneman Creek and also involved intensive PIT tagging (Munger et al. 1997; Engle and Munger 1998; Idaho Conservation Data Center 1999; Engle 2001a; Munger and Barnett 2002; Munger and Lingo 2002, 2003). Therefore, I assumed that a frog growing to maturity on the surveyed stretch of Stoneman Creek would have been captured and PIT tagged during one of the numerous surveys taking place on Stoneman Creek over the years.

Results and Discussion

Did the creation of an artificial reservoir facilitate beaver reintroduction?

Beaver activity at the reservoir was evident by the spring of 2002. The presence of beaver was confirmed by the repairs made to the irrigation dam (Figure 22). In addition, numerous smaller dams (Figure 23) were newly built throughout the stream channel (Figure 24). There were no smaller dams along the surveyed stretch of Stoneman Creek prior to beaver reintroduction.

Figure 22. Repairs made to the irrigation dam by newly-resident beaver during the summer months of 2002. Five beaver were reintroduced, during August and September of 2001. The irrigation dam was designed to preserve spotted frog habitat in the reservoir above, and to encourage settlement by beaver released at the site.

Figure 23. A newly-constructed beaver dam on Stoneman Creek in 2003. Five beaver were released at a large reservoir 200m downstream from this dam in 2001.

The additional dams further changed the flow patterns of Stoneman Creek. The areas of standing and slow moving water created by the smaller dams were observed to be used by spotted frogs for basking.

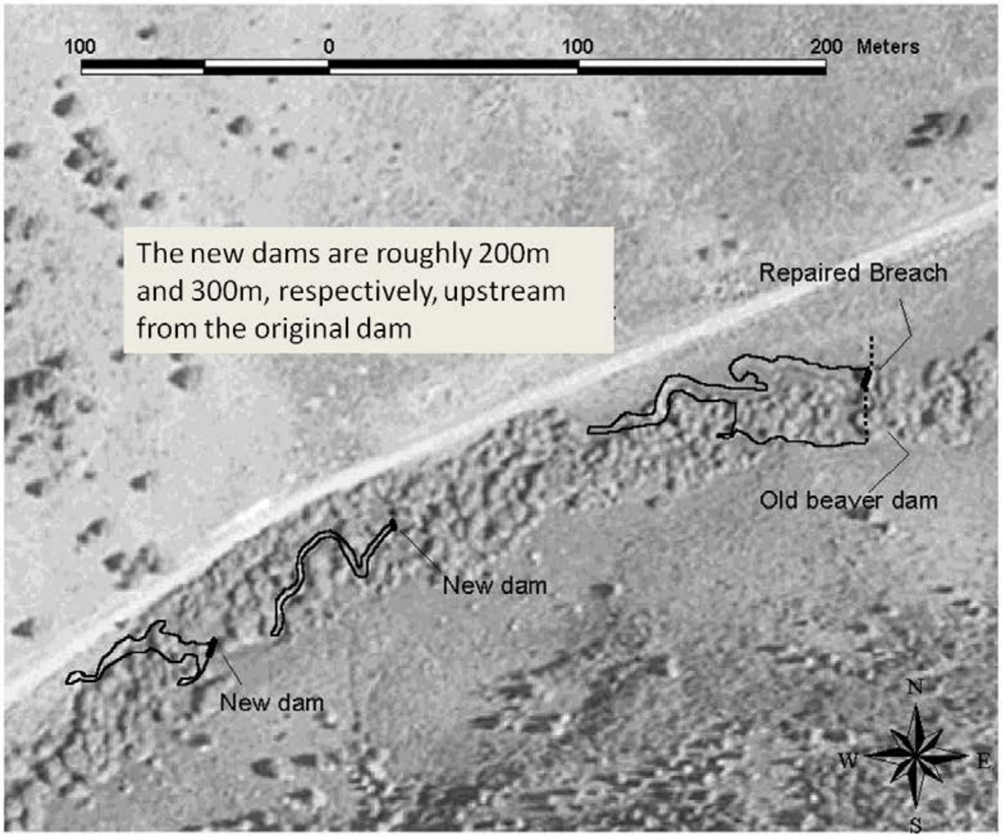


Figure 24. Small dams constructed by beaver in 2002 along Stoneman Creek, in addition to the preexisting dam. Five beavers were released on Stoneman Creek in the late summer of 2001 at the location labeled 'Old beaver dam.' At least one beaver settled at the reservoir and built smaller dams along Stoneman Creek. The smaller dams contributed to the wetted area of Stoneman Creek, possibly providing suitable spotted frog habitat. This image consists of GPS points collected along the perimeter of the wetlands and then overlayed onto aerial photos of the creek. Aerial photographs of the creek provided by the Bureau of Land Management (BLM) Boise, Idaho Field Office.

The gender of the resident beaver was not determined. It was also unclear whether the observed beaver was solitary, or if more than one beaver had settled in the reservoir. The animal(s) were left undisturbed.

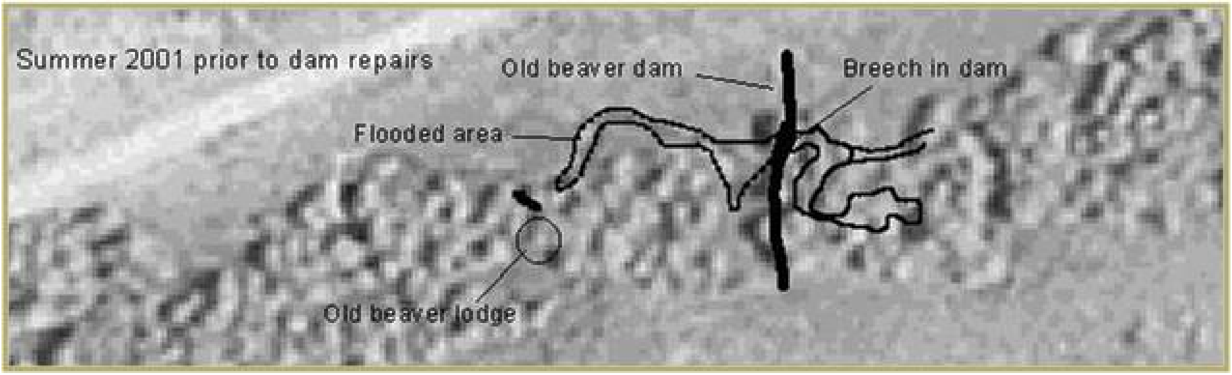
The beaver that settled on Stoneman Creek remained in place for 8 years following its release (Tim Carrigan, Bureau of Land Management, Pers. Comm.). Mature beaver generally form monogamous pairs and frequently occur in more-or-less equal sex ratios (Baker and Hill 2003). They live in close-family groupings traditionally called ‘colonies,’ that include the breeding pair, the year’s offspring, and, in some cases, older young. Dispersing beaver (floaters) of both genders wander until they encounter an unmated beaver, or they build a dam to attract a mate (Baker and Hill 2003). I only ever directly observed one beaver at any given time. Due to their territorial nature, it is likely that a dominant male settled along the stretch of suitable habitat and forced the other translocated beaver away (Toby Boudreau, Idaho Department of Fish and Game, Pers. Comm.).

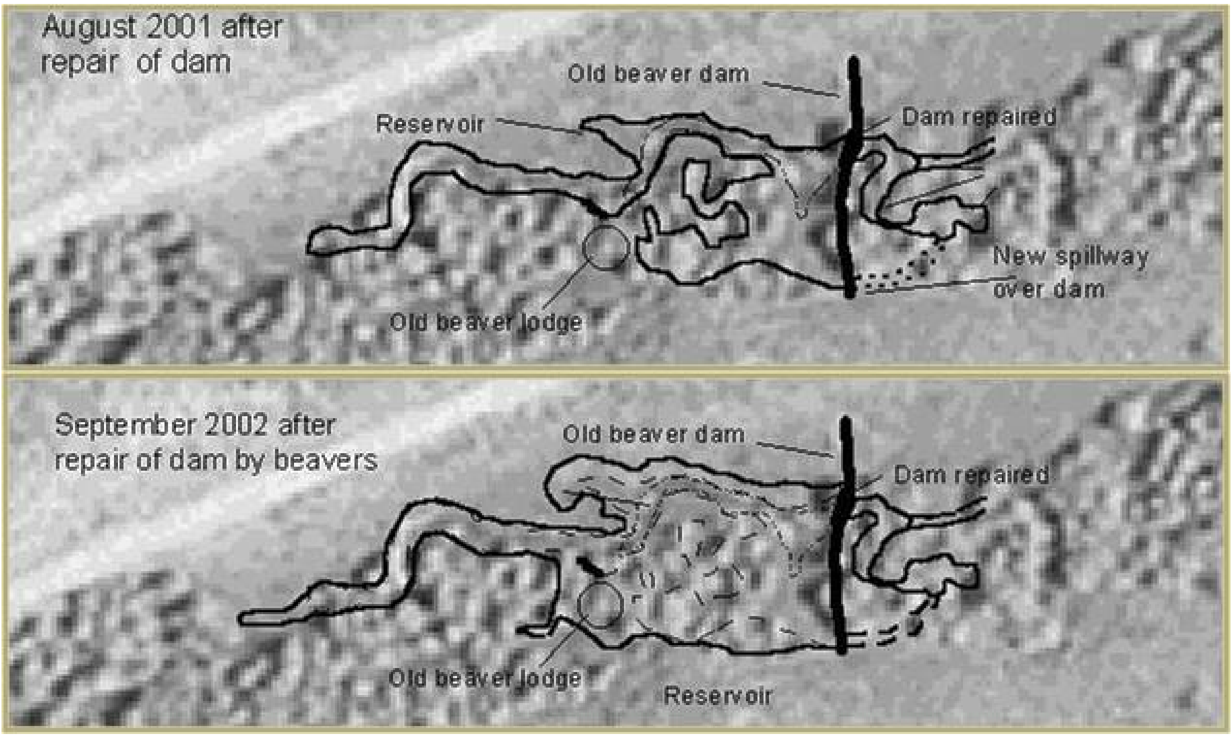
I conducted extensive surveys of the watersheds surrounding Stoneman Creek during the summers of 2002 and 2003 in order to collect information on the surrounding spotted frog populations (Munger and Lingo 2002, and 2003). In a few of the drainages surrounding Stoneman Creek I found evidence of past beaver activity, but no evidence of present beaver habitation. Therefore, the lone male that settled along Stoneman Creek may have simply waited for a mate to encounter his dam in an area where beaver population numbers are not conducive to many floaters.

Beaver reach sexual maturity at 1.5-3 years of age, depending on habitat quality and the number of nearby colonies (Baker and Hill 2003). I did not observe beaver kits during the summers of 2002 or 2003. Beaver are mostly crepuscular and nocturnal (Baker and Hill 2003). I did not attempt overnight surveys at Stoneman Creek, when the probability of observing young may have been highest. However, spotted frog surveys kept me at Stoneman Creek until daylight had faded on several occasions, without sighting any kits. Early morning is an active period for beaver kits and would have been a good time to check for their presence (Toby Boudreau Personal Comm.). However, early morning is not an active period for spotted frogs, so Stoneman Creek was not surveyed during those hours.

Does beaver reintroduction result in increased standing water, potentially improving spotted frog habitat?

The newly resident beaver rapidly repaired and enlarged the artificial dam. With repairs to the dam, a large marsh developed upstream of the dam. Based on measurements taken from the coordinates taken along the changing pond margin, the area of the reservoir went from 188 m2 in 2001 prior to beaver reintroduction to 2,086 m^2 the year following beaver reintroduction (Figures 25a, 25b, and 25c). By 2007 the temporary dam began to crumble under the weight of materials placed by the beaver (Figure 26). Beaver activity and expansion of the existing wetland complex continued into 2009 (Figure 27).





Figures 25a, 25b, and 25c. The quantity of water above and below the dam as beaver made repairs to, and expanded the existing dam. Figure 25a. The upstream (to the left) wetland extended 39m in linear distance. The wetland at the dam measured 6m in width. The wetland below the dam measured 17m across. Figure 25b. The upstream wetland extended 99m in linear distance. The wetland at the dam measured 28m in width. The wetland below the dam measured 30m across. Figure 25c. The upstream wetland extended 108m in linear distance. The wetland at the dam measured 32m in width. The wetland below the dam measured 30m across. The images were created by walking the perimeter of the reservoir collecting GPS points, and then plotting those points over aerial photos provided by the Bureau of Land Management (BLM), Boise Field Office, Idaho, USA.

Figure 26. The remains of the irrigation dam (orange arrows). Originally built to encourage beaver settlement, the irrigation dam became barely visible underneath repairs made by reintroduced beaver. This picture was taken in 2007, six years after the reintroduction of five beavers at the dam site.

Figure 27. The artificial dam, constructed on Stoneman Creek in 2001 to encourage settlement by beaver, had been significantly enlarged by beaver activity in 2007. The end of the original dam is marked in the photograph with an orange arrow. New dam activity extends past the foreground of the photograph. Five beavers were released at this location in the late summer of 2001.

Spotted frogs require standing or very slow moving water for egg mass deposition (Turner 1962). In addition, breeding habitat needs to retain enough water for larval frogs to be able to swim and respire throughout the summer months as metamorphosis occurs. As the reservoir behind the repaired dam grew in size it provided several areas of shallow, standing water where egg mass deposition occurred (Figure 28 and 29).

Figure 28. Shallow pond margins, like the one in the lower left above, provide habitat for spotted frog egg masses. Egg masses were observed along this margin in 2002, 2003, and 2004 (Munger and Lingo 2002 and 2003; Blankinship and Munger 2004). The pond was enlarged and maintained by reintroduced beaver along Stoneman Creek.

Figure 29. The shallow pond margin (to the left) was the site of egg mass deposition in 2003. The depth along the pictured margin was between 0.6m in May, and 0.2m in August during the 2003 active season. Spotted frogs did not deposit egg masses along that pond margin prior to beaver reintroduction in 2001.

Spotted frogs may use wetland areas, like those found throughout the beaver impoundment (Figure 30), to forage and for travel among key habitat components. Insects, the preferred prey of spotted frogs, are frequently dense in beaver-created wetlands (Baker and Hill 2003). In addition, with their high water table, wetlands provide a moist microclimate that enables frogs to leave water for foraging and travel without undue risk of desiccation. By raising the water table, connectivity among key amphibian habitat features is enhanced through beaver activity (Cunningham et al. 2007). For example, the wetland immediately downstream from the expanded beaver dam was a common site of observations of foraging frogs. Connectivity of key habitat features is so important to highly aquatic amphibians, that its presence can determine whether potential habitat is occupied (Rothermel 2004).

Figure 30. A large wetland resulting from beaver activity on Stoneman Creek. This photograph was taken six years after the release and successful establishment of beaver along Stoneman Creek. Wetlands provide spotted frogs with foraging and

migratory habitat where they can undertake terrestrial movements with limited risk of desiccation.

Other studies have found that as beaver ponds age, they improve as amphibian habitat (Stevens et al. 2006). The removal of the riparian canopy cover by beaver opens up basking sites, while encouraging the growth of submerged vegetation that larvae use for cover and as a feeding surface. The open, standing water raises thermal degree-days, facilitating transformation of larvae and aiding frog metabolic function.

Another important result of beaver-caused flooding is the overall increase in plant and animal diversity on a broader landscape scale (Metts et al. 2001; Wright et al. 2002; Cunningham et al. 2007). Before and after vegetation plots along Stoneman Creek would have been an ideal way of measuring shifts in the plant community resulting from beaver activity. The positive relationship between beaver activity, landscape-level species diversity, and stream health is drawing more attention as beaver begin to recolonise North America (Wright et al. 2002; Cunningham et al. 2007; Karraker and Gibbs 2009; Stoffyn-Egli and Willison 2011).

Did the numbers of spotted frogs along Stoneman Creek change following the release of beaver?

Spotted frogs along Stoneman Creek increased in numbers following successful beaver reintroduction (Figure 31). Of course, increasing spotted numbers could have merely correlated with beaver presence and correlation does not equal causation. In order to determine whether there was a regional increase in spotted frog numbers, trends in spotted frog capture numbers at two neighboring sites are offered for comparison to what was observed at Stoneman Creek.

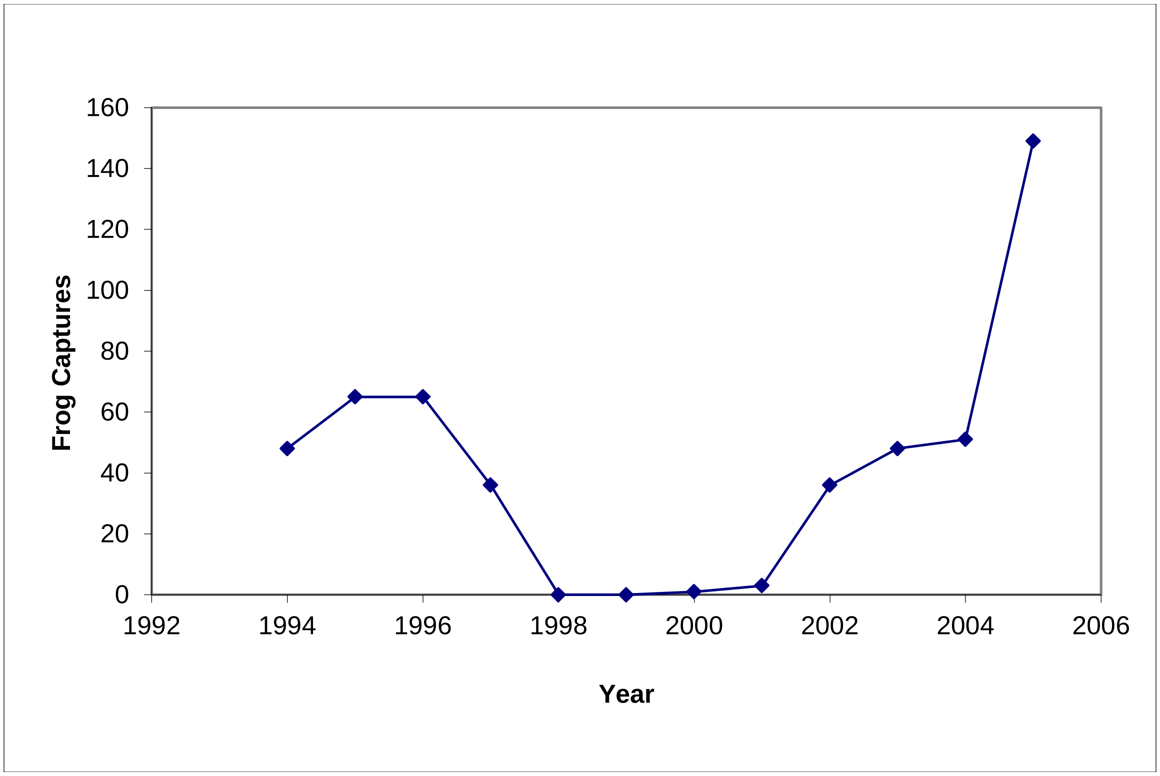


Figure 31. Frog captures at Stoneman Creek from 1994 to 2005 (Munger et al. 1994; Munger et al 1997; Engle and Munger 1998; Idaho Conservation Data Center 1999; Munger and Barnett 2002; Munger and Lingo 2002; Munger and Lingo 2003; Blankinship and Munger 2004; Munger and Oelrich 2005). The beaver on Stoneman Creek were killed in 1992 and the dam began to erode, disrupting the lentic spotted frog habitat associated with the dam. Following repairs to the dam and successful beaver reintroduction in 2001, the spotted frog population began to increase.

Circle pond, located roughly 8 km from Stoneman Creek, is a spotted frog breeding site that is surveyed several times annually as part of a monitoring protocol designed to track spotted frog numbers in the Owyhees (Engle 2001a). The pond is located near the head of Anne Valley and has ephemeral connectivity to Hurry Back Creek (Figure 32). The survey area consists of a small springhead that flows into an outlet with thick grasses and sedges, and eventually to the excavated pond and its outlet. The spring’s flow typically ceases to reach the pond by July. Spotted frog captures at Circle Pond did not share the pattern of rapid increases seen at Stoneman Creek (Figure 34).

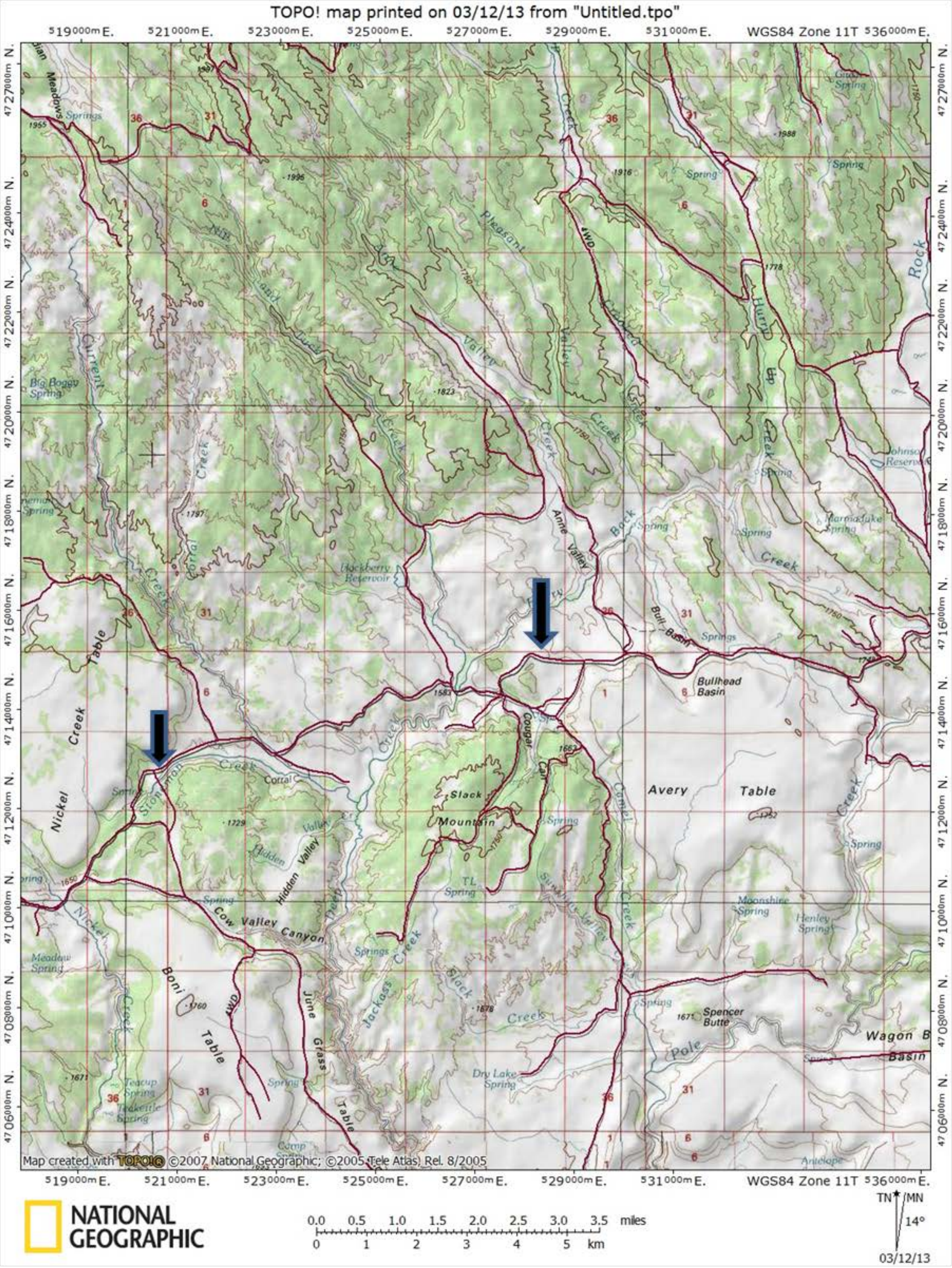


Figure 32. Circle Pond spotted frog survey site and its location relative to Stoneman Creek. Despite their close proximity, frog numbers at Circle Pond declined, while those at Stoneman Creek increased. Due to the distance separating the two sites (8 km) and lack of a shared drainage, it is unlikely that the frogs appearing along Stoneman Creek came from Circle Pond. Map generated in TOPO! National Geographic 2007.

Figure 33. Circle Pond in late July, 2003. The sedges in the center of the photograph are typically submerged vegetation. I found incompletely metamorphosed spotted frogs within the sedges that, most likely, did not survive the drying of Circle Pond.

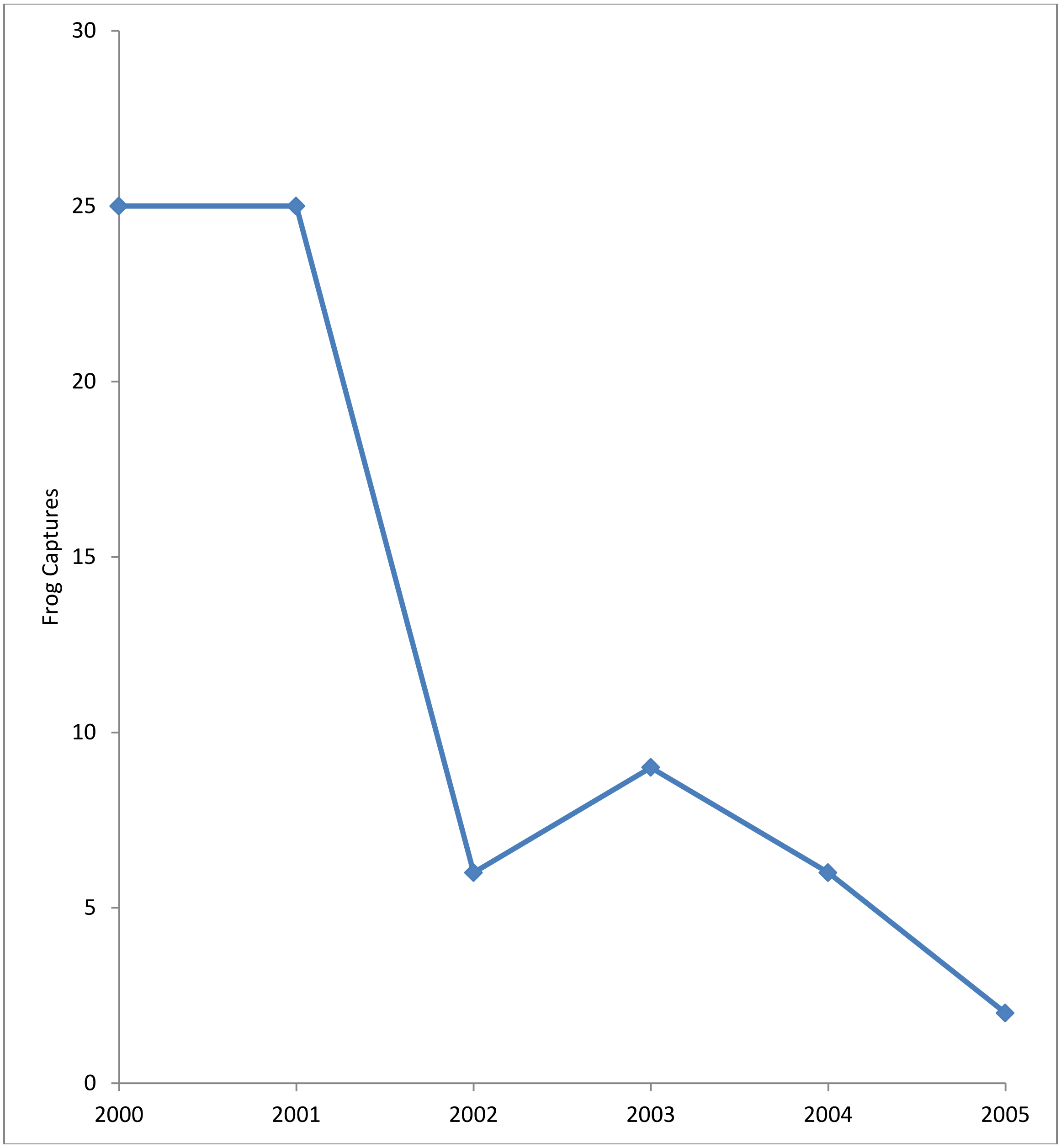


Figure 34: Spotted frog captures on Circle Pond from 2000-2005 (Engle 2000; 2001a; Munger and Lingo 2002, 2003; Blankinship and Munger 2004; Munger and Oelrich 2005). Spotted frog captures at Circle Pond were in decline at the same time that spotted frog captures were increasing at Stoneman Creek. A likely reason for the difference in frog observations between the two sites was that spotted frog habitat had improved at Stoneman Creek through beaver reintroductions, but habitat improvement efforts had not taken place at Circle Pond.

Another heavily-surveyed site in the Owyhees, Cottonwood Creek, consists of a wetland formed where a culvert meant to facilitate the stream's course under Mud Flat

Road, had, in fact, slowed the stream's flow. The wetland was the location of egg mass deposition in 2002 and 2003 and frogs were frequently found throughout the area. The surveyed area of Cottonwood Creek is 13.7 km from the beaver reservoir on Stoneman Creek (Figure 35). At the same time that frog captures were increasing at Stoneman Creek, capture numbers on Cottonwood Creek were fluctuating.

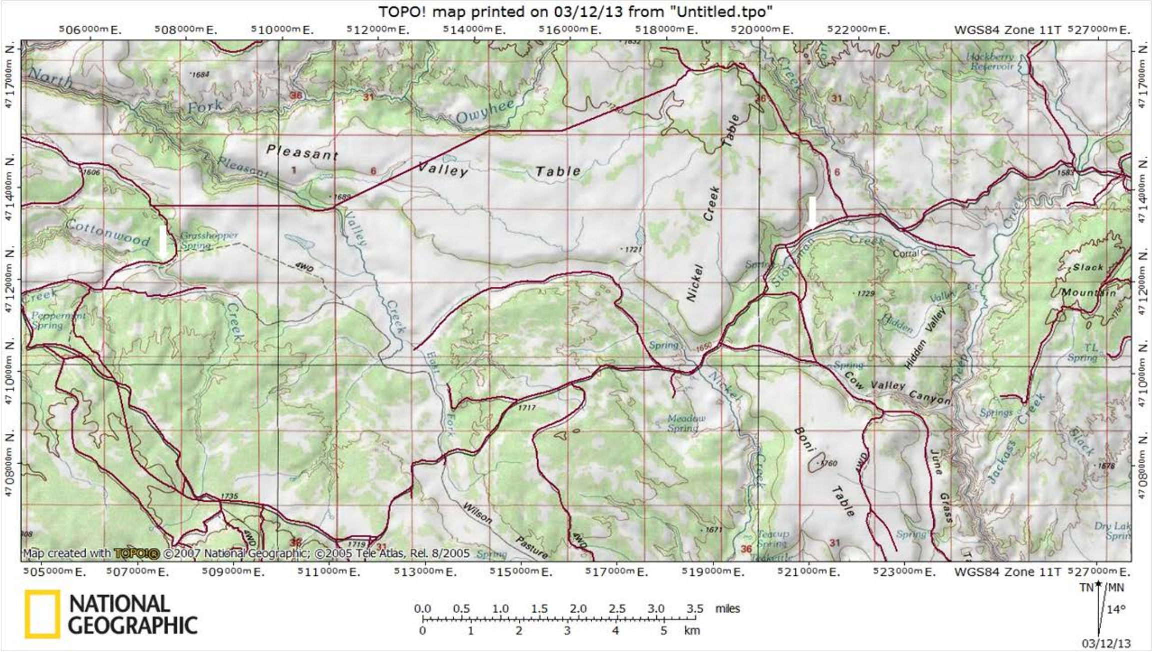


Figure 35. The location of the spotted frog population on Cottonwood Creek relative to the location of the beaver dam on Stoneman Creek (both shown with black arrows). Despite their proximity, Cottonwood Creek's spotted frog population appeared to decline while Stoneman Creek's spotted frog population appeared to increase in numbers. Map generated in TOPO! National Geographic 2007.

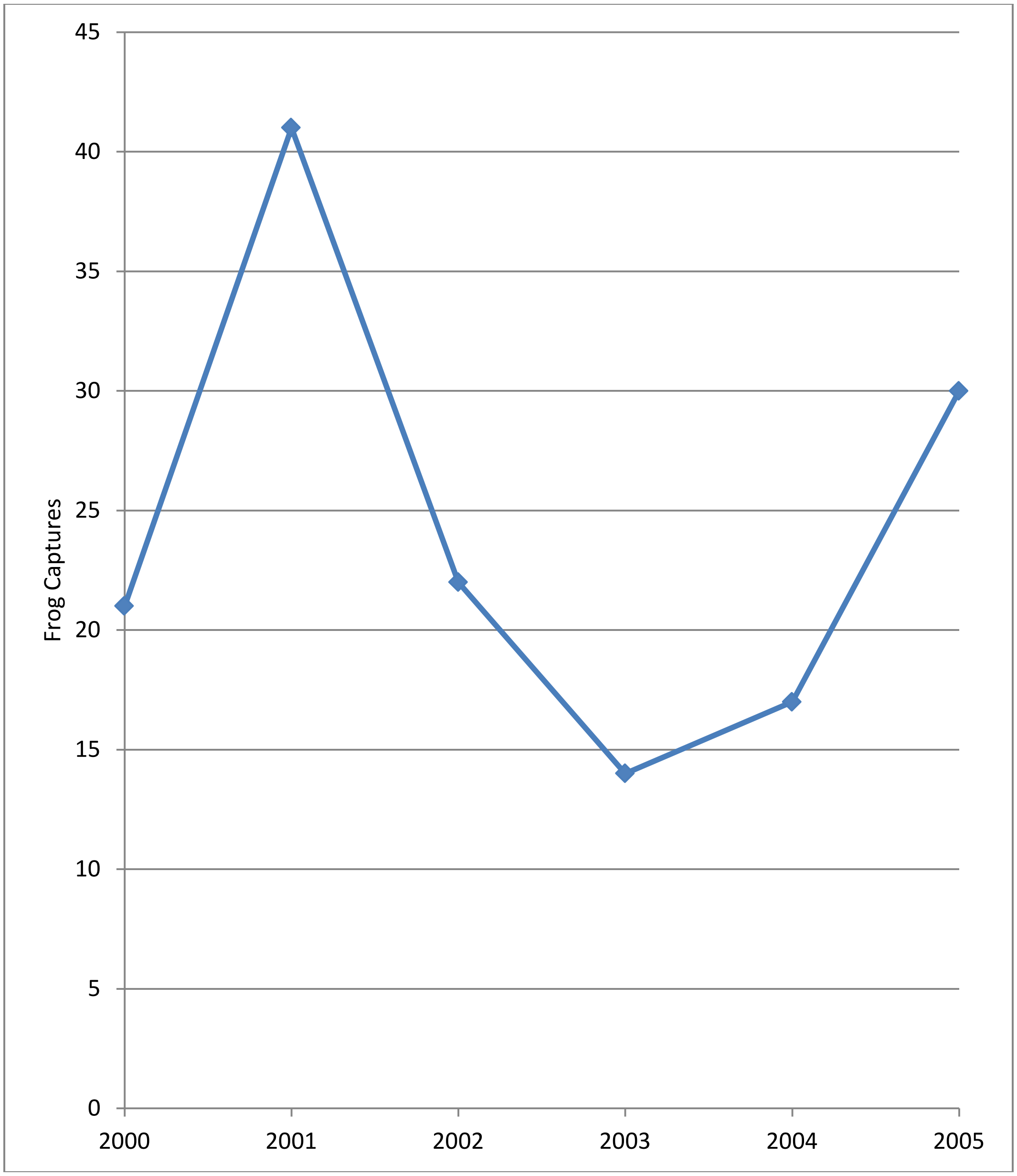


Figure 36: Spotted frog captures along Cottonwood Creek from 2000-2005 (Engle 2000, 2001a; Munger and Lingo 2002, 2003; Blankinship and Munger 2004; Munger and Oelrich 2005). Spotted frog capture patterns along Cottonwood Creek differ from those seen at Stoneman Creek. A likely reason for the difference is the habitat improvement that took place on Stoneman Creek due to beaver activity. No beaver activity took place at Cottonwood Creek during 2000-2005.

The pattern of rapidly rising numbers seen at Stoneman Creek in 2002 and 2003 was not seen at two other heavily-surveyed sites in the Owyhee Uplands. Although, neither Circle Pond, nor Cottonwood Creek are meant to be controls for Stoneman Creek, it is interesting to note that, while Stoneman Creek frogs went up in numbers following beaver reintroductions, frog numbers over that same time period declined at two nearby sites. It is unlikely, given the intervening distance and topography, that the spotted frogs that appeared on Stoneman Creek came from either Circle Pond.

Patches of habitat occupied by Columbia spotted frogs in the Owyhees are mapped by the Idaho Department of Fish and Game (Idaho Conservation Database Center 1999; Moser 2007). Written for Ranid frogs in general (Hammerson 2002), specific guidelines define a distinct and separate subpopulation as recorded observations of one or more individuals, by a reliable observer, that are separated by one or more of the following:

1. Any major barrier to dispersal, such as a busy highway, urban developments dominated by buildings and pavement, a major river (greater than 50 m wide), or habitat in which site-specific data indicate that frogs virtually never occur there (e.g., some semiarid shrubland habitats);
2. Any distance greater than 2 km across habitat that is considered unsuitable for frog residence, but is traversable;
3. Any distance of greater than 5 km over suitable habitat when subpopulations occupy connected drainages in montane regions;
4. A distance of at least 10 km of suitable habitat for subpopulations within a drainage in montane habitat.

For both 2 and 3, a lesser distance can be used if site-specific data indicate that individuals in adjacent populations are not likely to come in contact with each other. All separation distances are measured from the outer edge of the occupied habitat (see mapping guidelines) (Idaho Conservation Data Center 1999). These guidelines enable researchers to identify a distinct breeding population and separate it from others.

Despite these specific guidelines, how to accurately separate observations, so that isolated subpopulations are properly depicted, poses a challenge to land managers and researchers (Munger and Lingo 2002). For example, potential barriers to frog movements may go unreported, because land ownership or impassable terrain makes an area inaccessible to surveyors (Engle 2001a; Munger and Lingo 2002 and 2003).

A likely source of adult spotted frogs seen in the beaver reservoir was the private land almost 2 km away where Stoneman Creek and Current Creek meet. The topography indicates a lowland that potentially contains suitable frog habitat. However, the confluence of the two creeks has never been surveyed for frogs, nor has the presence of suitable habitat been confirmed along that stretch of stream. Given the requirements for isolated subpopulations it is almost impossible to determine whether the frogs that settled along Stoneman Creek can truly be classified immigrants from a neighboring subpopulation, or whether they are immigrants from a portion of the Stoneman Creek subpopulation that did not previously occupy the reservoir area.

Are increased frog numbers a result of recruitment through reproduction, or recruitment through immigration?

Recruitment through both immigration and reproduction increased following dam repairs on Stoneman Creek (Figure 37). What is not clear is the source of the large (> 57 mm SVL) adult frogs. Did the beaver impoundment provide a natal site where frogs rapidly grew to maturity, or did large adult frogs immigrate into the habitat provided by the beaver impoundment? The latter is possible given that both Current and Deep

Creeks were within 3 km of the study site and both of the neighboring creeks had records of spotted frog presence.

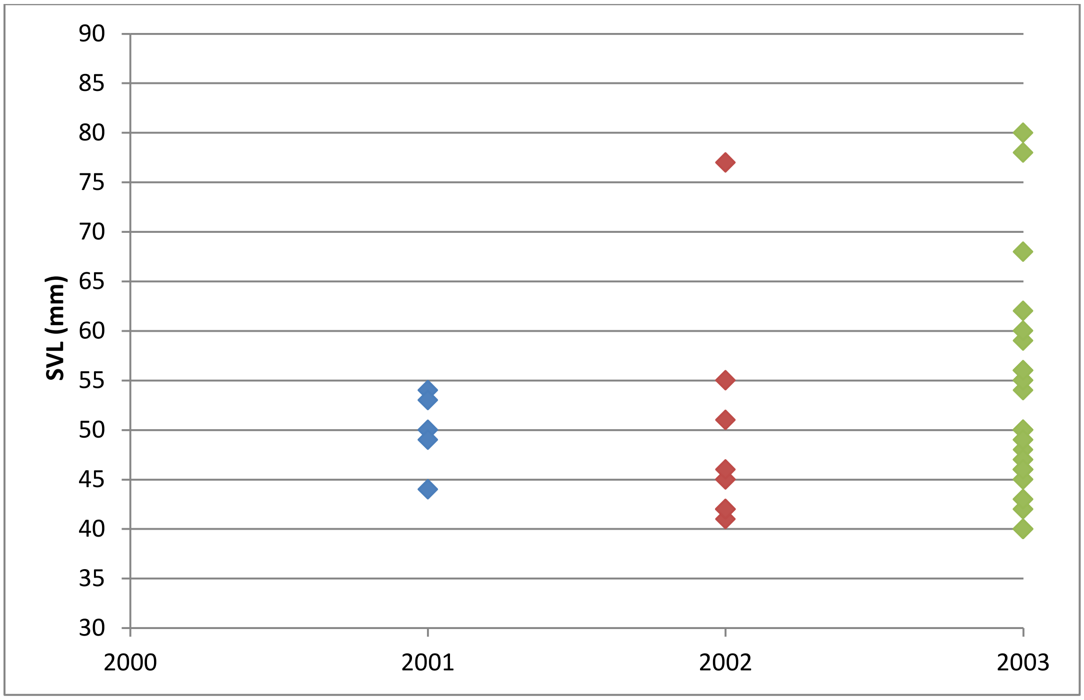


Figure 37. Recruitment along Stoneman Creek immediately following artificial repairs to the beaver dam (2001), and the two years following beaver reintroduction (2002 and 2003). Recruitment, for the purposes of the present study, is considered any frog reaching PIT tag size, which is a minimum of 40mm. A large (sexually mature) adult is considered to be over 57mm. Data include both males and females.

Of the frogs captured in 2003, seven met all three of the criteria designed to determine whether a captured frog was an immigrant (over 57mm in SVL, no VIE mark, and no PIT tag). Therefore, these adult frogs appeared to be new arrivals, and possibly immigrated into the Stoneman Creek survey stretch following habitat restoration. Note that three of the potential immigrants were large female frogs (68, 77, and 80 mm SVL), a demographic commonly thought to have high levels of site fidelity (Engle 2001a; Bull 2005). One possibility is that the large frogs captured during 2003 had lived along Stoneman Creek for the three-four years required for a female to reach such a large SVL. The three females could have evaded capture and then been mistaken as immigrants in

2003. However, Moser (2007) found that four surveys in a single year were needed to establish mark-recapture estimates with an acceptable level of error. Stoneman Creek was surveyed three times in 1996; eight times in 1997; for the years of 1998-2000 surveys took place but no frogs were captured, so there is no information on survey efforts. In 2001 there were five surveys; and in both 2002 and 2003 there were eight surveys. Given the intensity of survey efforts along Stoneman Creel over the years, it seems unlikely that large frogs would have gone unnoticed.

Immigrant frogs tended to be larger individuals, rather than smaller metamorphs immigrating into the reservoir area from other natal sites (Females: Mann-Whitney U = 2 P = 0.04; Males: Mann-Whitney U = 1.5 P = 0.05) (Figure 38). Although the juvenile life stage is commonly thought to be the age at which amphibians undergo dispersal-type movements (Berven and Grudzien 1990; Funk et al. 2005; Roznik and Johnson 2009), research has shown that larger-bodied frogs may be better suited to traverse adverse conditions (Chan-McLeod 2003; Chelgren et al. 2008), and may travel farther distances than smaller frogs (Pilliod et al. 2002; Chelgren 2003).

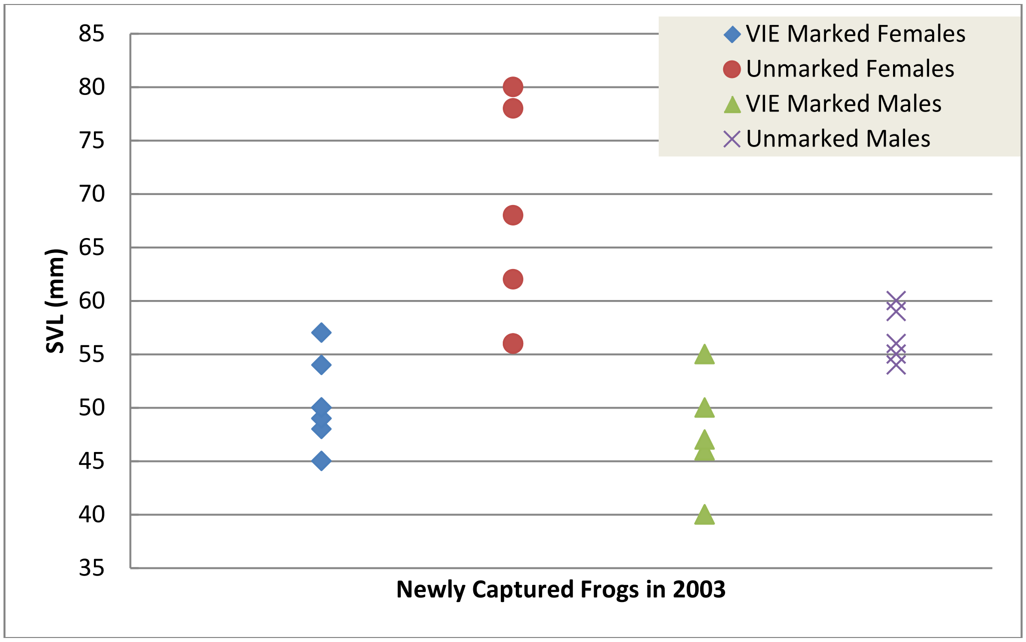


Figure 38. Newly PIT tagged (not previously captured at a size suitable for PIT tag implantation) frogs in 2003. Blue diamonds are VIE marked females (captured and VIE marked at the reservoir as a metamorph). Red circles are unmarked females (possible immigrants). Green triangles are VIE marked males (captured and VIE marked at the reservoir as a metamorph). Purple X's are unmarked males (possible immigrants).

In addition to the 184 metamorphs that were VIE marked in 2002, egg mass numbers provided evidence that breeding activity increased population numbers following beaver dam repairs. 1997 was the last year that egg masses were noted prior to repairs to the beaver dam (Engle 2001a). However, the year following beaver reintroduction, frogs began to deposit egg masses in the reservoir again (Table 2.1).

Table 2.1. Egg mass counts along Stoneman Creek from 2000-2009. Late-April breeding surveys have been conducted at Stoneman Creek since 2000 as part of an attempt to monitor the Owyhee subpopulation of spotted frogs, due to concerns about dropping numbers (Engle 2000, and 2001a; Munger and Lingo 2002 and 2003; Blankinship and Munger 2004; Munger and Oelrich 2005; Moser and Patton 2006; Moser 2007; Lohr and Haak 2009). Following beaver reintroductions in 2001, egg mass counts at the Stoneman Creek beaver reservoir increased in numbers.

Year	Egg Masses
2000	0
2001	0
2002	1
2003	10
2004	30
2005	51
2006	120
2007	Present
2008	93
2009	79

Conclusions

The present study, while admittedly limited given its sample size and lack of controls, suggests that beaver reintroduction may be a useful technique for improving habitat for spotted frogs. Not all streams in the Owyhees are suitable for beaver habitation. Streams where beaver releases take place should be less than 6% gradient and less than 1 m deep to ensure dam-building behavior. Additionally, woody plants that provide bark, such as the aspen grove along Stoneman Creek, help ensure overwinter survival of beaver (Collen and Gibson 2001).

Because beaver are highly territorial and form monogamous bonds (Baker and Hill 2003), translocating a previously mated pair may ensure the development of a colony (familial group) at a release site. A colony may more permanently occupy a site as young mature and continue construction and maintenance on established dams (Naiman et al.

1986). Additionally, translocations must be timed to allow the released beaver to stockpile sufficient food for the winter (Toby Boudreau, Idaho Department of Fish and Game, Pers. Comm.). Releases should take place before September when shallow water begins to freeze in the Owyhees.

There are several drainages in the Owyhees where spotted frogs are known to occur and that would be suitable for beaver habitation. Spotted frogs in breeding condition appear to undergo movements of at least 2 km along low-gradient (4-6%) stream corridors. Therefore connectivity between streams where beaver are reintroduced and streams where frog populations are known to occur may be important to successful immigration of frogs into improved habitat. Given this possibility, additional beaver reintroductions to confirm, or refute this study’s findings are warranted.

CHAPTER III: AN EXPERIMENTAL, BEHAVIORAL APPROACH TO UNDERSTANDING NEWLY METAMORPHOSED COLUMBIA SPOTTED FROG (*Rana luteiventris*) TERRESTRIAL MOVEMENT PATTERNS

Introduction

Successful movements, sometimes over terrestrial habitats, by amphibians are critical at both the metapopulation scale and the population scale. Frogs fit a metapopulation model well because so many species are confined to water that is surrounded by inhospitable uplands (Marsh and Trenham 2001). Thus, localized water sources such as ponds and wetlands are viewed as subpopulations while more regional watersheds constitute a metapopulation of frogs. In practice, breeding ponds form discrete habitat patches that researchers can easily identify, characterize, and survey for presence or absence (Sjogern 1994; Marsh and Trenham 2001).

Metapopulation models then provide a basis for predicting the persistence of a species, given habitat patch shape, connectivity, and spatial scale (Sjogren 1991; Sjogren 1994; Sjogren 1998). A useful guideline is that as long as habitat patch recolonization rates match or exceed local extinction rates, a metapopulation will persist on the regional scale (McCullough 1996). In addition, a species' range is delineated into areas where within-patch extinctions exceed colonization and recolonization rates (Carter and Prince 1981 *in* Sjogren 1994). Thus, persistence and expansion of metapopulations rely on the ability of an amphibian species to undertake movements.

Terrestrial movements by amphibians are critical to the survival of local populations because pond dwelling amphibians require access to different key habitat elements for the successful completion of their life cycles (Sjogren 1998). Accessibility of ponds for breeding, wetlands for foraging, and suitable overwintering habitat can determine whether or not frogs populate potential habitat (Rothermel 2004). Thus, amphibians require the ability to successfully complete terrestrial movements to ensure the survival of local populations and for the species to persist at the landscape level.

The Owyhee Uplands of southwestern Idaho comprise a disjunct portion of the Great Basin Population of Columbia spotted frogs *Rana luteiventris* (Turner 1993; Munger et al. 1994, 1997, 1998; Engle 2001a; Munger and Lingo 2002, 2003; Blankinship and Munger 2004; Munger and Oelrich 2005; Moser 2007; Funk et al. 2008; Lohr and Haak 2009,;Funk and Robertson 2011). Areas of suitable spotted frog habitat in the Great Basin are highly fragmented as a result of seasonally arid conditions, limited resources, and their ephemeral nature (Engle 2001a; Gourley and Romin 2002; CSFTT 2003). Most occupied patches persist as small, seemingly semi-isolated subpopulations (Engle 2001a; Munger and Lingo 2002, 2003; Funk and Robertson 2011).

Past research on the movements of spotted frogs in the Owyhees has shown that they display high levels of breeding site fidelity as adults (Engle 2001a, 2001b). However, it is commonly believed that the age responsible for most interpond terrestrial movements by frogs is the juvenile life stage (Berven and Grudzien 1990; Funk et al. 2005; Roznik and Johnson 2009). The dispersal ability of newly-metamorphosed spotted frogs in arid regions is unknown (Reaser 2000).

To better understand the movement patterns of newly-metamorphosed spotted frogs, I inserted a series of artificial ponds into two wetlands, one with a long hydroperiod and one with a short hydroperiod, within the Owyhees. Each artificial pond was surrounded by one of three randomly assigned substrates: bare soil, mid-height grass, or tall and undisturbed grass. Every pond was populated with newly-metamorphosed spotted frogs. The following variables are ones that I attempted to link to terrestrial movements by spotted frog metamorphs.

Temperature

Cooling temperatures and precipitation have been shown to correlate with terrestrial movements by amphibians through habitats that would otherwise pose a high risk of desiccation (Chan-McLeod 2003; Blomquist and Hunter 2010). Because the present study took place in an arid region and during the summer months, a time period when the risk of desiccation is high, I predicted that terrestrial movements by spotted frog metamorphs would increase during cooling temperatures.

Time-of-day

Frogs in the family Ranidae, the family to which spotted frogs belong, have been observed to undertake overnight movements (Sjogren 1998; Pilliod et al. 2002; Roznik and Johnson 2009). The risks of desiccation and predation associated with overland movements by amphibians are probably reduced at night (Yetman and Fergusen 2011). Therefore, I expected frogs to leave experimental ponds more during the overnight hours in order to avoid the high risk of desiccation. Similarly, I expected the rate of daytime movements to rise when temperatures fell and the risk of desiccation decreased.

There is evidence that amphibians time movements to align with favorable conditions (i.e., lowering temperatures and increasing precipitation) before entering habitats where the risk of desiccation is high (Chan-McLeod 2003; Blomquist and Hunter 2010). Thus, there is a potential relationship between upland substrate and overnight movements. I predict that the metamorphs in the ponds surrounded by drier uplands would be more reliant on overnight movements than the metamorphs in ponds surrounded by wetter uplands.

Body Size

Larger-bodied amphibians are generally able to withstand desiccation better than smaller individuals (Thorson 1955). The size of amphibians at metamorphosis is a function of several factors, one of the most important being competition during the larval phase (Chelgren et al. 2006). It is likely that the most effective competitors (i.e., larger individuals) have the greatest vigor and are the most capable of surviving terrestrial movements. Chelgren et al. (2008) found that red-legged frogs (*Rana aurora*) with larger SVL (snout-to-vent length) measurements were found farther from ponds than the frogs with smaller SVL. Therefore, I hypothesized that larger spotted frog metamorphs would leave experimental ponds in greater numbers than metamorphs with smaller bodies.

Given the resiliency of larger-bodied amphibians to desiccation, I predicted that metamorphs leaving ponds surrounded by bare ground upland substrates and within the short hydroperiod meadow would be relatively large and that metamorphs leaving ponds in wetter conditions would show no effect of size. Moreover, I predicted that larger frogs should be better suited to leave ponds during rising temperatures than smaller frogs.

Substrate

Each experimental pond was surrounded by one of three randomly-assigned upland substrates: bare soil, mid-height grass, and tall grass. The bare upland substrate provided metamorphs with the least protection from desiccation, therefore I expected there to be the fewest movements within that treatment. The duration of stay should be the shortest in ponds surrounded by grass treatments. The grass treatments provided metamorphs with better cover for movements than the other ponds, thus, I predicted that metamorphs would cross the grass substrates immediately.

There is evidence that amphibians avoid areas where the risk of desiccation is high, but then enter those same areas during times of cooling weather and increased precipitation (Chan-McLeod 2003). Because the bare substrate posed the greatest risk of desiccation to metamorphs, I predicted that movements within the bare soil substrate would be negatively correlated with temperature, and that movements across mid-height grass and tall grass substrates would occur independently of changes in temperature.

Microhabitat

Amphibians prefer to move through microhabitats that provide cover from desiccation (Popescu and Hunter 2011). In addition to providing moist soil, the tall grass associated with the wet meadow provided a protective overstory. Therefore, I predicted that terrestrial movements by frogs within the wet meadow (microhabitat) would occur in higher numbers than movements within the short hydroperiod meadow (dry microhabitat).

Wetter microhabitats increase a frog’s physiological performance by maintaining hydration (Koehler et al. 2011) and by reducing stress associated with water loss (Shoo et al. 2011). Thus, the metamorphs within the wet microhabitat would be better able to undertake terrestrial movements during times when the risk of desiccation would be high for metamorphs within the dry microhabitat. I expected that terrestrial movements in the wet microhabitat would be unrelated to the weather, but that movements within the dry microhabitat would have a negative correlation with daily temperatures. In addition, I hypothesized that movements within the wet microhabitat would take place at all times, but that terrestrial movements within the dry microhabitat would be limited to overnight hours.

Methods

Study Area

Sam Noble Springs is located on state land 1.6 km north and 1.6 km east of the Mud Flat BLM Administrative Site (the location of the Mud Flat weather station) (Figure 37). The study site is located on the 7.5 minute quad map titled Hurry Up Creek at Latitude: 423738N, Longitude: 1163200W. The area consists of a series of six spring-fed ponds that were excavated in 1977 and reconstructed in the early 1990’s (Figure 38). All have outlets that flow into a stream. The stream flows throughout the summer in some years and is ephemeral in its upper portion during drier years. The stream eventually flows into the larger drainage of Rock Creek.

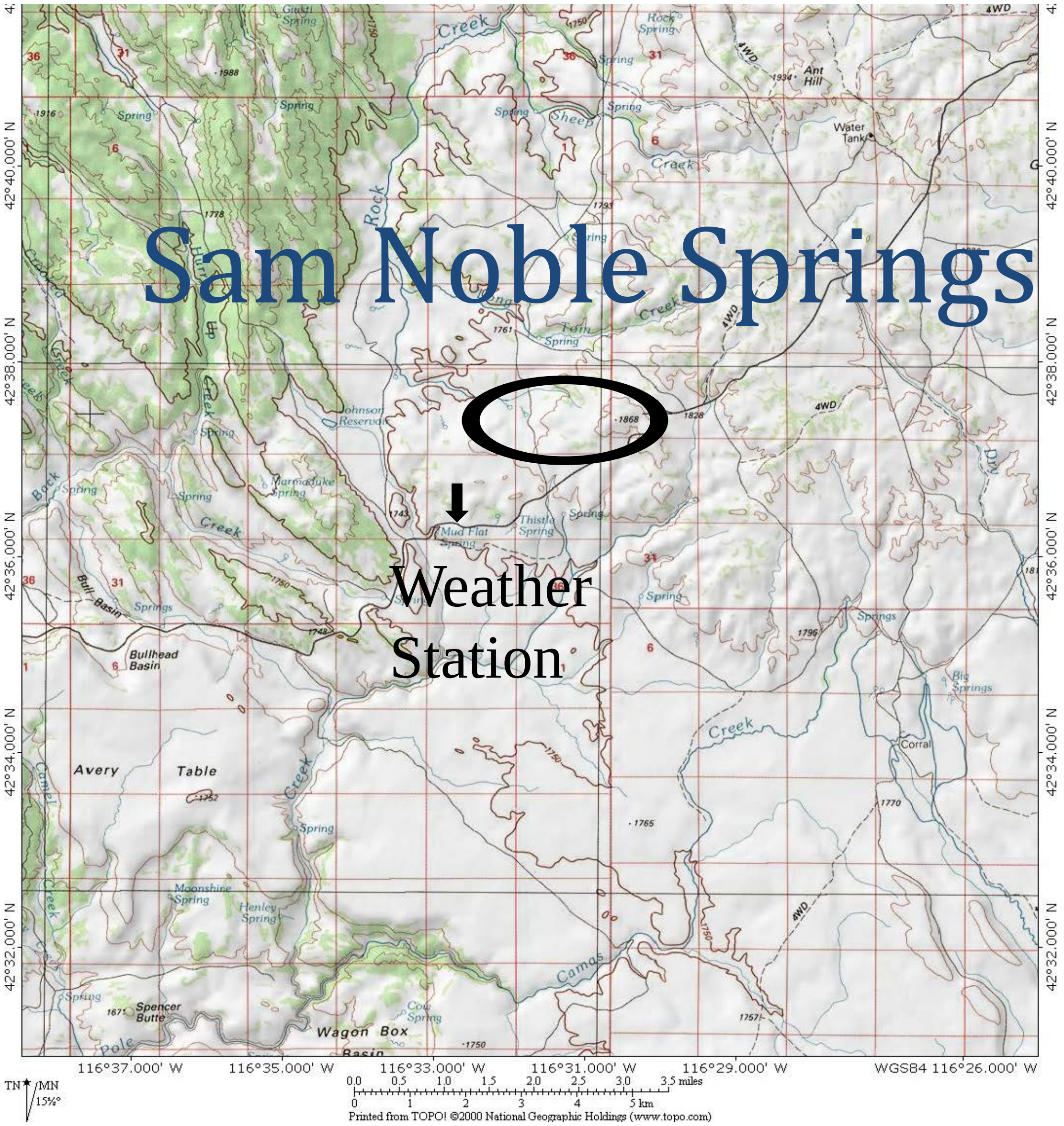


Figure 37. The location of Sam Noble Springs (black circle) within the larger watershed. Note the proximity of the Mud Flat weather station (Natural Resources Conservation Service [NRCS] 2013) to Sam Noble Springs. The creek draining Sam Noble Springs flows into Rock Creek, which also has spotted frogs, as does Long Tom and Sheep Creeks (Engle 2000; Munger and Lingo 2003). Map generated in TOPO! National Geographic 2007.

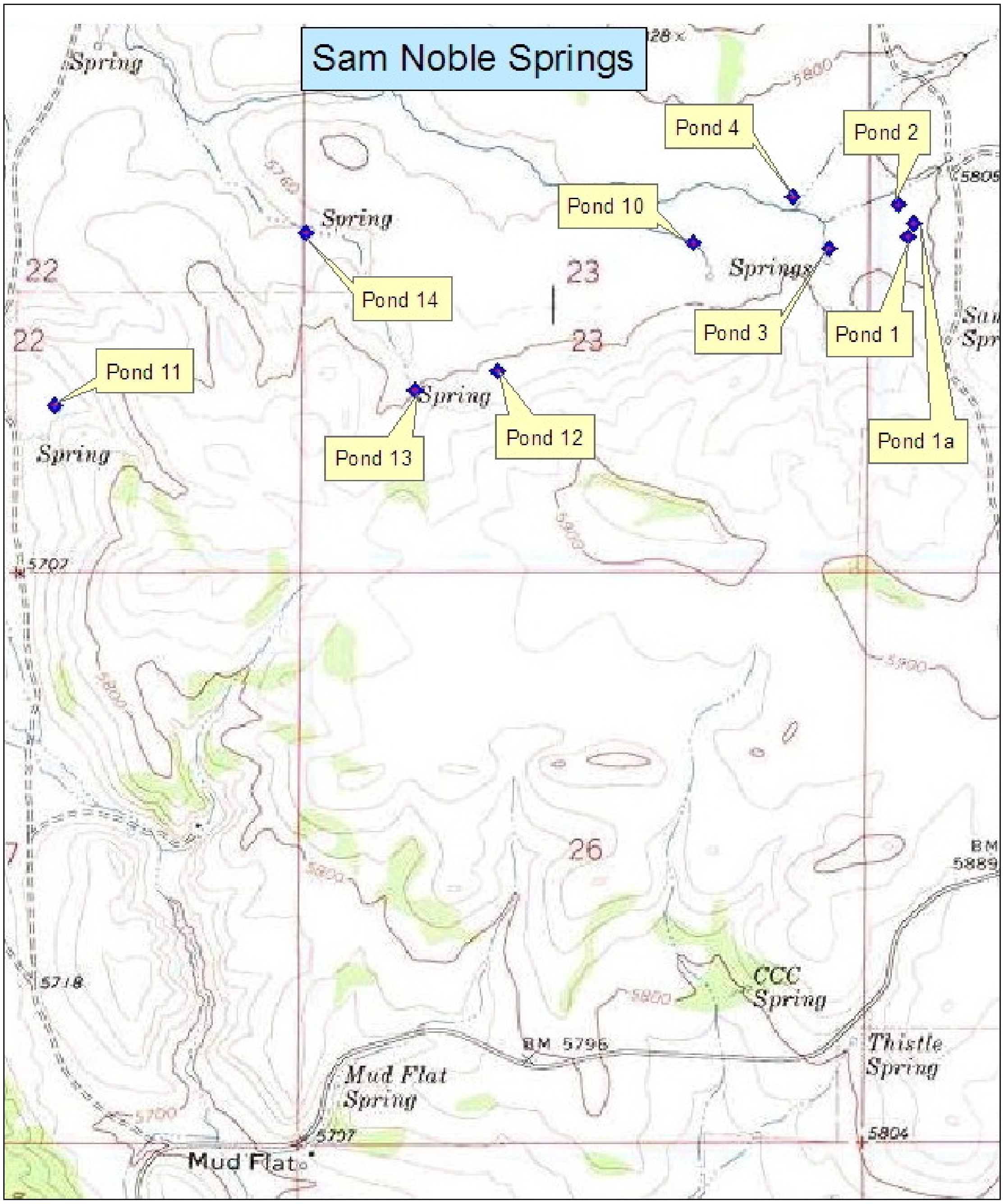


Figure 38. The layout of ponds at Sam Noble Springs (Moser 2007). Ponds 1, 1a, 2, 3, 4, and 10 lie within a grazing exclosure fence. Ponds 11-14 were excavated following the present study and lie outside of the exclosure fence. The labeled ponds are surveyed as an apex site in ongoing spotted frog monitoring efforts conducted by the Idaho Department of Fish and Game (Moser 2007).

The spring complex sits at roughly 1730 meters in elevation and gets snow yearly. The active season for spotted frogs runs from April to September, or October, depending on the first freezing temperatures of the year. Spotted frogs emerge from hibernation and males begin calling during early April, often with portions of the ponds still frozen and snow on the ground (Engle 2001a). Egg mass deposition is completed by the end of April on most years. The ponds begin to freeze in middle to late September. By October frogs are in hibernation.

In past years, cattle were typically grazed during two time periods: 400 to 1977 yearlings for 7 to 18 days sometime during the period of July through September, then 300 to 475 cows for 0 to 24 days sometime during the period of August through December. Ponds 1, 1a, and 2 and adjoining wetlands were fenced from grazing during the field seasons of 2002 and 2003 (Figure 39). For the present study, one grid of experimental ponds was inserted into the wetland adjacent to Ponds 1 and 1a. A second grid of experimental ponds was inserted into the dry meadow bordering Ponds 1a and 2 (Idaho Department of Lands permit TP-60-0429). For a further description of the grids, see the Experimental Grid Construction section below. A small stream bordered both grids to the west.

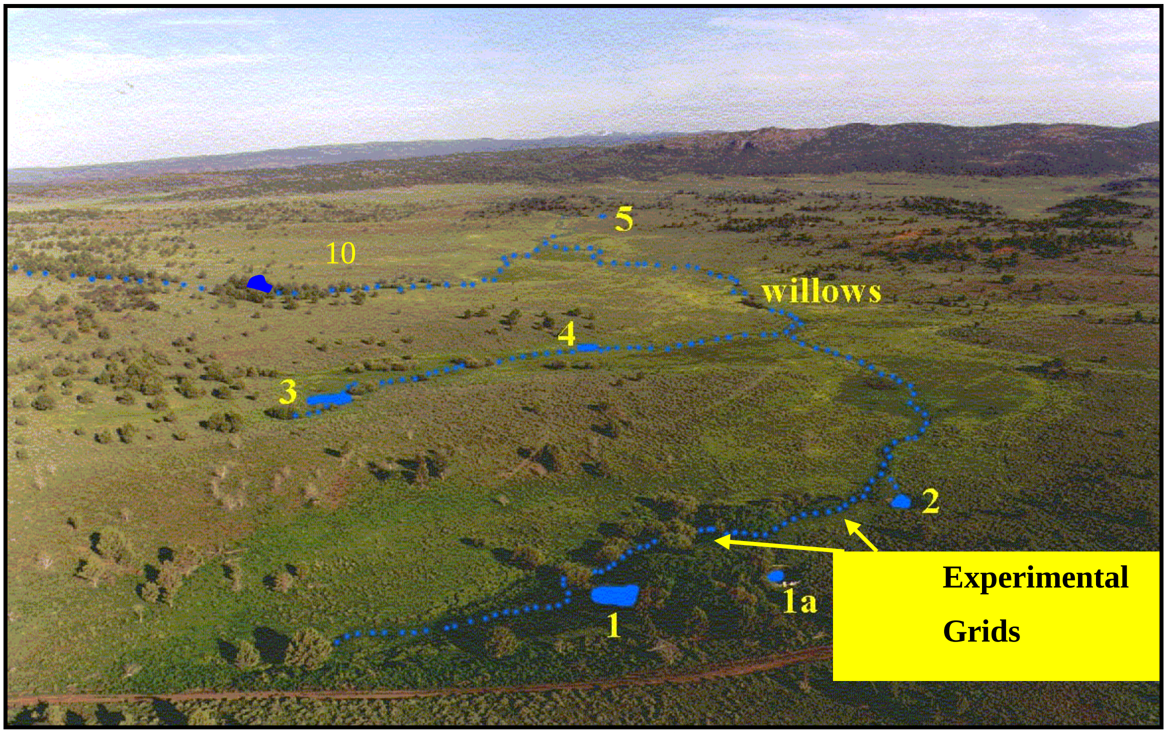


Figure 39. Sam Noble Springs and the location of the experimental ponds (shown with arrows). The foreground is east, and the ridgeline near the top of the picture is west. Metamorphs from the pond labeled 5 were not included in the study because it lies on private land. Photo and graphics by Janice C. Engle (2001a).

Pond 1 is the largest of the Sam Noble Springs ponds with a 19m diameter (area = 283.5 m^2). Pond1a is smaller in diameter at 9m (area=38.5m^2). Ponds1 and 1a are connected by a wetland dominated by willows that is easily traversed by all but the egg mass and larval life stages (Engle 2001a). Pond 2 has a diameter of 11m (area=95m2). Pond 3 has a diameter of 13m (area=132m2). Pond 4's diameter is 10m (area=78.5m^2). Pond 10 has a diameter of 8m (area=50m^2). Note that all measurements were made in May, when the ponds are large relative to their size later in the summer. The distances separating each pond vary (Table 3.1).

Table 3.1 The distances intervening each pond at Sam Noble Springs in kilometers. The travel distance between each pond varies whether it is via wetland and stream, or over dry land. The distances of overland routes are shown in parentheses.

	Pond1	Pond 1a	Pond 2	Pond 3	Pond 4	Pond 10
Pond 1	*	0	0.13	0.45 (0.29)	0.4 (3.5)	1.17 (0.66)
Pond 1a	0	*	0.13	0.45 (0.29)	0.4 (3.5)	1.17 (0.66)
Pond 2	0.13	0.13	*	0.39 (0.29)	0.38 (0.24)	1.2 (0.64)
Pond 3	0.45 (0.29)	0.45 (0.29)	.39 (.29)	*	0.27 (0.19)	1.1 (0.35)
Pond 4	0.4 (3.5)	0.4 (3.5)	0.38 (0.24)	0.27 (0.19)	*	0.82 (0.37)
Pond 10	1.17 (0.66)	1.17 (0.66)	1.2 (0.64)	1.1 (0.35)	0.82 (0.37)	*

Surveys, Capture, and Marking

Our equipment and personal wear (boots, shoes, etc.) were cleaned in preparation for each survey in accordance with the Declining Amphibian Populations Task Force (DAPTF) fieldwork code of practice (DAPTF 2002). We used a solution of at least 1 part bleach to 32 parts water to clean nets, boots, containment bags, and livewells before each survey. All debris clinging to sampling gear and equipment was removed on site following surveys, so as to prevent the unnatural spread of local plants, fungi, bacteria, and other potential pathogens. All cleaning materials used, such as bleach water, were disposed of well away from any water sources and, when possible, their use was limited to the Mud Flat Guard Station to avoid introducing bleach into water sources.

Our goals during surveys were to capture a sufficient number of metamorphs to run the field experiment (240 were required for the study and 10 additional metamorphs were captured to have on hand in the event of escape or mortality), and to put captured frogs in as little peril as possible. With those considerations in mind, I developed the following methods of capture and collection of spotted frog metamorphs.

We used visual encounter surveys to locate frogs (Olson and Leonard 1997). Visual encounter surveys consist of slowly walking the margin of a pond in an attempt to flush hidden frogs and search for those frogs partially submerged in water for capture. In an attempt to correctly identify the natal pond of each captured metamorph, surveys did not extend beyond the pond's high water mark into surrounding uplands. There was the potential that captures in the wetlands separating ponds could be foraging metamorphs from surrounding natal ponds.

Within-pond surveys were limited by depth and substrate. Surveyors were allowed to use their own discretion in determining how deep to wade into ponds in the pursuit of a sighted frog. Long-handled dipnets with circular baskets were the most effective means of capturing metamorphs in deep water. In shallower areas, we often caught metamorphs by hand.

Captured metamorphs were held in lidded livewells during the survey period. The livewells consisted of 18.9 L buckets with 2.5 cm holes, separated by no more than 5 cm, which we drilled through the walls on all surfaces. The holes allowed air and oxygenated water to flow through the livewells. The flow of fresh water prevented the water temperature within livewells from rising above that of the pond.

Metamorphosing frogs used in the experiment were taken from Ponds 1, 2, and 10. Because of heavy use by cattle at Ponds 3 and 4 during emergence, metamorphosing frogs were not visible and, thus, not taken from those ponds. Only a few metamorphs from Pond 2 were used because of low numbers of emerging young at that pond during

2003. The metamorphs collected for experimental purposes were transported to the Mud Flat Administrative site, just over 1.6 km from Sam Noble Springs, in coolers filled with water and detritus from the natal ponds. Cattle tanks were used to house metamorphs until the experiment began because they provided protection from predation and allowed for a minimum of crowding (Rothermel 2004).

Only metamorphosing frogs that had developed the pointed snout and more pronounced nares of older metamorphs, indicative of developmental stage 46 (Gosner 1960), were used (Figure 40). Younger metamorphs (pre-Gosner stage 46) often retained their tail and had the fragile skin of fully aquatic larvae, so clearly they were not suited to movements over land (Figure 41).

Figure 40. Spotted frog metamorph suitable for marking. Note that the metamorph has fully absorbed its tail and has the more rugose skin characteristic of a fully-developed frog. This spotted frog metamorph is at Gosner developmental stage 46 and would be more capable of terrestrial movements than a metamorph still retaining its tail (Gosner 1960).

Figure 41. The late stages of metamorphic development. Neither frog pictured was suitable for marking. The frog in the foreground was in Gosner developmental stage 44-45. The frog in the back was still fully aquatic and in Gosner Developmental stage 42-43 (Gosner 1960).

Captured metamorphs were marked subcutaneously with soft, biocompatible alpha-numeric (VIAlpha) tags (Northwest Marine Technologies [NMT] 2012). The tags were 1.0 x 2.5 mm. VIAlpha tags are designed for fisheries research, and are meant to be inserted into the non-pigmented areas of fish, especially the adipose eyelid tissue. As such, they are made of a soft, brightly-colored, biocompatible material.

The VIAlpha tags were inserted into the dorsal surface of each frog's thigh (Chelgren 2003) with a specialized syringe (Figure 42). Although the syringe was designed for tag injection, we found that the insertion process was easier when we made an initial opening with surgical scissors. Tags were moved to the ventral thigh surface, near the knee joint where there is a lack of ventral pigmentation in metamorphic frogs (Figure 43). Our tags were red with a black alphanumeric combination (a single letter, followed by a digit ranging from 00-99) unique to each metamorph.

Figure 42. VI Alpha tag being loaded into a specialized syringe (NMT 2012). Although the syringe was designed to implant tags, the process went more smoothly if a small incision was first made in the dorsal thigh surface with a pair of surgical scissors. The needle was then inserted through the incision and the tag implanted.

Figure 43. Spotted Frog Metamorph with VIAlpha Tag in the dorsal thigh. Note the lack of pigmentation in the frog's dorsal thigh. As spotted frogs mature, white and orange pigmentation develop on that surface rendering the VIAlpha tag invisible in adults.

Each metamorph also received a subcutaneous, visible, injected, polymer-hardened elastomer (VIE) dye mark (NMT 2012) in the hind foot (Figure 44). The biocompatible VIE dye is made of two parts: a color elastomer and a curing agent. The two were mixed together in a 10:1 ratio. Following injection the compound hardens into a flexible solid within a few hours. The hardening process can be slowed by storing the VIE mixture on ice in the field. VIE marks showed each metamorph's natal pond (Table 3.2). VIE marks are visible throughout a frog's life.

Figure 44. VIE mark (NMT 2012) depicted in the webbing of a spotted frog's hind foot. A 1cc insulin syringe was inserted at the metacarpals (blue arrow) and moved distally toward the phalanges. The dye was then injected into the webbing of the hind foot (shown here in orange). The dye was injected away from the needle insertion point to ensure that the color did not exit through the insertion point before hardening.

Table 3.2. Color scheme of VIE marks (NMT 2012) by natal pond 2003. The number of metamorphs removed from each natal pond was based solely on availability (n = 250). Although the experiment required 240 metamorphs, I captured 10 additional individuals to ensure a sufficient number by the start of the experiment. The VIE marks expedited the return of metamorphs from the experiment to their natal pond. VIE marks are permanent in spotted frogs.

Pond	Red	Orange	Green
Pond 1	118		
Pond 2			34
Pond 10		98	

Experimental Grid Construction

Construction of the experimental ponds began in late June of 2003 and was completed in mid-August of the same year. I built 2 grids consisting of 12 ponds each (Figure 45). Each pond was randomly assigned a surrounding upland substrate: bare soil, mid-height grass, or tall grass. Randomness of assigned treatments was achieved by first assigning each plot a number from 1-24. Next I programmed a calculator to select random numbers from 1-24. The three treatments were then written on separate pages of paper. A paper listing a treatment was then blindly drawn and the plot was assigned by the randomly generated number provided by the programmed calculator. The plot surrounding each pond was square in shape and each edge measured 5.75 meters.

Figure 45. One experimental grid with randomly-assigned upland treatments. Each square (n = 12 squares in each grid) was assigned one of three potential upland treatments: bare soil, mid-height grass or, tall grass. The pictured grid is located in the wet meadow.

The barren ground treatment was meant to represent an area that had been entirely devegetated, and it was created by first cutting down all of the grass, then spreading landscaping plastic over the plot and covering the plastic with soil. Mid-level grass represented an area that had undergone moderate to heavy vegetation removal; we created it by cutting the grass to a 2.54 cm stubble height with a weed trimmer. The tall grass treatment was the control and represented an area where no disturbance had taken place. The nature of the tall grass and medium grass treatments depended upon plot's microclimate (described below).

One grid of 12 ponds was placed into a wet meadow and a second grid of 12 ponds was placed into a dry meadow (Figures 46a and 46b). The wet meadow (microhabitat) was characterized by a high water table, numerous, dense sedges (*Carex spp.*), and dense sod soil. The dry meadow (microhabitat) had a shorter wet season and was more arid with sagebrush growing in dry soil, and wetland grasses sparsely distributed throughout. The wet meadow was typical of habitat that frequently borders streams and naturally-surfacing springs in the Owyhees. The dry meadow was what frequently surrounds ponds that are separate from larger water sources, such as, a small spring that is excavated to create an ephemeral pond. Each upland habitat treatment (bare ground, mid-height grass, or tall grass) was replicated four times per meadow. However, note that there was only one replicate for each meadow type (microhabitat): one wet meadow and one dry meadow.

Figure 46. Meadow types (microhabitats) where experimental pools were built: wet meadow (left), and dry meadow (right). The wet meadow is dominated by sedges, retained moisture through the experiment, and had a sod-type soil surface. The dry meadow had a mix of sage brush and grasses with patches of exposed, dry soil.

Each pond was constructed to be 0.75m diameter by 0.25m depth and therefore contained approximately 74L of water per pond. I lined each pond with two layers of impermeable landscaping plastic. A layer of green shade cloth was placed to overlap the waterproof barrier so as to provide a surface with traction for the metamorphs to climb out of the ponds (Figure 47). A siphon hose was used to add water to the pools from ponds 1 and 2 to maintain water levels without creating turbulence that would disturb metamorphs within the experimental ponds, and to ensure that each pond received water of the same temperature and chemistry.

Figure 47. Experimental pond lined with green shade cloth. Landscaping plastic lined the ponds beneath the shade cloth. The purpose of the shade cloth was to provide traction for metamorphs to climb out of ponds.

Each experimental pond and its surrounding upland treatment were completely surrounded by a square drift fence constructed from landscaping plastic (Figure 48). The plastic was affixed to wooden stakes that held the drift fences upright. Each drift fence was buried to 15 cm below the surface of the ground and rose 45 cm above surface. Pitfall traps were inserted into the four corners of each plot.

Figure 48. Layout of experimental plots. Each pool and upland plot is fully surrounded by a plastic drift fence with a pitfall trap in each of the corners. The foreground of the photo shows a mid-height grass treatment to the right, a bare soil treatment to the left, and a tall grass treatment in the background.

Pitfall traps consisted of 1 L buckets, and were placed in each corner of each drift fence square. The buckets were buried so that each bucket's lip was even with the ground. The bottom of each bucket was filled with roughly 2 cm of water to prevent captured frogs from desiccating (Figure 49).


'03 9 11

Figure 49. Pitfall trap. The opening of each bucket was formed by cutting its lid to create an overhang. The overhang prevented frogs from crawling out of the pitfall trap.

<u>Experimental Setup, Data Collection, and Analysis</u>

Each experimental pond received 10 randomly-assigned juvenile frogs. Thus, each pond had the same population density and a random mix of metamorphs from the various natal ponds. All metamorphs were measured and returned to their natal pond, either as the metamorph was removed from a pitfall trap, or upon being removed from the ponds at the end of the experiment. Each metamorph was used only one time in the experiment. The metamorphs that were removed from pitfall traps (i.e., had left ponds) I call ‘transient.’ The metamorphs that remained in ponds for the duration of the experiment I call ‘resident.’

Running every replicate of the experiment at one time was not possible, as I could not capture and hold such a large number of metamorphs at one time. Therefore, I ran the experiment in rounds where half of the replicates were run from August 11 to 27 and the second half of replicates from August 25 to September 12, 2003. Round 2 was shorter in duration than Round 1 by two days because the experimental ponds began to freeze. Each round consisted of 120 metamorphs placed into 1 of 3 treatments, so that at the start of each round there were 40 metamorphs surrounded by each upland substrate and 60 metamorphs in each microhabitat.

Temperature

Weather data was collected by the Mud Flat Weather Station, located at the Mud Flat Administrative Site just 1.6 km from Sam Noble Springs. Precipitation was measured to the 0.25 mm and posted by the Natural Resources Conservation Service (NRCS, 2013). Unfortunately, the weather station did not accurately represent precipitation patterns at the experiment locality. On days where precipitation was noted at the experiment locality, the weather station posted precipitation as zero.

I used dropping temperatures as a correlate for precipitation. On a large scale, observed monthly mean temperature and precipitation have correlated within North America and Europe (Madden and Williams 1978; Trenberth and Shea 2005). The relationship stems from the fact that, over land, dry conditions favor more sunlight and less evaporative cooling, whereas wet summers tend to have lower temperatures (International Panel on Climate Change [IPCC] 2007). As these are generalizations that are meant to be applied to larger time and landscape scales than those of the present study, cooling temperatures are treated as a correlate for rainfall and are used in lieu of precipitation out of necessity.

The date of capture in pitfall traps was recorded for each individual that left a pond. Thus, for each day of the experiment, I had temperature data and information about frog movement patterns. I used a logistic regression model to evaluate the influence of temperature on the probability of metamorphs undergoing terrestrial movements on a particular day. Two potential predictors were entered into the analysis: changing temperatures, and experimental run (i. e., Round 1 or 2).

Time of Day

The time interval (overnight, morning, midday) of the metamorphs' movements was tracked by checking pitfall traps three times each day, at 0700, 1200, and 1900. I compared the proportion of metamorphs that moved during different parts of the day using Chi-squared goodness of fit tests. Mann-Whitney non-parameteric tests were used to compare the influence of changing temperatures on daytime versus overnight movements. Because the time intervals were uneven, comparisons among time intervals were made on the per-hour rate of metamorphs leaving within each time interval.

Size

A total of 213 metamorphs were used to examine the influence of size on movements. Each metamorph was weighed with a handheld Pesola scale to the nearest 0.25 gram. The SVL was measured to the nearest millimeter.

In all body size comparisons between transients and residents, I used the same statistical approach. I used an ANOVA to determine if a body metric differed between transients and residents, and included the number of days spent in ponds as a covariate in the statistical model.

Similarly, I used an ANOVA with number of days as a covariate to test whether there was a size difference among metamorphs that moved within the different substrate treatments, and moving within two microclimates. Additionally, I used an ANOVA with days as a covariate to see if larger metamorphs were the ones who left ponds during times of rising temperatures.

The number of days spent in ponds was a necessary covariate because the transients had less time to grow than the residents whose metrics were taken after 16 or 18 days. Because each metamorph's body metrics were taken twice, at the beginning and end of its use in the experiment, the extent to which body metrics changed over time was also compared between transients and residents.

Substrate

There were three potential outcomes for each metamorph in the experiment: (1) it left the experimental pond, (2) it stayed in the experimental pond, or (3) it was lost from the experiment. I used a Chi-squared goodness of fit test and ANOVA to determine whether dispersal patterns were influenced by the substrate composing a pond's margin (barren ground, mid-level grass, and tall grass heights). Losses were also compared among treatments with a Chi-squared goodness of fit test.

To establish if changing temperature influenced the probability of movement over the three substrates in different ways, I conducted three separate logistic regression analyses, one for each of the three substrates (bare ground, medium grass, and tall grass).

Microhabitat

To best understand whether the meadow (microhabitat) in which a grid was placed affected metamorph movements, I used a Chi-square goodness of fit test to determine the relative proportion of individuals that left the pools and fell into pitfall traps, and the relative proportion of metamorphs that remained in the pools until the end of the experiment. Additionally, I looked at the relationship between weather and movement patterns within each microhabitat, both graphically and with logistic regression analysis, run separately on each meadow type.

Losses between the two meadows were compared with a Chi-squared goodness of fit test. The metamorphs lost from bare ground treatments within each meadow were not included in analyses because the bare ground treatment was the same in both meadows.

Results

A total of 240 spotted frog metamorphs were placed into experimental ponds. Over the course of the experiment, 158 (65.8%) metamorphs left experimental ponds and were considered ‘transient.’ Fifty-five (22.9%) metamorphs remained in the ponds for the duration of the experiment and were considered ‘residents.’ An additional 32 metamorphs (13.3%) were not recovered and were considered ‘lost.’ One metamorph bearing obvious bite marks was found dead in an experimental pond, however, no other mortality was directly observed. The first round of the experiment lasted 18 days and the second round ended 2 days earlier, on day 16, because of freezing conditions.

Temperature

Dropping temperatures appear important in triggering out-of-pond movements (Figure 50). Of the two independent variables within a logistic regression model testing the influence temperature and round of the experiment over the likelihood of a metamorph leaving a pond, only change in temperature had a statically significant influence over whether or not metamorphs left ponds (Wald $\chi^2 = 9.8$, df = 1, P = 0.0017). The results indicate an inverse relationship between temperature and probability of movement.

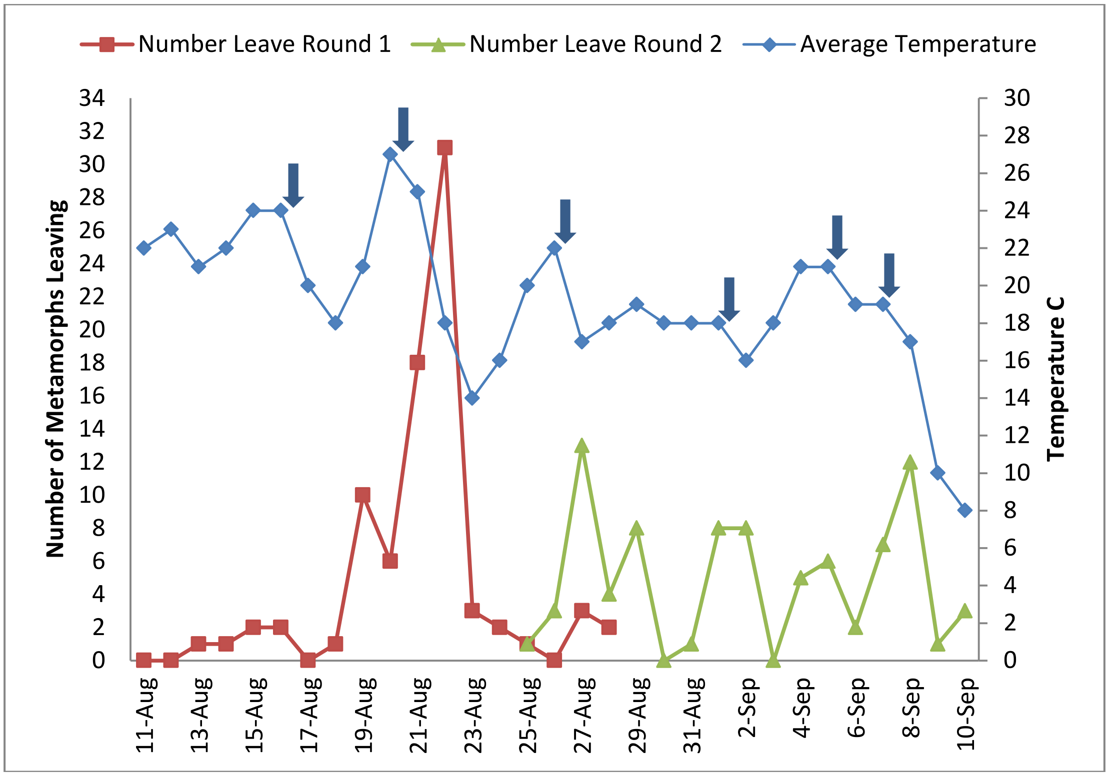


Figure 50. Comparison of average temperature (°C) within each day and the number of frogs leaving experimental ponds during that day from August 11-September 10, 2003 (n = 158). Temperature data are published by the Natural Resources Conservation Service (NRCS) and gathered from the US Geological Survey (USGS) snotel gauge (NRCS, 2013).

Time of Day

Metamorphs showed a clear preference for overnight movements (χ^2 = 18.69, df = 1, P < 0.0001). Out of the 158 movements evaluated, 67.3% of those movements took place overnight. Additionally, frogs showed a preference for overnight movement regardless of the upland substrate surrounding the experimental pond (χ^2 = 2.139, df = 2, P > 0.25). Metamorphs moved overnight (n = 105) more often than during the day (n = 51) fairly consistently among each of the three treatments (Tall Grass = 73% overnight, Medium Grass = 68% overnight, Bare Ground = 60% overnight). In both the wet (n = 84, 64% overnight) and dry (n = 72, 70% overnight) microhabitats metamorphs moved more frequently at night than during the day. There was no difference in the timing of movements within the two microhabitats (χ^2 = 0.756, df = 1, P > 0.725).

When viewed graphically, the rate of daytime movements appeared to increase when the temperature dropped, whereas, the rate of nighttime movements did not seem to be affected by changing temperatures (Figure 51). The median rate at which metamorphs moved at night did not differ between days when the temperature rose and days when the temperature fell (n_1 = 9, n_2 = 7, U = 37, P = 0.3). However, the median rate at which metamorphs left ponds during the daytime was lower during rising temperatures and higher during falling temperatures (n_1 = 6, n_2 = 6, U = 28.5, P = 0.04).

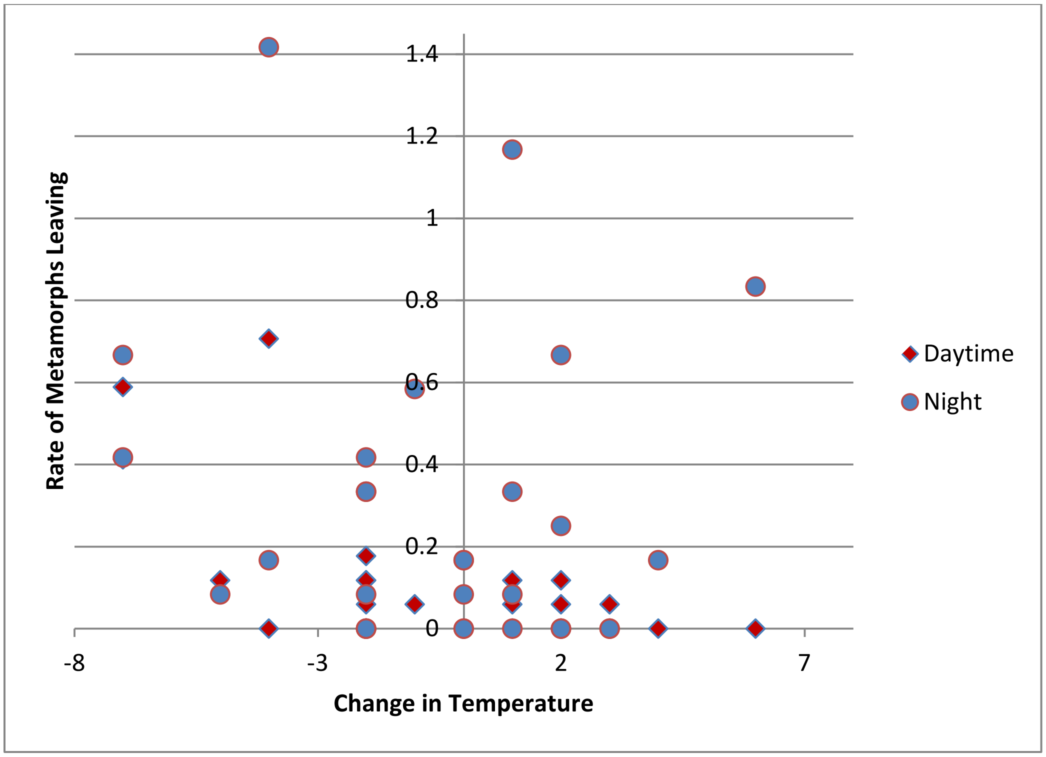


Figure 51. Per-hour rate of frogs leaving experimental ponds during changing temperatures. The y-axis shows the per-hour rate at which frogs left ponds. To the left of the x-axis is falling temperatures and to the right is rising temperatures. Note that the daytime (orange) movements tend to have their highest peaks only during periods of falling temperatures, whereas overnight (blue) movements have high numbers during both rising and falling temperatures.

Body Size

Size (mass and SVL) did not differ significantly between transients and residents (Mass: $F_{1,210} = 0$, $P = 0.98$; SVL: $F_{1,210} = 0.13$, $P = 0.72$). However, residents, on average, gained more weight than transients ($F_{1,210} = 5.23$, $P = 0.0233$).

The mass of transients in the wet meadow was, on average, higher than the mass of the transients in the dry meadow with marginal statistical significance ($F_{1, 155} = 4.02$, $P = 0.47$). However, the influence of mass on that difference was not particularly strong ($R^2 = 0.067$). The mass did not differ among transients in the three treatments ($F_{2, 154} =$

0.63, $P = 0.53$). There was no difference in mass among transients that left on cooling days and transients that left on warming days ($F_{1, 155} = 0.58$, $P = 0.35$).

The SVL of metamorphs crossing the wet meadow did not differ from that of metamorphs crossing the dry meadow ($F_{1, 155} = 0.12$, $P = 0.72$). Nor did the SVL of transient metamorphs differ among treatments ($F_{2, 154} = 1.86$, $P = 0.16$). Transients that left on days when the temperature was cooling tended to have larger SVL measurements than transients that left on days when the temperature was rising ($F_{1, 155} = 4.91$, $P = 0.028$).

Substrate

There was no detectable influence by substrate on the number of metamorphs leaving ponds ($\chi^2 = 0.19$, df = 2, $P > 0.25$). Each of the three substrate treatments had essentially the same number of residents (Tall Grass n = 18, Medium Grass = 18, Bare Ground = 19). On average, transient frogs remained in experimental ponds for about a week (7.6 – 8.7 days), regardless of the surrounding substrate. The substrate along a pond’s margin did not affect the likelihood of a frog leaving (Wald $\chi^2 = 0.051$, df = 1, $P = 0.81$).

The probability of a metamorph crossing the bare and medium grass substrate treatments was positively linked to cooling weather (Medium Grass, Wald $\chi^2 = 5.51$, df = 1, $P = 0.0189$; Bare Ground, Wald $\chi^2 = 8.73$, df = 1, $P = 0.0031$). However, the probability of movement by a metamorph within a tall grass treatment was not significantly influenced by changing temperatures (Wald $\chi^2 = 1.13$, df = 1, $P > 0.9$). Losses did not differ among the substrate treatments ($\chi^2 = 1.261$, df = 2, $P > 0.25$).

Microhabitat

There was no difference in transient numbers between the wet and dry microhabitats ($\chi^2 = 0.573$, df = 1, P > 0.25). However, the patterns of movement appeared to differ between the wet and dry microhabitats (Figure 52). On days when the temperature dropped, metamorph movements across the dry microhabitat were highest in numbers (Wald $\chi^2 = 10.81$, df = 1, P = 0.001). However, movements within the wet microhabitat occurred independently of changing weather (Wald $\chi^2 = 1.39$, df = 1, P = 0.24). Metamorphs were lost from the experiment in higher numbers from the wet microhabitat than the dry microhabitat ($\chi^2 = 12.46$, df = 1, P = 0.002).

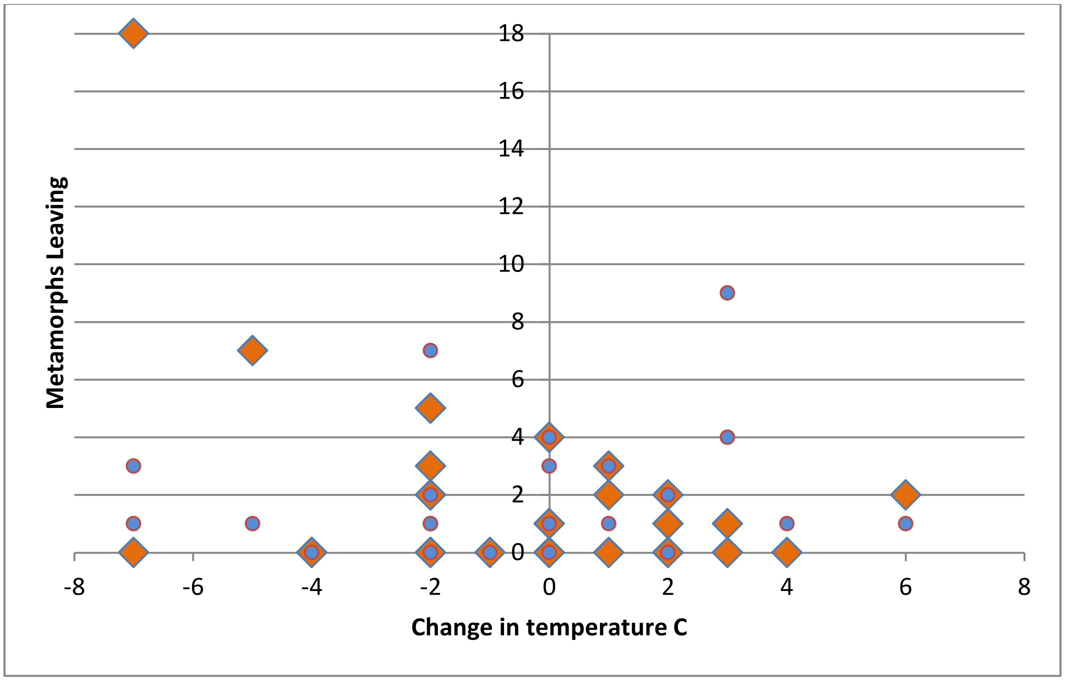


Figure 52. Metamorphs leaving experimental ponds within the dry microhabitat (orange n = 59) and experimental ponds within the wet microhabitat (blue n = 50). Datapoints to the left depict the number of movements within each microhabitat on a day when the temperature fell and datapoints to the right depict the number of movements within each microclimate taking place on a day when the temperature rose.

Discussion

The experimental setting was successful in detecting some of the movement patterns of spotted frog metamorphs in the Owyhees. However, it is important to remember that a straight-line movement from an experimental pond to a pitfall trap would be a distance of 3.7 m. In order to complete a true dispersal-type movement, a metamorph would need to traverse a distance of 50 meters over shrub-steppe (Hammerson 2002). The metamorphs classified as transient could easily have been foraging away from ponds, or simply sampling their surroundings without intending to permanently leave the experimental ponds. With that caution in mind, I did manage to capture some of the requirements of spotted frogs attempting upland movements.

Temperature

My finding that frog activity is, at least partially, tied to temperature supports the idea of habitat permeability being increased by weather conditions. Similar to Chan-McLeod's (2003) finding that extreme heat decreased the permeability of clearcuts to red-legged frogs, the spotted frog metamorphs that I inserted into drier conditions (i.e., bare and medium grass substrates, or the dry meadow microclimate) were more reliant on cooling temperatures for their movements than those metamorphs in the wetter substrate treatment and microclimate.

It would be misleading to imply that cooling temperatures alone can trigger amphibian movements. Cooling temperatures accompanying drought conditions would likely not increase the permeability of the Owyhee's shrub steppe uplands. Although terrestrial movements by juvenile spotted frogs in the Owyhees, were frequently cued by dropping temperatures, the precipitation accompanying dropping temperatures was probably more important. Past research on amphibian movement patterns has shown a positive correlation between precipitation and dispersal propensity among a variety of amphibian taxa and regions (Berven and Grudzien 1990; Dodd and Cade 1998; Sjogren 1998; Metts et al. 2001; Vasconcelos and Calhoun 2004; Cook and Jennings 2007; Chelgren et al. 2008; Graeter et al. 2008). In a seasonally arid region of Africa, heavy rainfall was observed to trigger migratory movements by ranid frogs toward breeding sites (Speiler and Linsenmair 1998). Mazarolle et al. (2001) made the observation, that in areas where hot, dry weather conditions prevailed, amphibian dependence on rain for movements intensified. In their studies on Columbia spotted frogs in Yellowstone National Park, Morris and Tanner (1969) found that spotted frogs had the greatest population turnover following heavy rains. Pilliod (2001) found that Columbia spotted frogs in Skyhigh Basin in Central Idaho tended to move during rain events, but were not entirely limited to rainy conditions for upland movements.

My reliance on cooling temperatures as a surrogate for rainfall was required because of the lack of accurate data on rainfall at the study locale. Despite the close proximity of a weather station purported to record rainfall to the 0.25 mm (NRCS 2013), the information on rainfall was not in accord with my observations in the field; on days when I recorded rain at the study locale, the weather station reported zero precipitation. Accurate precipitation data would likely have been more illustrative about the relationship between movement probability and precipitation.

Time of Day

For the most part spotted frog movements occurred at night, consistent with the notion that nocturnal movements reduce a frog's exposure to predators and the risk of desiccation. Other studies on frogs report similar patterns of nocturnal movements (Sjogren 1998; Roznik and Johnson 2009; Yetman and Fergusen 2011). For example, a pond-breeding species of bullfrog (*Pyxicephalus adspersus*) living in arid grasslands and savannas of Africa limited movements almost exclusively to overnight, probably to offset the risk of desiccation and predation (Yetman and Fergusen 2011). Pitfall traps along stream corridors that were left open overnight in the Owyhees frequently captured spotted frogs (Engle 2000, 2001a). In a study on spotted frogs occupying high elevation sites in central Idaho, out-of-pond movements by spotted frogs tended to occur overnight, though not exclusively (Pilliod et al. 2002), as was consistent with my observations.

Pilliod et al.'s (2002) study also found that relatively warm and rainy nights cued terrestrial movements by spotted frogs. Within the present study, there appeared to be a correlation between temperature and daytime movements, but not between temperature and nighttime movements. There were only high rates of movement during the day when temperatures were dropping. High rates of movement occurred overnight, even during times of rising temperatures. Of course, temperatures are an imperfect correlate for rainfall, which was more likely the cue to movements, as noted by Pilliod.

Body Metrics

The size of an amphibian's body influences its resistance to desiccation through their surface area to volume ratio (Thorson 1955). Thus, it is often the frogs with larger bodies that are most resistant to desiccation when undergoing terrestrial movements. However, in my study, the metamorphs who had gained more mass remained in residence and the metamorphs that gained less mass left ponds. This difference may have stemmed from intra-specific competition where the better competitors were driving the metamorphs that were gaining less mass from the ponds. However, given the equality in metamorph density and food availability across all of the experimental ponds, that observation is conjecture and observations on competition were not the goal of the present study.

There was little influence by size on movement patterns observed within the experiment. In general, amphibians with larger bodies tend to be better able to undertake terrestrial movements. Red-legged frogs that were able to enter clearcuts, where ground-level sunlight was more intense than the surrounding habitat, tended to be those with a relatively large mass to SVL ratio, and the probability that a frog would enter a clearcut was positively related to mass (Chan-McLeod 2003). On the African savannah, bullfrogs with better body condition were the ones that were able to forage over the greatest distances (Yetman and Fergusen 2011). In a study of the movement patterns of newly metamorphosed red-legged frogs (*Rana aurora*), Chelgren et al. (2008) noted that the metamorphs that moved the greatest distances away from standing water sources were those with the largest SVL measurements. There is a lot more variability among body size as amphibians increase in age. A similar study in the Owyhees on older frogs may provide more definitive results.

Substrate

My observations that spotted frog metamorphs traversed each of the three upland substrate treatments in roughly equal numbers initially came as a surprise given past observations on frog behavior. In general, ponds surrounded by substrates that pose barriers to movement remain unoccupied (Vasconcelos and Calhoun 2004; Scherer et al. 2012). Because frogs appear highly sensitive to the substrate surrounding ponds, I had assumed that the upland substrates that were associated with a high risk of desiccation would be avoided and that those frogs would simply remain within the experimental ponds.

However, there is evidence that, for amphibians, the permeability of certain habitats can be increased by cooler and/or wetter weather (Chan-McLeod 2003; Schalk and Luhring, 2010; Popescu and Hunter 2011; Gravel et al. 2012). For example, clearcuts on Vancouver Island, British Columbia, Canada, were actively avoided by red-legged frogs (*Rana aurora*) until days with moderately cool temperatures and periods of rain increased the permeability of those same clearcuts to transient frogs (Chan-McLeod 2003). In eastern Canada, Gravel et al. (2012) found that some pond-dwelling amphibians offset the risk of desiccation associated with crossing roads by moving in greater numbers during periods of rainfall. My observations support the notion that weather conditions influenced the permeability of upland habitat for transient amphibians. Spotted frog metamorphs were dependent on decreasing temperatures (likely associated with rainfall) for upland movements across the barren and mid-height grass substrates. However, terrestrial movements occurred independently of weather conditions within the tall grass substrate.

Although the present study did not focus on movement distance, Pilliod et al. (2002) found that adult spotted frogs in a high mountain basin in Central Idaho traveled at least 500m across dry upland and did not appear to actively seek out moist habitat for movements. The authors also noted that juveniles moved the least of all life stages, and were never found more than 350m from breeding sites. Green frogs (*Rana clamitans*) showed random radial dispersal out of natal ponds until individuals encountered suitably moist traveling habitat such as ditches, streams, and small ponds, which they then used as a movement corridor (Schroeder 1976). Future studies on the movement patterns of spotted frog metamorphs therefore need to examine long-distance movements. The small scale of the present study, 3.7 m, limits the inferences that can be made about the habitat required for successful dispersal by juvenile spotted frogs in the Owyhees.

The duration of stay by metamorphs within each of the three substrates was about one week. I feel that this result is less about the substrate treatments and more illustrative about the response of metamorphs to their placement in the experiment. Had their capture, handling, and use in the experiment evoked a crisis response, I would have expected different behavior. At ponds 3 and 4 within the Sam Noble Springs complex, grazing overlapped with metamorph surveys. No metamorphs were observed in Ponds 3 and 4 during the time period of use by cattle, despite the earlier presence of spotted frog egg masses and larvae. The water within those ponds was turbid and cattle frequently waded through the ponds creating a potential disturbance from the perspective of the metamorphs. Those metamorphs either immediately left the ponds being used by cattle, or took refuge in the pond substrate. I observed neither of those behaviors by the metamorphs within the experiment.

Microhabitat

I expected to see fewer transients within the dry meadow than in the wet meadow because there is considerable evidence that frogs will actively seek out microhabitats that offset the risk of desiccation during terrestrial movements (Cook and Jennings 2007; Blomquist and Hunter 2010; Koehler et al. 2011; Popescu and Hunter 2011). However, the pattern of habitat permeability being liked to cooling temperatures was repeated within the microhabitat analyses. Within the wet meadow, movements occurred independently of changes in the temperature, whereas in the dry meadow movement likelihood was positively linked to cooling temperatures. The latter pattern has been seen in other studies on amphibian movements. For example, a study on habitat use patterns in leopard frogs (*Rana pipiens*) found that, when given the choice to travel through forests or clearcuts, the frogs would enter clearcuts only when the humidity levels were high (Graeter et al. 2008). Chelgren et al. (2008) found that red-legged frogs (*Rana aurora*) could cross deforested pond margins and that those movements were closely tied to precipitation.

Although cooling temperatures appear to increase the permeability of otherwise inhospitable habitat, the importance of wetlands to amphibian survival and movement should not be underestimated. Pickerel frogs (*Rana palustris*) select ephemeral streambeds for movements, because streambeds provide moist microclimates and thick vegetation for predator-avoidance (Gibbs 2000). When released into young clearcuts, juvenile wood frogs (*Lithobates sylvaticus*) seek out old growth forest for the protection of the canopy cover (Popescu and Hunter 2011). Wet microclimates for foraging and movements are so important to amphibians that, with increasingly arid climatic conditions, land managers are encouraged to augment the moisture in microclimates surrounding amphibian breeding ponds (Shoo et al. 2011).

Although there appeared to be fewer constraints on movements within the wet meadow, garter snakes (*Thamnophis sirtalis*) were observed within the wet meadow, but not in the dry meadow. Garter snakes are common predators of amphibians in the Northwestern United States (Nussbaum et al. 1983), and they are known to prey on spotted frogs of all life stages (Pers. obs.). During the course of my study, I noted that losses (metamorphs disappearing from the experimental plots) were higher in the wet meadow than the dry meadow. The presence of predators in the wet meadow and higher losses of spotted frog metamorphs within the wet meadow indicate that predation might have played a role in losses. However, without direct confirmation of predation, there is the possibility that metamorphs escaped the experimental enclosures in some way.

A Note on Natal Pond-Related Behavior

Although spotted frog metamorphs from each of the natal ponds (1, 2, and 10) attempted to disperse, those from natal Pond 10 seemed to be most driven to leave experimental ponds. This observation was especially interesting in light of the observation that of the 82 metamorphs marked at Pond 10 during the late summer of 2002, none were observed, despite repeated surveys, during the spring of 2003 (Munger and Lingo 2003). In contrast, metamorphs marked at the other natal ponds were recaptured frequently. Pond 10 appears to provide suitable habitat for all spotted frog life stages and lies between several occupied sites along the drainage. In addition, adults have consistently bred at Pond 10 since surveys began at Sam Noble Springs in 1997 (Engle 2001b). The reason for the propensity for metamorphs to disperse away from Pond 10 remains a mystery.

Conclusions

Temperature appeared to be an important factor that triggered out-of-pond movements by spotted frogs. Understanding the relationship between temperature and movement patterns helps with our understanding of connectivity among pond-dwelling amphibian populations that are separated by potential barriers to movements, such as arid uplands (Gravel et al. 2012). Spotted frog metapopulation function may be limited in the Owyhees during times of severe drought, because metapopulation function hinges on the ability of a species to disperse from one area of suitable habitat to another. In an arid region that has undergone a series of drought years, such as the Owyhees, population contractions may result from the lack of connectivity between occupied sites, potential habitat, and complimentary habitat features such as breeding, foraging and overwintering habitat. Thus, when examining population trends within the Owyhees spotted frog population, observations of weather patterns should accompany any long-term data on frog numbers.

The majority of movements by spotted frog metamorphs took place overnight. Thus, future studies on movement patterns, especially those that rely on direct observations of movements, should include a nocturnal component. In addition, spotted frog surveys, especially those designed to detect upland use, may benefit from having a nocturnal component, as this appears to be a time when movements into arid conditions are more likely to occur.

There is a history of research on the influence of amphibian body size on mobility that dates back to Thorson’s work in the 1950’s and, in general, larger-bodied amphibians are more mobile than smaller-bodied amphibians of the same species and gender. It is unclear why my results do not align with those found in the literature. However, there is little variability in size among a cohort of emerging spotted frogs.

At the scale of 3.7 meters, spotted frog metamorphs appeared to cross entirely denuded upland substrates and dry microclimates. However, that is not a sufficient distance to ensure a dispersal-type movement. Observations on spotted frog movements across upland habitats more on the scale of 50 m (Popescu and Hunter 2011), would provide more information on the ability of spotted frog metamorphs to undertake terrestrial movements in the Owyhees.

REFERENCES

Amburgey, S., W.C. Funk, M. Murphy, E. Muths. 2012. Effects of hydroperiod duration on survival, developmental rate, and size at metamorphosis in boreal chorus frog tadpoles (*Pseudacris maculata*). Herpetologica 68(4):456-467.

Baird, S.F. and C. Girard. 1853. Communication. Proceedings of the Academy of Natural Sciences Philadelphia. 6: 378-379.

Baker, B.W., and E.P. Hill. 2003. Beaver (*Castor canadensis*). P 288-310. In: G.A. Felhammer, B.C. Thompson, and J.A. Chapman, eds. Wild Mammals of North America: Biology, Management, and Conservation. Second Edition. The Johns Hopkins University Press, Baltimore, Maryland, U.S.A.

Barnett, H.K., J.S. Richardson. 2002. Predation risk and competition effects on the life history characteristics of larval Oregon spotted frog and larval red-legged frog. Oecologica. 132(3): 436-444.

Berry, S. S. 1923. Observations on a Montana beaver canal. Journal of Mammology. 4(2): 92-103.

Berven, K.A., T.A. Grudzien. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. Evolution. 44(8): 2047-2056.

Blankinship, M.E., J.C. Munger. 2004. Columbia spotted frogs monitoring in the Owyhee Mountains of southwestern Idaho: year 2004 results, including a survey of Long Tom Creek. Boise State University and the U.S. Bureau of Land Management.

Blaustein, A. R. and D. B. Wake. 1990. Declining amphibian populations: A global phenomenon? Trends in Ecology and Evolution 5:203-204.

Blaustein, A.R. 1994. Chicken little or Nero’s fiddle? A perspective on declining amphibian populations. Herpetologica. 50(1): 85-97.

Blomquist, S.M. 2000. Monitoring and modeling the viability of the Columbia spotted frog *Rana luteiventris*. Masters Thesis. University of Nevada, Reno.

Blomquist, S.M., and M.L. Hunter, Jr. 2010. A multiscale assessment of amphibian habitat selection: wood frog response to timber harvesting. Ecoscience. 17(3): 251-264.

Bos, D.H., and J.W. Sites, Jr. 2001. Phylogeography and conservation genetis of the Columbia spotted frog (*Rana luteiventris*; Amphibia, Ranidae). Molecular Ecology. 10: 1499-1513.

Bull, E.L. 2005. Ecology of the Columbia spotted frog in northwestern Oregon. General Technical Repprt PNW-GTR-640. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 46p.

Bury, R.B. 1999. A historical perspective and critique of the declining amphibian crisis. Wildlife Society Bulletin. 27(3): 1064-1068.

Chan-McLeod, A.C. 2003. Factors affecting the permeability of clearcuts to red-legged frogs. Journal of Wildlife Management. 67(4): 663-671.

Chelgren, N.D. 2003. Effects of body size on the survival and timing of newly metamorphosed northern red-legged frogs. Masters Thesis. Oregon State University, Corvallis, Oregon, USA.

Chelgren, N.D., D.K. Rosenberg, S.S. Heppell, and A.I. Gitelman. 2006. Carryover aquatic effects on survival of metamorphic frogs during pond emigration. Ecological Applications. 16(1): 250-261.

Chelgren, N.D., D.K. Rosenburg, S.S. Heppel, and A.I. Gitelman. 2008. Individual variation affects departure rate from the natal pond in an ephemeral pond breeding anuran. Canadian Journal of Zoology. 86(4): 260-267.

Columbia Spotted Frog Technical Team (CSFTT). 2003. Conservation agreement and strategy: Columbia spotted frog (*Rana luteiventris*) Great Basin Population, Nevada, northeastern subpopulations: Jarbridge-Independence and Ruby Mountain. Northeastern Nevada, U.S.A. 52p.

Collen, P., and R.J. Gibson. 2001. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish – a review. Reviews in Fish Biology and Fisheries. 10: 439-461.

Cook, D.G., and M.R. Jennings. 2007. Microhabitat use of the California red-legged frog and introduced bullfrog in a seasonal marsh. Herpetologica. 63(4): 430-440.

Connell J.H. 1979. Tropical rain forests and coral reefs as open non-equilibrium systems. p 141-163. In: Andersen R.M., B.D. Turner, and L.R. Taylor eds. *Population Dynamics*. Blackwell Scientific Publications, Oxford.

Corkran, C.C., and C.R. Thoms. 1996. Amphibians of Oregon, Washington, and British Columbia: a field identification guide. Lone Pine Publishing, Renton, Washington, USA; Vancouver, British Columbia; Edmonton, Alberta, Canada. 175p.

Columbia Spotted Frog Technical Team. 2003. Conservation agreement and strategy, Columbia spotted frog (Rana luteiventris), Great Basin population, Nevada; Northeastern subpopulations, Jarbidge-Independence and Ruby Mountain. U.S.A.

Cunningham, J.M., AJ.K. Calhoun, W.E. Glanz. 2007. Pond-breeding amphibian species richness and habitat selection in a beaver-modified landscape. The Journal of Wildlife Management. 71(8): 2517-2526.

Debinski, D.M., R.D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology. 14(2). 342-355.

DAPTF (Declining Amphibian Population Task Force). 2002. Recommended protocols for species management: DAPTF fieldwork code of practice. http://ventura.fws.gov//SurveyProt/DAPTF_prot.htm

DeVries, P., K.L. Fetherston, A. Vitale, and S. Madsen. 2012. Emulating riverine landscape controls of beaver in stream restoration. Fisheries. 37(6): 246-255.

Dodd, C.K., Jr. and B.S. Cade. 1998. Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. Conservation Biology 12(2): 331-339.

Engle, J. C. and J. C. Munger. 1998. Population structure of spotted frogs in the Owyhee Mountains. BLM Technical Bulletin 98-20.

Engle, J.C. 2000. Columbia spotted frog Great Basin Population (Owyhee Mountains Subpopulation) long-term monitoring plan Owyhee County, Idaho. US Fish and Wildlife Service. Boise Field Office, Boise, Idaho, U.S.A.

Engle, J. C. 2001a. Population biology and natural history of Columbia spotted frogs (*Rana luteiventris*) in the Owyhee Uplands of Southwest Idaho. Master’s thesis. Boise State University, Boise, ID, U.S.A.

Engle, J.C. 2001b. Columbia spotted frog project: The translocation of two male Columbia spotted frogs between breeding sites within an element occurrence in the Owyhee subpopulation of the Great Basin Population. Technical Report to The Idaho Department of Fish and Game. Section 6 Endangered Species Act, Threatened and Endangered Species Project E-26-1.

Fahrig, L., G. Merriam. 1985. Habitat patch connectivity and population survival. Ecology. 66(6): 1762-1768.

Fellers, G.M., and C.A. Drost. 1993. Disappearance of the Cascades frog *Rana cascadae* at the southern end of its range, California, USA. Biological Conservation. 65: 177-181.

Franklin, A.B., B.R. Noon, T.L. George. 2002. What is habitat fragmentation? Studies in Avian Biology. 25: 20-29.

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

Funk, W.C., C.A. Pearl, H.M. Draheim, M.J. Adams, T.D. Mullins, S.M. Haig. 2008. Range-wide phylogeographic analysis of the spotted frog complex (*Rana luteiventris* and *R. pretiosa*) in northwestern North America. Molecular Phylogenetics and Evolution. 49: 198-210.

Funk, C.W., and J.M. Robertson. 2011. Population genetic structure of Columbia spotted frogs (*Rana luteiventris*) in southwestern Idaho. BLM Annual Report. Fort Collins, Colorado. USA.

Gates, J.E., L.W. Gysel. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. Ecology. 59: 871-883.

Gibbs, J.P. 2000. Wetland loss and biodiversity conservation. Conservation Biology. 14: 314-317.

Gomez, D. 1994. Conservation assessment for the spotted frog (*Rana pretiosa*) in the intermountain region. USDA Forest Service Intermountain Region.

Graeter, G.A., B.B. Rothermel, and J.W. Gibbons. 2008. Habitat selection and movement of pond-breeding amphibians in experimentally fragmented pine forests. The Journal of Wildlife Management. 72(2): 473-482.

Gravel M., M.J. Mazerolle, and M.A. Villard. 2012. Ineractive effects of roads and weather on juvenile amphibian movements. Amphibia-Reptilia 33: 113-127

Green, D. M., T. F. Sharbel, J. Kearsley, and H. Kaiser. 1996. Postglacial range fluctuation, genetic subdivision and speciation in the western North American spotted frog complex, *Rana pretiosa*. Evolution, 50(1), 374-390.

Gosner, K.L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica. 16: 183-190.

Gourley, J., L. Romin. 2002. Endangered wildlife and plants; 12-month finding for a petition to list the Wasatch Front Columbia spotted frog as threatened throughout its range. Federal Register. 67(169): 55758-55767.

Hammerson, G. 2002. Element Occurrence Specifications for Ranid frogs. AAABH00001. Idaho Department of Fish and Game.

Hayes, M.P., M.R. Jennings. 1986. Decline of Ranid frog species in western North America: are bullfrogs (*Rana catesbeiana*) responsible? Journal of Herpetology. 20(4): 490-509.

Heaton, T. H. 1990. Quaternary mammals of the Great Basin: extinct giants, Pleistocene relics, and recent immigrants. In R.M. Ross. Causes of Evolution: a Paleontological Perspective. University of Chicago Press. Chicago, IL, U.S.A. 494 pages.

Hossak, B.R., W.H. Lowe, and P.S. Corn. 2012. Rapid increases and time-lagged declines in amphibian occupancy after wildfire. Conservation Biology. 27(1): 219-228.

Howard, A. and J.C. Munger. 2003. Effects of livestock grazing on the invertebrate prey base and on survival and growth of larvae of the Columbia spotted frog, *Rana luteiventris*. Bureau of Land Management Technical Bulletin No. 03-7. Boise, Idaho. April 2003. 28pp.

Huston, M. 1979. A general hypothesis of species diversity. The American Naturalist. 113(1): 81-101.

Idaho Conservation Data Center, Idaho Department of Fish and Game. 1999. Element Occurrence Record (EOR) Database. Boise, ID.

International Panel on Climate Change (IPCC). 2007. Climate change: the Scientific Basis. Cambridge University Press.

Jennings, M.R., M.P. Hayes. 1994. Decline of native Ranid frogs in the Desert Southwest. Herpetology of the North American Deserts Proceedings of a Symposium. P.R. Brown and J.W. Wright eds. Special Publication Number 5. Southwestern Herpetologist’s Society. Serpent’s Tale Books. Excelsior, MN.

Johnston, C.A., R.J. Naiman. 1990. Aquatic patch creation in relation to beaver population trends. Ecology. 71(4): 1617-1621.

Karraker, N.E., and J.P. Gibbs. 2009. Amphibian production in forested landscapes in relation to wetland hydroperiod: a case study of vernal pools and beaver ponds. Biological Conservation. 142. 2293-2302.

Kendell, K. 2001. Northern leopard frog reintroduction: Raven River-year 2(2000). Alberta Sustainable Resource Development, Fish and Wildlife Service, Alberta Species at Risk Report No. 13., Edmonton, AB. 43pp.

Kohler, A., J. Sadowska, J. Olszewska, P. Trzeciak, O. Berger-Tal, and C.R. Tracy. 2011. Staying warm or moist? Operative temperature and thermal preferences of common frogs (Rana temporaria), and effects on locomotion. The Herpetological Journal. 21(1): 17-26.

Lohr, K., B. Haak. 2009. Columbia spotted frog Great Basin Population (*Owyhee Subpopulation*) Long-term Monitoring Plan: year 2009 results. Progress Report. Idaho Department of Fish and Game. Nampa, Idaho, U.S.A.

Lord, J.M., D.A. Norton. 1990. Scale and the spatial concept of fragmentation. Conservation Biology. 4(2): 197-202.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey, USA.

Madden, R.A., and J. Williams. 1978. Correlation between temperature and precipitation in the United States and Europe. Monthly Weather Review. 106(1): 142-147.

Marsh, D.M., and P.C. Trenham. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology. 15(1): 40-49.

Mazarolle, M.J. 2001. Amphibian activity, movement patterns, and body size in fragmented peat bogs. Journal of Herpetology. 35: 13-20.

McCoy, E.D., and H.R. Mushinski. 2007. Estimates of minimum patch size depend on the method of estimation and the condition of the habitat. Ecology 88(6): 1401-1407.

McCullough, D.R. 1996. Spatially structured populations and harvest theory. Journal of Wildlife Management. 60(1): 1-9.

McKinstry, M.C., and Anderson, S.H. 1999. Attitudes of private- and public-land managers in Wyoming, USA, toward beaver. Environmental Management. 23(1): 95-101.

McKinstry, M.C., P. Caffrey, and S.H. Anderson. 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. Journal of the American Water Resources Association. 37(6): 1571-1577.

McMenamin, S.K., E.A. Hadly, C.K. Wright. 2008. Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. Proceedings of the National Academy of Sciences of the United States of America. 105(44): 16988-16993.

Meffe, G.K., C.R. Carroll. 1994. Principles of Conservation Biology. Sinauer Asscociates Incorporated pubs. Sunderland, Massachusettes. 600p.

Metts, B.S., J.D. Lanham, K.R. Russell. 2001. Evaluation of herpetofaunal communities on upland streams and beaver-impounded streams in the upper Piedmont of South Carolina. The American Midland Naturalist. 145(1): 54-65.

Morris, R.L. and W.W. Tanner. 1969. The ecology of the western spotted frog, *Rana pretiosa pretiosa* Baird and Girard, a life history study. The Great Basin Naturalist. 29: 45-81.

Moser, A, and G. Patton. 2006. Columbia spotted frog Great Basin population (Owyhee subpopulation) long-term monitoring plan: Year 2006 results at Sam Noble Springs. Idaho Department of Fish and Game Report. Boise, Idaho. December 2006. 16pp.

Moser, A. 2007. Columbia spotted frog Great Basin population (Owyhee subpopulation) long-term monitoring plan: Revised 2007. Idaho Department of Fish and Game and Owyhee Columbia spotted frog working group. Boise, Idaho. August 2007. 17pp.

Munger, J.C., L. Heberger, D. Logan, W. Peterson, L. Mealy, and M. Cauglin. 1994. A survey of the herpetofauna of the Bruneau Resource Area, with focus on the spotted frog, *Rana pretiosa*. Idaho Bureau of Land Management Technical Bulletin 94-7.

Munger J.C., M. Gerber, M. Cauglin, and T. Bert. 1995. Status and habitat associations of the spotted frog, *Rana pretiosa*, in southwestern Idaho. Idaho Bureau of Land Management Technical Bulletin #96-1.

Munger, J. C., A. Ames and B. Barnett. 1997. 1996 Survey for Columbia spotted frogs in the Owyhee Mountains of southwestern Idaho. Idaho Bureau of Land Management Technical Bulletin 97-13.

Munger, J.C., M. Gerber, K. Madrid, M. Carroll, W. Petersen, L. Herberger. 1998. U.S. National Wetland Inventroy classifications as predictors of the occurrence of Columbia spotted frogs (*Rana luteiventris*) in and Pacific tree frogs (*Hyla regilla*). Conservation Biology. 12(2): 320-330.

Munger, J.C., and B. Barnett. 2002. 1997 survey for Columbia spotted frogs in the Owyhee Mountains of southwestern Idaho. Report from a challenge cost share agreement between US Bureau of Land Management and Boise State University. BLM order# 1422D010P970107.

Munger, J.C., and H.A. Lingo. 2002. Columbia spotted frog Great Basin Population, Owyhee subpopulation long-term monitoring plan year 2002 results. Report from a challenge cost share agreement between US Bureau of Land Management and Boise State University. BLM order# 1422D010P970107.

Munger, J.C. and H.A. Lingo. 2003. Reintroduction of beaver to aid restoration of the spotted frog population at Stoneman Creek. Technical Report Submitted to the US Bureau of Land Management. Boise, Idaho.

Munger, J.C., K. Oelrich. 2005. Columbia spotted frog Great Basin Population, Owyhee Subpopulation long-term monitoring plan year 2005 results. Report from a challenge cost share agreement between US Bureau of Land Management and Boise State University. BLM order# 1422D010P970107.

Naiman, R.J., J.M. Melillo, J.E. Hobie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology. 67(5): 1254-1269.

Naiman, R.J., C.A. Johnston, and J.C. Kelley. 1988. Alteration of North American streams by beaver. BioScience. 38: 753-762.

Nauwelerts, S., J. Coeck, P. Aerts. 2000. Visible implant elastomers as a method for marking adult anurans. Herpetological Review. 31(3): 154-155.

Northwest Marine Technology (NMT). 2012. NMT, Inc. Northwest Marine Technology. 14 November, 2012. http://www.nmt.us/

Natural Resources Conservation Service (NRCS). 2013. United States Department of Agriculture. National Water and Climate Center. Mud Flat Snotel Site (Site number 654). http://www.wcc.nrcs.usda.gov/

Nussbaum, R.A., E.D. Brodie, and R.M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. University of Idaho Press, Moscow, Idaho, USA.

Olson, D.H. and W.P. Leonard. 1997. Amphibian Survey and Monitoring: a Standardized Approach for the Pacific Northwest. Northwest Fauna 4: 1-21.

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

Pilliod, D.S., C.R. Peterson. 2001. Local and landscape effects of introduced trout on amphibians in historically fishless watersheds. Ecosystems. 4(4): 322-333.

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

Pimentel, D., U. Stachow, D.A. Takacs, H.W. Brubaker, A.R. Dumas, J.J. Meaney, A.S. O'Neil, D.E. Onsi, D.B. Corzilius. 1992. Conserving biological diversity in agricultural/forestry systems. BioScience. 42:5 p354-362

Pope, S.E., L. Fahrig, H.G. Merriam. 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecology. 81(9): 2498-2508.

Popescu, V.D., and M.L. Hunter, Jr. 2011. Clear-cutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements. Ecological Applications. 21(4): 1283-1295.

Reaser, J.K. 1997. Amphibian declines: conservation science and adaptive management. PhD. Dissertation, Stanford University, Reaser, J.K. 2000. Demographic analysis of the Columbia spotted frog *(Rana luteiventris)*: case study in spatiotemporal variation. Canadian Journal of Zoology. 78: 1158-1167.

Reaser, J.K. and D.S. Pilliod. 2005. Columbia spotted frog (*Rana luteiventris*). In: Lanoo, M.J., ed. Amphibians Declines: The Status and Conservation of United States Amphibians. Berkekey, CA: University of California Press: 559-563.

Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs. 52: 199-221.

Ross, D.A., M.C. Stanger, K. McDonald, D.L. Shirley, P.A. White, and L.D. Lentsch. 1994. Distribution, habitat use, and relative abundance indicies of spotted frogs in the West Desert, Utah, 1993. Native Wildlife Section, Utah Division of Wildlife Resources. Salt Lake City, Utah. Publication Number 93-15.

Rothermel, B.B. 2004. Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. Ecological Applications. 14(5): 1535-1546.

Roznik, E.A., and S.A. Johnson. 2009. Burrow use and survival of newly-metamorphosed gopher frogs (*Rana capito*). Journal of Herpetology. 43(3): 431-437.

Sada, D.W., G.L. Vinyard. 2002. Anthropogenic changes in biogeography of Great Basin aquatic biota. Smithsonian Contributions to the Earth Sciences. 33: 277-293.

Schalk, C.M., and T.M. Luhring. 2010. Vagility of aquatic salamanders: implications for wetland connectivity. Journal of herpetology. 44(1): 104-109.

Schroeder, E.E. 1976. Dispersal and movements of newly transformed green frogs (*Rana clamitans*). American Midland Naturalist. 95(2): 471-474.

Scherer, R.D., E. Muths, and B.R. Noon. 2012. The importance of local and landscape scale processes to the occupancy of wetlands by pond-breeding amphibians. Population Ecology. 54: 497-498.

Shoo, L.P., D.H. Olson, S.K. McMenamin, K.A. Murray, M. Van Sluys, M.A. Donnelly, D.A. Stratford, J. Terhivuo, A. Merino-Viteri, S.M. Herbert, P.J. Bishop, P.S. Corn, L. Dovey, R.A. Griffiths, K. Lowe, M. Mahoney, H. McCallum, J.D. Shuker, C. Simpkins, L.F. Skerratt, S.E. Williams, and J.M. Hero. 2011. Engineering a future for amphibians under climate change. Journal of Applied Ecology. 48: 487-492.

Sjogren, P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). Biological Journal of the Linnaean Society. 42: 135-147.

Sjogren, P.G. 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. Ecology 75(5): 1357-1367.

Sjogren, P.G. 1998. Spatial movement patterns in frogs: Differences between three *Rana* species. Ecoscience. 5(2): 148-155.

Spieler, M., and K.E. Linsenmair. 1998. Migration patterns and diurnal use of shelter in a Ranid frog in a west African savannah: a telemetric study. Amphibia-Reptilia. 19(1): 43-64.

Stevens, C.E., C.A. Paszkowski, G.J. Scrimgeour. 2006. Older is better: beaver ponds on boreal streams as breeding habitat for the wood frog. The Journal of Wildlife Management. 70(5): 1360-1371.

Stoffyn-Egli, P., and J.H.M. Willison. 2011. Including wildlife habitat in the definition of riparian areas: the beaver (*Castor Canadensis*) as an umbrella species for riparian obligate animals. Environmental Reviews. 19: 479-493.

Thompson, H.B. 1913. Description of a new subspecies of *Rana pretiosa* from Nevada. Proceedings of the Biological Scocietyof Washington. 26: 53-56.

Thorson, T.B. 1955. The relationship of water economy to terrestrialism in amphibians. Ecology. 36: 100-116.

Trenberth, K.E., and D.J. Shea. 2005. Relationships between precipitation and surface temperature. Geophysical Research Letters. 32(14): Article Number: L14703.

Turner, F.B. 1962. An analysis of geographic variation and distribution of *Rana pretiosa*. American Philosophical Society Yearbook 1962. 325-328.

Turner, J. F. 1993. Endangered and threatened wildlife and plants; finding on petition to list the spotted frog. Federal Register 58(87):27260-27263.

UDWR (Utah Department of Wildlife Resources). 2006. Columbia spotted frog (*Rana luteiventris*) Conservation agreement and strategy. Compilation of conservation activities (1998-2006). Publication Number 10-5. Utah Division of Wildlife Resources. Salt Lake City, Utah, U.S.A. 36pp.

US Fish and Wildlife Service (USFWS). 2006. Proposed candidate conservation agreement with assurances for the Columbia spotted frog at Sam Noble Springs, Owyhee County, Idaho. Federal Register. 71(21): 5358-5359.

Wente, W.H., M.J. Adams, and C.A. Pearl. 2005. Evidence of decline for *Bufo boreas* and *Rana luteiventris* in and around the northern Great Basin, western U.S.A. Alytes. 22: 95-108.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3(4): 385-397.

Wilcox, B. A. and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation and extinction. Am. Nat. 125:879-887.

Wright, J.P., C.G. Jones, and A.S. Flecker. 2002. An ecosystem engineer, the beaver increases species richness at the landscape scale. Oecologia. 132: 96-101.

Wyman, R. 1990. What's happening to the amphibians? Conservation Biology. 4: 350-352.

Vasconcelos, D., and Calhoun A.J.K. 2004. Movement patterns of adult and juvenile Rana sylvatica (LeConte) and Ambystoma maculatum (Shaw) in three restored seasonal pools in Maine. Journal of Herpetology. 38(4): 551-561.

Yetman, C.A., and W.H. Fergusen. 2011. Conservation implications of spatial habitat use by adult giant bullfrogs (*Pyxicephalus adspersus).* Journal of Herpetology. 45(1): 56-62.