Columbia Spotted Frog (*Rana luteiventris* formerly *R. pretiosa*): A Technical Conservation Assessment

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AUTHORS' BIOGRAPHIES

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Doug Keinath is the Zoology Program Manager for the Wyoming Natural Diversity Database, which is a research unit of the University of Wyoming and a member of the Natural Heritage Network. He has been researching Wyoming's wildlife for the past nine years and has 11 years experience in conducting technical and policy analyses for resource management professionals. His broader scope of research focuses on bat and small mammal ecology, survey, and monitoring at the population and landscape scales, and more recently on the spatially explicit predictive distribution modeling of sensitive elements (i.e., animals, plants, communities) of the Rocky Mountain West. Mr. Keinath earned a B.S. in Interdisciplinary Engineering (1993; *magna cum laude*) and a B.S. in Natural Resource Management (1993; with Distinction) from the University of Michigan and a M.S. in Wildlife Biology from the University of Wyoming.

COVER PHOTO CREDIT

Columbia spotted frog (*Rana luteiventris*), Yellowstone National Park. Photo by Matthew Chatfield.

Summary of Key Components for Conservation of the Columbia Spotted Frog

Four populations of Columbia spotted frog (*Rana luteiventris* formerly *R. pretiosa*) are currently recognized: a main population, which extends from northwestern Wyoming through western Canada and includes the species' range in USDA Forest Service Region 2, and three disjunct populations to the south. Although some local declines have been documented, the main population is generally considered secure and has no federal status as endangered or threatened.

Within Region 2, Columbia spotted frogs exist on the Bighorn National Forest as a small, geographically isolated population restricted to a single watershed. There are no records showing that the status of this disjunct population has been reviewed by federal or state agencies. This species is also known to occur on the Shoshone National Forest. Although this forest is immediately adjacent to other federal lands that contain this species, spotted frogs appear to be common in only one portion of the Shoshone National Forest. Survey efforts have probably been inadequate to determine if the species is common or rare throughout the Shoshone National Forest. The Columbia spotted frog is not known to occur on any other national forest within Region 2, and historical data are too scarce to determine if declines have occurred in Region 2.

Habitat loss, degradation, and fragmentation are potential threats to spotted frogs in Region 2. Sport fish introduction, water manipulation, road construction, and livestock grazing are identified as the activities most likely to affect habitat. Drought is also a threat to frogs and their habitat, and its effects may be exacerbated by management activities and land uses. Two infectious diseases, chytridiomycosis and ranavirus, have been found in spotted frogs elsewhere in northwestern Wyoming and could threaten the persistence of local populations and the abundance of frogs. Spotted frog populations also may be directly affected, in terms of survival and reproduction, by elevated mortality rates from a variety of human and management activities (e.g., roadkill, trampling), predation by fish, and exposure to toxic chemicals. On the Bighorn National Forest, the spotted frog population is particularly vulnerable due to its geographical isolation and the small number of active breeding sites.

The main conservation concerns for the Columbia spotted frog involve maintaining the viability of the disjunct population on the Bighorn National Forest and determining the distribution, abundance, and status of populations on the Shoshone National Forest. Identification of breeding, overwintering, and migration areas is necessary to determine if populations are at risk from site-specific land uses and management activities, particularly on the Bighorn National Forest, but also on portions of the Shoshone National Forest where spotted frogs may be uncommon or relatively isolated. Forest management practices need to be evaluated for their impacts on spotted frogs to ensure that viable populations are maintained on both national forests.

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Introduction

This assessment of the Columbia spotted frog (*Rana luteiventris* formerly *R. pretiosa*) is part of the Species Conservation Project for Region 2 of the USDA Forest Service (USFS). The Columbia spotted frog was selected for assessment because it is classified as a sensitive species in Region 2. Within the National Forest System, a sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downward trends in abundance and/or in habitat suitability that would reduce its distribution. A sensitive species may also be one with a limited distribution such that population stability or permanence appears to be at risk (FSM 2670.5 (19)). Because a sensitive species may require special management, knowledge of its biology and ecology is critical. This report addresses the biology, ecology, conservation status, and management of the spotted frog throughout its current range.

Goal and Scope

Our goal in this conservation assessment is to provide a current summary of published information and expert interpretation of this information that can be used to develop management plans for the Columbia spotted frog. Since there is little information on spotted frogs specifically from Region 2, this assessment draws from spotted frog and other amphibian studies conducted outside the region. Of these studies, spotted frog surveys, monitoring, and research conducted in the Greater Yellowstone Ecosystem (GYE; defined as the mountainous area surrounding Yellowstone National Park) are most applicable to spotted frogs in Region 2. The regional boundary separating the Shoshone National Forest from other national forests and lands in the GYE is ecologically artificial, and spotted frog populations of these adjacent land management units are logically considered together.

In creating this assessment, we consulted with expert scientists and reviewed refereed scientific literature, research reports, unpublished documents, and Natural Heritage Program data. Whenever possible, we emphasize the peer-reviewed literature over unpublished reports, but much of the relevant information on spotted frogs, particularly conservation management material, has not been published. Occurrence information from Natural Heritage Programs and survey-monitoring data in the GYE were used extensively to estimate the distribution of this species. These occurrence data were standardized to the methods and level of accuracy used in the Wyoming Natural Diversity Database. This assessment is based on the best information currently available, but it should be noted that new research on spotted frogs and the findings of on-going monitoring projects in the GYE are likely to provide additional insights and management tools in the near future.

Uncertainty and Limitations

In this assessment we compiled and synthesized information from multiple sources, and we have attempted to indicate which findings were supported by evidence and which were more speculative or subject to challenge. The extent and causes of amphibian population declines in western North America are subject to active research in recent years, with hypotheses and concepts under frequent examination and revision. Current knowledge supports the hypothesis that amphibian populations are declining in some areas and at risk in others. There is significant uncertainty whether hypothesized causes apply broadly to many species of amphibians and to spotted frogs in particular in Region 2. Some findings and generalizations that we applied, based on current knowledge, may be challenged and discredited with further research, or they may be found not to apply to spotted frogs in Region 2. Limitations reflect the lack of information on the species' distribution and abundance patterns in Region 2, poor information on its population biology, the location and intensity of potential threats to spotted frogs and their habitat in Region 2, and the paucity of research detailing how this species responds to human activities and habitat modification.

The text was largely written and reviewed in 2002 and 2003; research and trend information published after 2003 has not been thoroughly incorporated or was not available for consideration by this assessment.

Publication and Peer Review

This species assessment will be published on the USDA Forest Service Region 2 World Wide Web site in order to facilitate its use by USFS personnel, other agencies, and the public. Web publication will make this information accessible more rapidly than publication as a report, and it will make revisions more efficient. A link to this publication will also be available on the Wyoming Natural Diversity Database Web site.

All assessments developed for the Species Conservation Project have been formally peer reviewed prior to release on the Web. An early draft of this assessment was reviewed by Dr. David Pilliod, California

Polytechnic State University, and his comments were incorporated. This report was also reviewed through a process administered by the Society for Conservation Biology, employing two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Federal Endangered Species Act

The U.S. Fish and Wildlife Service (USFWS) currently recognizes four populations of Columbia spotted frogs: the Northern (or main) population, which extends from northwestern Wyoming through western Canada and includes spotted frogs in USFS Region 2; and three smaller, disjunct populations, the Wasatch population in Utah, the West Desert population in Utah, and the Great Basin population in eastern Oregon, southwestern Idaho, and Nevada (U.S. Fish and Wildlife Service Region 6 2002). The Northern population currently has no status under the Endangered Species Act (ESA). In 1993, the USFWS ranked the three disjunct populations as warranted but precluded for listing under the ESA (Worthing 1993). In April 1998, USFWS determined that the status of the species in Utah had improved and that the spotted frog no longer warranted listing under the ESA (63 FR 16218). With this finding, the Wasatch and West Desert distinct population segments were removed as candidates for listing on October 25, 1999 (64 FR 57533). This action was challenged in federal court with regards to the Wasatch Front spotted frogs. A legal settlement stipulated that the USFWS remand the 1998 “not warranted” finding and start a new status review and 12-month finding on the Wasatch Front population. A status review by USFWS in 2002 confirmed the “not warranted” designation for the Wasatch population (U.S. Fish and Wildlife Service Region 6 2002). In 2001, the Great Basin population was assigned an elevated priority rating (from priority 9 to priority 3, the highest rank possible for a subspecies); this change was based on the discovery of chytrid disease in the Owyhee subpopulation, declining numbers, and imminent threats (U.S. Fish and Wildlife Service Snake River Basin Office 2002).

Bureau of Land Management

The Columbia spotted frog is currently on the Bureau of Land Management sensitive species list in Wyoming (Bureau of Land Management Wyoming 2001). Spotted frogs do not occur in the other Region 2 states (i.e., Colorado, South Dakota, Nebraska, Kansas).

USDA Forest Service

Both Region 2 and Region 4 of the USDA Forest Service classify the Columbia spotted frog as a sensitive species (USDA Forest Service 1994, USDA Forest Service 1999).

State wildlife agencies

The Wyoming Game and Fish Department (WGFD) ranks the Columbia spotted frog as a Native Species of Special Concern 4 (NSS4) (Wyoming Game and Fish 2005). This classification means that the department considers spotted frogs to be common (i.e., widely distributed throughout its native range, population status stable), and its habitat to be stable.

Natural Heritage Program ranks

Global heritage ranks (G-ranks) and state heritage ranks (S-ranks) follow a numerical scoring system (NatureServe Explorer 2002, Keinath and Beauvais 2003, Keinath et al. 2003). The Columbia spotted frog is given a global rank of G4 (apparently secure) by the Natural Heritage Programs (NatureServe Explorer 2002). A rank of G4 means that the species is considered uncommon and widespread (although it may be rare in parts of its range, particularly on the periphery). While there may be a cause for concern due to declines in the disjunct southern populations, which face major threats (e.g., habitat loss and degradation, exotic species, and possibly global climate change), the species is not considered vulnerable in most of its moderately large range in the Rocky Mountains and northwestern North America. In Canada, the Committee on the Status of Endangered Wildlife in Canada considers the Columbia spotted frog ‘Not at Risk’ by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2000).

Wyoming is the only Region 2 state that ranks the spotted frog on its sensitive species list. The statewide population is ranked as S3 (vulnerable), while the Bighorn Mountain population is ranked as T1Q/S1 (critically imperiled; the taxonomic distinctiveness of this entity is questionable) (Keinath et al. 2003). The Natural Heritage Programs of nine other states and provinces rank the spotted frog at widely disparate S-ranks, indicating substantial geographic variation in endangerment (**Table 1**).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Existing regulatory mechanisms

The National Forest Management Act (16 U.S.C. 1600 et seq.) includes a sensitive species policy that directs the USFS to manage for sensitive species such as the Columbia spotted frog. There are no plans or strategies for the spotted frog written at the Region 2 level. Furthermore, no habitat protection measures specific to spotted frogs are included in the current forest plans for the Bighorn or Shoshone national forests. Species with sensitive status must be addressed in the National Environmental Protection Act process for any project or planning activity that requires such compliance. Biological evaluations are prepared to evaluate the effects on sensitive species and to identify mitigating measures.

Existing management plans and conservation strategies

A conservation agreement and strategy was prepared for the Columbia spotted frog in Utah (Perkins and Lentsch 1998) as a collaborative effort among resource agencies to expedite the implementation of conservation actions for this species. It describes specific actions and strategies and requires annual assessments of actions that are implemented. A habitat conservation assessment and accompanying conservation strategy have been drafted for the Columbia spotted frog in southwestern Idaho (Munger et al. 2002). We are unaware of any management plans or conservation strategies written for spotted frog subpopulations in its core range.

Table 1. Natural Heritage Program Rank of Columbia spotted frog in states and provinces in which it is known to occur (NatureServe 2002). Region 2 state is in bold.

State/Province	Natural Heritage Program Rank[1]
Wyoming	S3 (vulnerable)
Alaska	S2? (probably imperiled)
Alberta	S3 (vulnerable)
British Columbia	S4 (apparently secure)
Idaho	S3S4 (between apparently secure and vulnerable)
Montana	S4 (apparently secure)
Nevada	S2S3 (between imperiled and vulnerable)
Oregon	S2S3 (between imperiled and vulnerable)
Utah	S1 (critically imperiled)
Washington	S4 (apparently secure)

[1] 1 = Critically Imperiled: At very high risk of extinction due to extreme rarity (often 5 or fewer populations), very steep declines, or other factors.

2 = Imperiled: At high risk of extinction due to restricted range, few populations (often 20 or fewer), steep declines, or other factors.

3 = Vulnerable: At moderate risk of extinction due to a restricted range, relatively few populations (often 80 or fewer), recent and widespread declines, or other factors. Such species are often rare or found locally in a restricted range.

4 = Apparently Secure: Uncommon but not rare; some cause for long-term concern due to declines or other factors. Such species are likely to be quite rare in parts of their range, especially at the periphery.

5 = Secure: Common; widespread and abundant. Such species are potentially rare in parts of their range, especially at the periphery.

? = Inexact Numeric Rank: Denotes inexact numeric rank (e.g., G2?).

Biology and Ecology

Description and systematics

Juveniles and adults

The Columbia spotted frog has a slender body shape, with a rather pointed snout (**Figure 1**). Body lengths of adult frogs range up to 100 mm in females, and 68 mm in males (Nussbaum et al. 1983). In Yellowstone and Grand Teton national parks in northwestern Wyoming, observed maximum snout-urostyle lengths approach 90 mm for females and 65 mm for males (Patla unpublished data). Size at metamorphosis is highly variable among breeding sites and ranges from 12 mm to 33 mm (Nussbaum et al. 1983, Patla unpublished data). The upturned eyes are usually bright yellow or gold, but they are sometimes dark in juveniles. Dorsal color is light to dark brown, tan, dull green, or olive. There are irregularly-shaped, large black spots on the back; often these spots have light-colored centers. The dorsal skin has a bumpy or warty texture. Dorsolateral folds are usually present. A white or yellowish jaw stripe (or lip line) extends from the tip of the snout, under the eye, to the front legs. Undersides of the hind legs and the lower abdomen of many but not all adults are brightly colored with yellow, orange, red, or salmon, resulting from a lipoid pigment (**Figure 2**). On some individuals, the pigmentation extends into the chest or throat and front legs. Belly pigmentation is more extensive on large females and develops at an earlier age than in males (40 mm body length for females, 50 mm for males) (Turner 1959b). Ventral areas of adults are also variously mottled with melanin pigment (Turner 1959b). The hind feet are large relative to the hind leg length and have webbing that extends nearly the length of the hind toes. Male spotted frogs have dark, roughened nuptial pads at the base of the thumbs (**Figure 3**), which do not become reliably apparent until frogs reach a snout-urostyle length (measured dorsally from tip of the snout to the terminus of the urostyle or coccyx bone) of about 45 mm (Turner 1960, Hollenbeck 1974, Patla 1997). Post-metamorphic juveniles are similar in appearance to adults except for the lack of reddish pigmentation on undersides (**Figure 4**).

Similar species in or near the range of the Columbia spotted frog are the northern leopard frog (*Rana pipiens*) and the wood frog (*R. sylvatica*). Leopard frogs can have dorsal coloration that is similar to spotted frogs, but leopard frogs are readily distinguished by their smooth skin and the light borders outlining oval-shaped spots. Wood frogs have a black mask, light upper jaw line, and dorsal coloration that can resemble spotted frogs; the smooth skin of wood frogs is probably the best field mark to distinguish them from spotted frogs. Juvenile spotted frogs may be confused with wood frogs, and records that consist only of juveniles should be considered with caution. Both leopard and wood frogs have white bellies. In Region 2, any healthy frog with reddish or orange coloration on the undersides is a spotted frog, but the lack of this pigmentation does not reliably identify spotted frogs.

Figure 1. Adult female Columbia spotted frog. Photo taken in Grand Teton National Park by Matthew Chatfield, Idaho State University and USGS.

Figure 2. Pigmentation on the underside of a spotted frog. This is a large female with extensive pigmentation. Photo taken in Yellowstone National Park (D. Patla).

Figure 3. The gender of adult spotted frogs is apparent due to the dark nuptial pads at the base of the thumbs (arrow) of male frogs. Photo taken in Yellowstone National Park (D. Patla, Idaho State University).

Tadpoles

Tadpoles are dark in color after hatching. As they grow, their color lightens to brown or greenish-brown, with gold or brassy flecks on the upper surface (**Figure 5**). Bellies are light in color, often showing a metallic, copper sheen (Maxell 2000). Tadpole size varies from 7 to 8 mm total length at hatching (Nussbaum et al. 1983) to a maximum of 90 mm (Maxell 2000) before the onset of metamorphosis, when tails begin to shrink. Spotted frog tadpoles have a long, robust tail that is more than 1½ to 2 times the body length (Maxell 2000). The tail fin is colorless or pale, flecked with black or gold.

Figure 4. Young-of-the-year spotted frog, September, Yellowstone National Park (D. Patla. Idaho State University).

There are small differences among spotted frog, leopard frog, and wood frog tadpoles; a diagnostic key is provided by Corkran and Thoms (1996). In spotted frog tadpoles, the height of the dorsal fin is greater than the thickness of the tail trunk at its base (side view); in leopard frog tadpoles, the height of the dorsal fin is equal to or less than the thickness of the tail trunk at its base. Leopard and wood frog tadpoles have somewhat shorter tails (less than or equal to 1 ½ times the body length when viewed from above) (Corkran and Thoms 1996). However, spotted frogs tadpoles have variable tail size (D. Patla personal observation), and in areas where the ranges of these species overlap, tadpoles may not safely be distinguished in the field except by experienced observers. Given the rarity of co-occurrence of these species in Region 2, however, it is fairly safe to assume that tadpoles matching the general description are indeed spotted frogs if adults and juveniles in the vicinity are positively identified as spotted frogs, and if wood frogs or leopard frogs have not been found historically or recently during surveys in the area.

Figure 5. Spotted frog tadpole. Photo by Charles R. Peterson, Idaho State University.

Eggs

Individual eggs are 10 to 12 mm in diameter, including ovum and two surrounding jelly layers. The ova are black in color, with a white spot. Eggs are deposited in a single, gelatinous mass (**Figure 6a**) that is round and ca. 12 to 20 cm in diameter (Nussbaum et al. 1983). Each egg mass contains from a few hundred to over 2,000 eggs (see Life history section for details). Egg masses are deposited in shallow water, where they initially rest on the bottom but soon float and become partially submerged and increasingly covered with algae and debris as they age (**Figure 6b**).

Systematics

Within the family of true frogs, Ranidae (order Anura), only the genus *Rana* occurs in North America, with approximately 26 species in North America (Duellman and Sweet 1999). Western North America hosts 29 endemic anuran species, including eight endemic ranid frogs. The subject of this report, *R. luteiventris*, is one of four anuran species (and the only ranid frog) that occurs in both the northern Rocky Mountains and the northern part of the Pacific-Cascade ranges. Recent phylogenetic analyses place *R. luteiventris* within the *R. boylii* group, which is restricted mainly to the cool, montane regions of western North America and includes the species *R. aurora*, *R. muscosa*, *R. boylii*, *R. cascadae*, and *R. pretiosa* (which is most closely related to *R. luteiventris*) (Duellman and Sweet 1999).

The species now known as *Rana luteiventris* was first described from Puget Sound in Washington as the western spotted frog (*R. pretiosa*) (Baird and Girard 1853). In 1913, two subspecies were recognized, *R. p. pretiosa* and *R. p. luteiventris* (Thompson 1913). The subspecies designations, which were based on differences in coloration and foot tubercles, were debated and contested for several decades, and they were eventually abandoned (Morris and Tanner 1969, Turner and Dumas 1972). Recent genetic analysis of spotted frogs, however, revealed the existence of two morphologically cryptic species, which had diverged into coastal and interior forms in the course of repeated glacial advances and retreats during the Quaternary (Green et al. 1996). The species occupying the type locality retained the name *R. pretiosa* (Oregon spotted frog), with a range comprised of Puget Sound, south-central Washington, the Oregon Cascades, and extreme southwestern British Columbia (Green et al. 1997). The name *R. luteiventris* (Columbia spotted frog) designates spotted frog populations in the remainder of spotted frog range (see Distribution and abundance section) (Green et al. 1997). The subject of this species account is *R. luteiventris* Thompson, 1913, the Columbia spotted frog, with no subspecies formally recognized.

The designation of two spotted frog species (*Rana luteiventris* and *R. pretiosa*) has been officially accepted by the scientific community, as evidenced by listing in Scientific and Standard English Names of Amphibians and Reptiles of North America North of Mexico (Crother 2003). This document is the official list of

(A)

(B)

Figure 6. Spotted frog egg masses. (A): Newly deposited spotted frog eggs. Photo taken in Yellowstone National Park by D. Patla, Idaho State University. (B): Floating spotted frog egg masses of various ages. Older egg masses are green with algae and spread out on the water surface. Photo taken in Yellowstone National Park by D. Patla, Idaho State University and USGS.

standard common and scientific names recognized by the Society for the Study of Amphibians and Reptiles, American Society of Ichthyologists and Herpetologists, and the Herpetologists' League.

The recent taxonomic change for spotted frogs occupying USFS Region 2 and Region 4 (from *Rana pretiosa* to *R. luteiventris*) may cause some confusion given that species lists, field guides, and most of the literature prior to 1998 use the name *R. pretiosa*. Adding to potential confusion in the future, there may be taxonomic re-designations resulting from continued genetic analysis of disjunct *R. luteiventris* populations, possibly resulting in three or more subspecies or "several weakly differentiated species" (Green et al. 1997).

Distribution and abundance

The Columbia spotted frog has an extensive distribution in western North America, from southern Alaska through British Columbia and western Alberta and the states of Washington, Oregon, Idaho, Montana, Wyoming, Utah, and Nevada (**Figure 7**). Disjunct populations exist south of the main range in southeastern Oregon, Nevada, southwestern Idaho, and Utah; and east of the main range in the Bighorn Mountains of north-central Wyoming. As explained in the Federal Endangered Species Act section, the disjunct populations south and east of the main range have been recognized as isolated, distinct population units. USFS Region 2 encompasses the Bighorn Mountain population, and the southeastern edge of the main population's range (**Figure 8**).

Figure 7. Distribution of Columbia spotted frog (Rana luteiventris) in North America. This map is adapted from Figure 1 in Green et al. (1997). (Permission to use granted by copyright notice, American Society of Ichthyologists and Herpetologists).

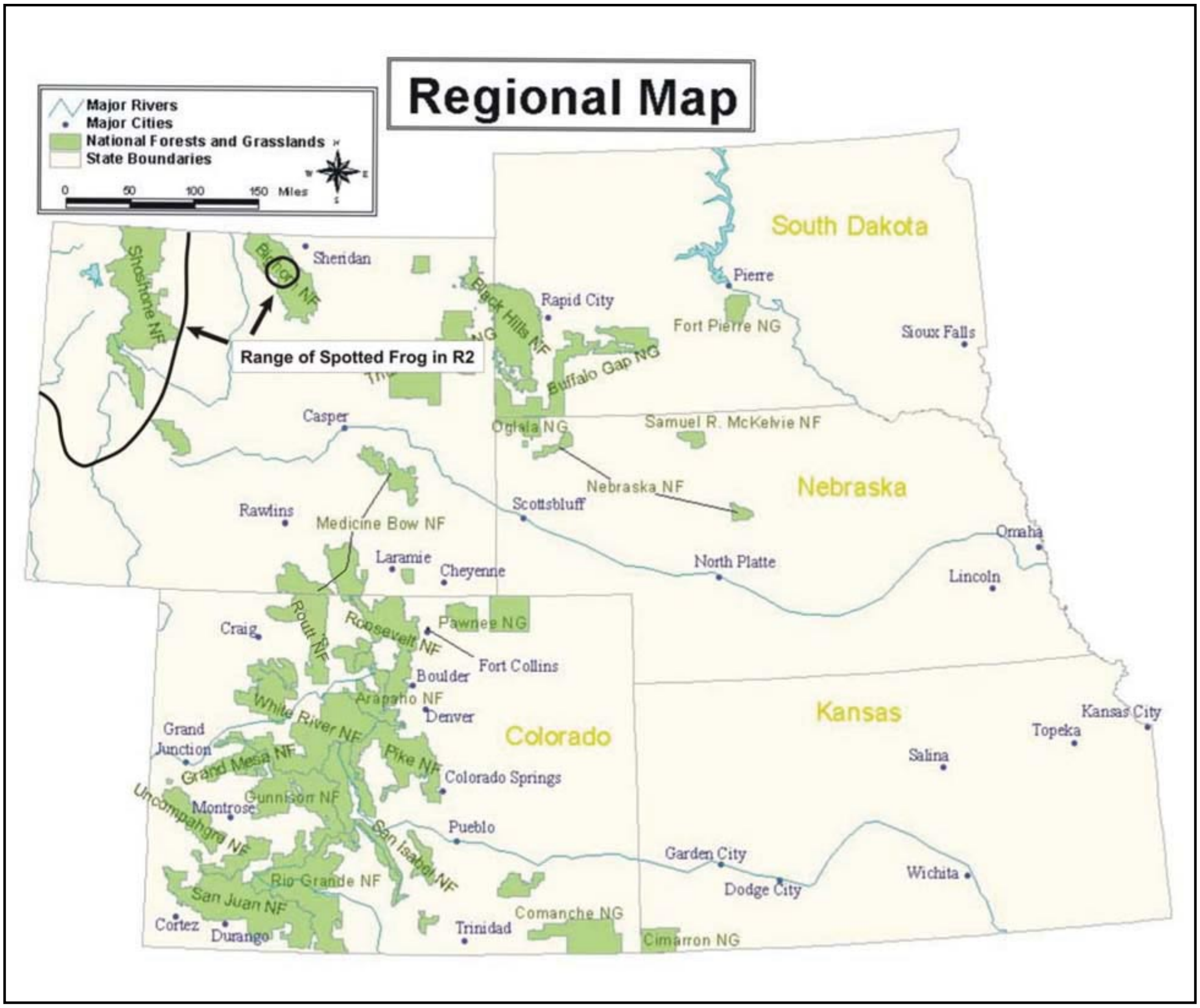

Figure 8. Range of the Columbia spotted frog in Forest Service Region 2.

In the southern part of the species range, the Great Basin and Wasatch Front populations have undergone significant decline, with wetland habitat loss and modification recognized as the primary causative factor (Worthing 1993). The West Desert population has suffered less habitat loss but is faced with limited habitat availability and potential habitat degradation from cattle grazing and agriculture (Worthing 1993). Spotted frogs in the southern disjunct populations are reported as locally abundant or occurring at high local densities in some areas, but uncommon and at low densities in others (Reaser and Pilliod 2005). In Nevada and Utah, spotted frogs were not found at many historically-occupied sites, but surveys also documented sites not previously recorded. Green et al. (1997) regard the two Utah populations (referred to as the "Bonneville spotted frog" and the "Provo River spotted frog") as the most threatened, based on their extremely limited distributions.

The main population of spotted frogs (western Alberta, British Columbia, eastern Washington and Oregon, northern and central Idaho, and western Montana and Wyoming) is regarded by USFWS as "common and abundant" although some declines have occurred (Worthing 1993). The Columbia spotted frog is reported to be the most common frog in western Montana's mountains and mountain valleys, but of uncertain status in the Big Snowy, Highwood, and Bighorn mountains (Maxell 2000). In Glacier National Park, surveys of randomly selected watershed units found spotted frogs breeding at 19 percent of 360 potential amphibian breeding sites surveyed in 2002 (USGS Amphibian Research and Monitoring Initiative 2002). In the mountains of central and northern Idaho, spotted frogs are the most commonly encountered amphibians, with locally abundant populations (Reaser and Pilliod 2005).

Information from northwestern Wyoming (portions outside Region 2) mostly verifies the USFWS assessment (Worthing 1993) that spotted frogs of the main population are still abundant. In Yellowstone and Grand Teton national parks, spotted frogs have been described as common to abundant (Koch and Peterson 1995). Surveys of widely-distributed and randomly-selected watershed units in the two parks identified spotted frogs breeding at 19 percent of 188 potential amphibian breeding sites surveyed in 2002; survey results from three years of surveys (2000 to 2002) indicate that the spotted frog is the second most abundant amphibian in the parks (Patla and Peterson 2003). In a non-refereed assessment of amphibian status in the Greater Yellowstone Ecosystem (GYE; construed broadly as the Yellowstone and Grand Teton national parks and surrounding mountains lands in Wyoming, Montana, and Idaho), the results of all identified survey efforts were compiled; spotted frogs were categorized as very widespread and abundant within the species' range, with no indications of a widespread decline based on comparison of historical and recent records (Van Kirk et al. 2000). Assessment of amphibian species status on the Bridger-Teton National Forest (B-TNF) in northwestern Wyoming found that spotted frogs were widespread and common on the northern districts of the B-TNF, but rare or absent on the southern districts (Patla 2000a). There is no evidence of a shrinking range based on the locations of previous and historical (prior to 1993) observations (**Figure 9** and **Figure 10**), other than the absence of recent records in the southern Wind River Mountains from where only one unverified historical record exists (Patla 2000a).

Spotted frogs in Region 2 occur in two separate areas, the Shoshone and Bighorn national forests of Wyoming (**Figure 8**, **Figure 9**, and **Figure 10**). Occurrence and breeding locations (**Figure 9** and **Figure 10**) were plotted from data records in the Wyoming Natural Diversity Database (with corrections for Bighorn National Forest locations provided by Harold Golden). Northern and central portions of the Shoshone National Forest are at the eastern periphery of and contiguous with the range of the spotted frog's main population, which extends through northwestern Wyoming and into Montana and Idaho. Based on existing information, spotted frogs appear to be much less common on the Shoshone National Forest than on mountainous lands to the west, the B-TNF and Yellowstone and Grand Teton national parks. To our knowledge, only five breeding sites have been identified and documented on the Shoshone National Forest between 1993 and 2002, and most of the recorded occurrences are clustered in tributaries of the upper Wind River (**Figure 10**). There are less than 25 non-breeding occurrences on record. Surveys in the vicinity of documented occurrences could reveal some additional breeding sites, unless frogs in those areas have disappeared or become rare. Amphibian surveys in previously unsurveyed areas could reveal many additional populations if abundance is similar to the northern B-TNF and Yellowstone National Park.

The apparent rarity of spotted frogs on much of the Shoshone National Forest may relate either to the actual scarcity of this species on the southeastern edge of its range or to low survey effort and/or lack of mechanisms for reliably recording incidental observations. An assessment of information availability for amphibians in the GYE gave ratings of "poor" to "fair" to relative information availability for watersheds of the Shoshone National Forest, compared to "best" ratings for the northern B-TNF and the national parks (Van Kirk et al. 2000). The only surveys on record in the WYNDD database were conducted by WYNDD in scattered locations on the Shoshone National Forest (Garber 1994, Garber 1995), by USFS Mark Hinschberger in the upper Wind River watershed 1994 to 1996, and by a volunteer team under the direction of Idaho State University Herpetology Lab in the upper Wind River watershed in 1999.

Spotted frogs of the Bighorn National Forest exist as a geographically-isolated, genetically distinct population on the northeast slope of the Bighorn Mountains; this population was first identified in 1973 (Dunlap 1977, Bos and Sites 2001). The USFWS listing decision (Worthing 1993), which provided candidate status for disjunct populations south of the main range of the spotted frog, does not mention the Bighorn Mountain population. Lack of recognition of the Bighorn population as a disjunct population segment by USFWS probably is further hampered by the fact that Green et al.'s (1997) genetic analysis of spotted frog species and populations did not include specimens from the Bighorn Mountains, where spotted frog distribution is extremely restricted. If accurate, all occurrences on record are within a 5 by 11 km rectangle, on tributaries of the Tongue River. Only three breeding sites have been identified since 1992; two of theses are within 2.6 km of each other, and the third is about 7.4 km to the south (H. Golden personal communication 2002). One of these breeding sites is the historical site at Sibley Lake, identified by Dunlap (1977) and described then as "an apparently abundant population". Garber (1994) tried to determine the exact distribution of spotted frogs in the Bighorn Mountains, surveying 49 sites but finding only two new sites and two breeding

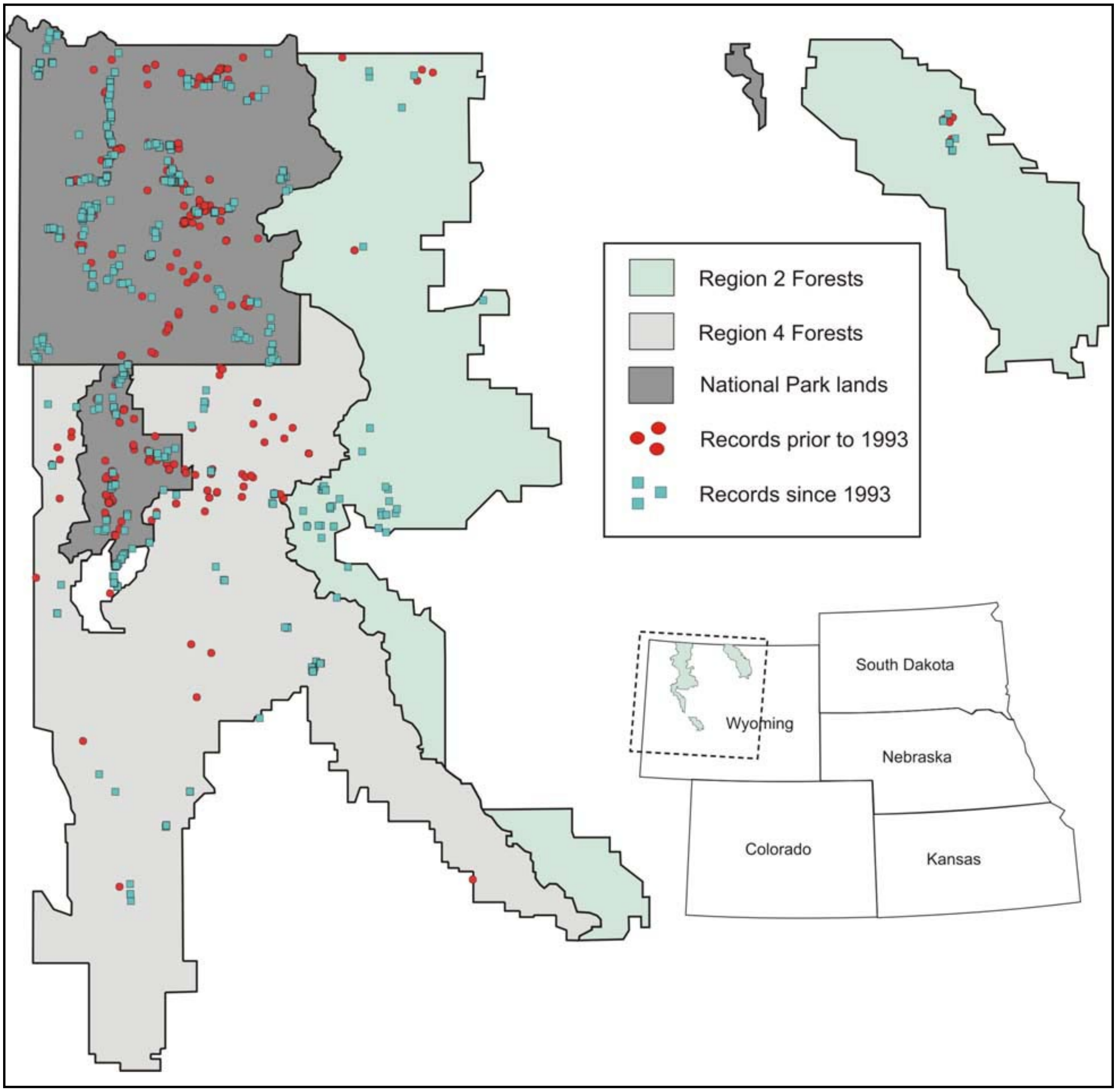

Figure 9. Historic (prior to 1993) and recent occurrence of Columbia spotted frogs in Region 2 and adjacent national forests and parks. Data from Wyoming Natural Diversity Database.

sites. He concluded that spotted frogs were restricted to a small area at the headwaters of the South Tongue River drainage and its tributaries, a much smaller range than depicted in Baxter and Stone (1985). There appears to be no subsequent information that would negate Garber's assessment of this restricted range. Surveys for amphibians have also been conducted by the Tongue Ranger District Biologist, Harold Golden, during several years since 1992, including surveys in the Cloud Peak Wilderness.

Keeping in mind that recorded information is scant, there is no evidence that spotted frogs are numerous at any location on the Bighorn National Forest; the maximum number of frogs observed and documented during any single survey is 20 adults, and 23 is the maximum number of egg masses ever recorded (Wyoming Natural Diversity Database, H. Golden personal communication 2002). By contrast, at some sites in the GYE, over 100 adult frogs can be caught in a single day, and 45 to 57 spotted frog egg masses have been observed at some sites (Koch and Peterson 1995, Patla and Peterson 2004).

A more precise measure of abundance within local populations may be determined through mark-

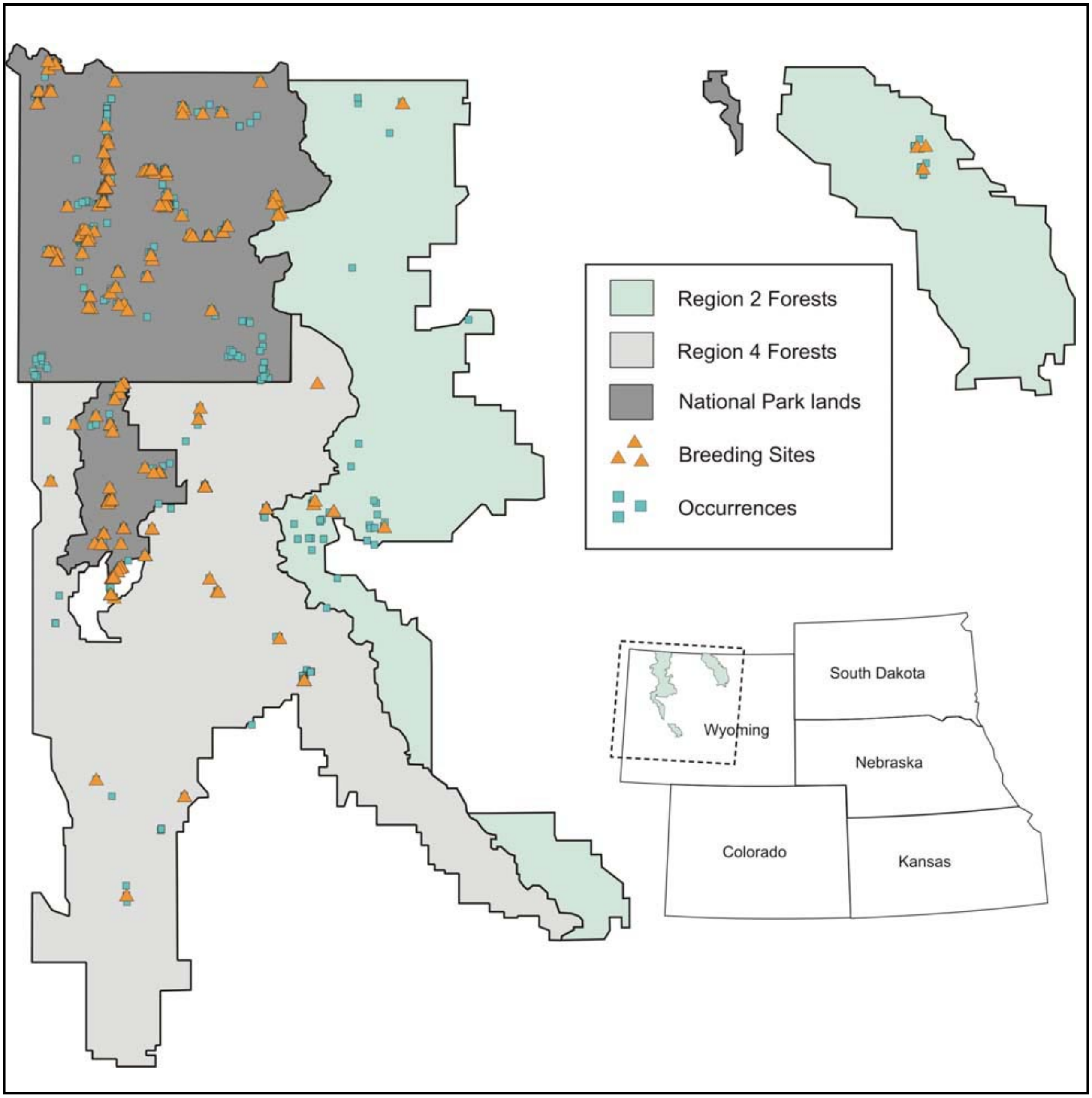

Figure 10. Columbia spotted frog breeding sites and non-breeding occurrences in Region 2 and adjacent national forests and parks since 1993. Data from Wyoming Natural Diversity Database.

recapture of individuals within a given area and the application of population estimation methods, but to our knowledge, no mark-recapture work has been conducted on spotted frogs on the Bighorn National Forest or elsewhere in Region 2. Egg mass counts may be used to estimate effective population size (number of breeding individuals in a given year), an approach that has been implemented by the Utah spotted frog Conservation Strategy (Perkins and Lentsch 1998). The Conservation Strategy assumes that every egg mass is the product of a single male and single female; thus every egg mass represents two frogs in terms of annual breeding population size. Using this index, based on the reported approximately 20 egg masses per year at one of the Bighorn National Forest breeding sites (see Population trend section), a rough estimate of breeding population size would be 40 frogs on average for this site. Egg mass counts are not available for the other two breeding sites on the Bighorn National Forest. However, it is important to note that the estimated breeding population size bears an unknown relation to actual population size, for several reasons:

- spotted frog females at upper elevation areas do not breed every year, and how often they breed is unknown

- one-to-one sex ratios of adult female to adult male frogs have not been observed in field studies

- although the assumption of one mass per reproductively active female is based on anecdotal evidence, the actual number of egg masses produced by a female is not known

- an unknown proportion of the population is made up of pre-reproductive juveniles and non-breeding adults.

Population trend

Amphibian populations at the local scale may exhibit extreme fluctuations in size from year to year as well as over the course of many years (e.g., Pechmann et al. 1991; Pechmann and Wilbur 1994 and references therein). This is particularly true for anuran amphibians of the North Temperate Zone, which respond to fluctuating environmental conditions with large variations in birth and survival rates (Green 1997). Researchers caution that determining the normal range of fluctuation for any single population, and the deviation from that norm that would signify a decline, could take decades, or longer than a human lifetime (Pechmann and Wilbur 1994, Green 1997). Given this fact, coupled with the difficulty of obtaining demographic data, biologists often define amphibian population trend in terms of changes in the numbers of populations (per species) over time, rather than changes in the size of local populations (Green 1997). In areas where declines of an amphibian species are accepted as indisputable, such as the boreal toad (*Bufo boreas*) in Colorado, the evidence consists of range reductions, the disappearance of the species at sites where it was historically or recently documented, and the failure to find significant numbers of previously unknown "new" breeding populations despite adequate survey efforts (Loeffler 2001). To assess broad-scale trends in widespread populations, the USGS Amphibian Research and Monitoring Initiative (USGS-ARMI) is developing occupancy methodology, which assesses trends based on changes in the number of occupied breeding sites over time.

Where anuran species have declined to a few breeding populations, population trend in terms of the estimated number of individuals is of interest. This emphasis on abundance, despite the preceding argument regarding variation, stems from 'small population' theory. Small and isolated populations are more vulnerable to extirpation while larger ones are more robust; thus declines in some or all of the few remnant breeding populations could indicate that the species is in increasing peril.

The abundance of the Columbia spotted frog has been described as greatly reduced from its historic levels in portions of Utah, Oregon, and Nevada (Worthing 1993). Assessment of population trends for the disjunct, southern populations is in progress by various researchers and agencies. Most extant populations of the Wasatch Front spotted frog are said to have increased or are of a larger size (additional occupied sites or greater density of sites found within known population boundaries) than previously thought (U.S. Fish and Wildlife Service Region 6 2002). Trends in the West Desert breeding populations are variable (Hogrefe 2001). Preliminary results (1997 to 2001) indicate that spotted frogs of southwestern Idaho (within the Great Basin population) are declining, with apparently only small numbers of frogs at most sites where they occur (Engle 2002). Concerns about the status of this population segment were heightened by the discovery of chytrid disease in 2001 (Engle 2002, U.S. Fish and Wildlife Service Snake River Basin Office 2002). In eastern Oregon, USGS-ARMI surveys of historic sites found that 65 percent were occupied by spotted frogs, and no new populations were found at 87 sites surveyed on BLM lands in southeastern Oregon in 2002 (http://armi.usgs.gov/2002_report_PNW.asp). These findings suggest that declines may be occurring in the Great Basin spotted frog population.

In the main population's range, surveys and assessment of broad-scale trends using occupancy methodology are in progress through USGS- in Glacier National Park and Yellowstone and Grand Teton national parks in the GYE (http://www.mesc.usgs.gov/research/rarmi). While trends have not yet been quantitatively assessed and published for the GYE, initial assessments indicate that spotted frogs are not experiencing a widespread decline in the national parks of the GYE, based on the number of new breeding sites found each year and the general persistence of the species in previously-identified occupied areas (Patla and Peterson 2003, Patla and Peterson unpublished data). However, some local declines of spotted frogs have been observed in the GYE. At a long-term study site in central Yellowstone, a spotted frog population declined almost 80 percent between the 1950s and the 1990s (Patla 1997, Patla and Peterson 1999, Patla and Peterson in prep). Spotted frogs have disappeared from a few sites in the national parks where they were previously observed (Patla unpublished data).

Information is insufficient to determine the population trend for spotted frogs in Region 2. On the Shoshone National Forest, surveys have been few and monitoring has not been conducted. Spotted frogs appear to be abundant and stable in areas west of Shoshone National Forest (i.e., Yellowstone National Park and B-TNF). However, the Shoshone National Forest is located at the edge of the main population's range, and therefore it may experience declines (or increases in populations via range expansion) not occurring elsewhere (Green et al. 1996). In addition, new amphibian diseases could be appearing in the region (see Parasites and disease and Threat sections).

On the Bighorn National Forest, the spotted frog population trend has been described by the district biologist as "stable (at a minimally viable level)" (Golden 2001). This judgment was based on the numbers of eggs masses (said to be 20 ± 5 per year) at one of the breeding sites since about 1994 (H. Golden personal communication 2002). However, this assessment must be evaluated with caution for several reasons:

- we were not able to verify or review information because written documentation of numbers of egg masses per year is not available from the USFS or elsewhere, to our knowledge
- no records of breeding effort (egg mass numbers) at the other two reported breeding sites (one of which is reported to be a pool only 3 by 3 m) are available
- there is no record of breeding success (e.g., presence or numbers of metamorphs around breeding sites).

Although egg mass census may be used as a surrogate for monitoring population size (as it is being used in Utah), maintaining records of dates and numbers is necessary. Lack of information about other breeding sites and reproductive success erodes confidence that the population can be considered stable. Unless additional information is acquired, trend of the disjunct spotted frog population occupying the Bighorn National Forest should be considered as uncertain.

Activity and movement patterns

Similar to other amphibians of the North Temperate Zone, spotted frogs seasonally occupy habitats providing resources for their primary annual activities: reproduction, nutritional acquisition, and hibernation (Sinsch 1990, Pilliod et al. 2002). Because suitable breeding, foraging, and over-wintering sites are spatially separated in many areas occupied by spotted frog populations, frogs migrate among habitat patches in the course of a year (Turner 1960, Patla 1997, Pilliod et al. 2002). These seasonal movements are essential for the survival of individuals and for the persistence of populations. Three major movement patterns have been identified in field studies: from hibernacula to breeding sites, from breeding sites to foraging areas, and from foraging areas back to hibernacula. The occupation of seasonal habitats, and the timing and documented distance of movements to these habitats, are described in the following sections, which are organized by season. Information relating to the size of the occupied area is provided in the Area requirements section.

As a preface to this section, it is important to note that the scale of movements depends on characteristics of the inhabited area. In some areas, all habitat components occur in a spatially-restricted area (e.g., one permanent pond isolated from other ponds). Frogs in a population inhabiting such an area do not exhibit movements (Bull and Hayes 2001). It is unknown how common such non-migratory populations might be. Moreover, field studies reveal that individual frogs within a population exhibit very different movements; some frogs remain at a given habitat patch while others leave. For example, Bull and Hayes (2001) found that 11 of 22 radio-tagged spotted frogs remained at breeding sites while the remaining 11 moved to other sites. Pilliod et al. (2002) found that 6 to 11 percent of male spotted frogs and 16 to 51 percent of females in a high mountain basin moved from breeding ponds to summer habitats. In a four year study in southwestern Idaho, Engle (2001) found that a large majority of the 2,094 spotted frogs she marked with PIT tags moved less than 100 m. A summary of maximum reported distances for seasonal movements in various types of habitat is provided in **Table 2**.

Some spotted frogs move long distances. The maximum straight-line movements per year on record are an adult female in Nevada moving 5 km (Reaser

Table 2. Summary of maximum reported seasonal movement distances of Columbia spotted frog populations.

Adults				
Breeding to over-wintering site	Breeding or over-wintering to foraging sites	Young of the Year: Natal site to over-wintering sites	Habitat	Source
600 m	1,033 m	350 m	Mountain basin in Idaho, 2,300 to 2,800 m elevation	Pilliod et al. 2002
100 m			Riparian zones in sage-juniper brushlands in Idaho, 1,325 to 2,035 m elevation	Engle 2001
400 m	620 m	480 m	Coniferous forest and adjacent meadows in Wyoming, 2,380 m elevation	Turner 1960, Patla 1997
	560 m		Coniferous forest and meadows in northeast Oregon, 920 to 1,500 m elevation	Bull and Hayes 2001
	444 m		Coniferous forest and willow bog in Montana, 2,040 to 2,070 m elevation	Hollenbeck 1974

1996) and a subadult in southwestern Idaho moving 6.5 km (Engle 2001). It is unknown if these long-distance movements signify a one-way dispersal resulting in occupation of a totally new area and a different set of breeding, foraging, and wintering sites, or if the frogs undertaking such long movements eventually return to their natal sites, which would suggest that the movements are part of a migration, perhaps extending over multiple years.

Emergence and early-season movements

Emergence from over-wintering sites by spotted frogs occurs from late February to early July, depending on elevation, latitude, and local conditions (Reaser and Pilliod 2005). In Utah, spotted frogs appear in March, following several days of air temperatures reaching 13 to 16 °C or after a rain storm (Morris and Tanner 1969). In Yellowstone National Park at an elevation of 2,380 m (7,800 ft.), spotted frogs emerge "not before the first or second week in May" (Turner 1958a), or later (into early June) (Koch and Peterson 1995), depending on snowmelt and air temperatures. Turner (1958a) reports that activity in May and early June is sporadic, with frogs remaining underwater during periods of low temperatures. A critical water temperature threshold occurs at 10 °C; below this temperature frogs are inactive and concealed at the bottom of ponds (Turner 1960, Morris and Tanner 1969).

Where breeding habitat is spatially separated from over-wintering sites, adults that are prepared to breed move (or migrate) from the hibernacula to breeding sites in spring. These movements likely take place immediately after emergence and in advance of the post-emergence movements of non-breeding adults and juveniles (Turner 1960, Patla 1997). The distance depends on the local configuration of habitat features (e.g., the location of springs or streams suitable for hibernation in relation to the location of pools suitable for breeding). Researchers have seldom succeeded in directly witnessing such movements due to the difficulty of accessing wintering sites in early spring and apprehending frogs prior to their breeding migration. Engle (2001) observed movements to breeding sites of 100 m or less, with one female traveling while the male was clasped to her back in amplexus. *Rana pretiosa* pairs have been observed to migrate in amplexus up to 0.7 km (J. Bowerman observation cited in Engle 2001). Based on fall locations of marked frogs at known winter-congregation sites and their subsequent re-location at breeding sites the following spring, Turner (1960) ascertained that some spotted frogs at a study site in Yellowstone moved a maximum of 200 to 400 m from their over-wintering site to the breeding site. Fall and subsequent early-summer recaptures at a study area in the mountains of central Idaho indicated that spotted frogs moved a maximum of about 600 m between over-wintering and breeding habitat (Pilliod et al. 2002). Most males and some females were reported to migrate 450 m or less between breeding and over-wintering sites in summer and fall (Pilliod et al. 2002); presumably their post-emergence migrations to breeding sites would be of similar distance. The maximum distance that adult spotted frogs are actually capable of moving after emergence from over-wintering to breeding sites is not known; Pilliod et al.'s (2002) documentation of 600 m appears to be the maximum reported value.

Summer

Outside of the breeding period, spotted frogs spend the warm months of the year meeting their nutritional needs. They may be active day and night. Spotted frogs often bask in sunshine along the edges of ponds, lakes, and stream edges, a habit causing them to be visually conspicuous to humans and leading to high observation rates relative to other amphibians. Low night temperatures inhibit activity, but frogs are active during warm nights (Turner 1959a).

In higher elevation areas, the season available for growth is even shorter than the active season. In Yellowstone National Park, Turner (1960) found that nearly all of the annual change in frog body lengths occurred between mid-June and early August. Access to good foraging sites is an important component of the life history of spotted frogs, as is evidenced by their considerable summer movements. In Yellowstone, Turner (1960) determined that frogs disperse to seasonally moist meadows, ephemeral pools, and intermittent streams in May and June and return to more permanent water sources as surface water evaporates, with maximum movement rates (up to 620 m) occurring during the first three weeks in July. In northeastern Oregon, spotted frogs moved from breeding sites to temporary and permanent ponds and streams (Bull and Hayes 2001). Distances of these movements ranged from 22 to 560 m. The only breeding pond where frogs remained through the summer was isolated from other permanent water and also considerably larger in size, leading Bull and Hayes (2001) to conclude that larger water bodies may provide adequate resources for year-round occupation. In the mountains of central Idaho, movements from breeding and wintering sites to summer habitats were found to differ among age and sex classes; over a four-year period, an average maximum of 32 percent of juvenile frogs moved to summer habitats, versus 51 percent of the adult females and only 11 percent of the adult males (Pilliod et al. 2002). Maximum straight-line distances of these movements in a four-week period were 424 m for males and 1,033 m for females (Pilliod et al. 2002).

While occupying summer habitats (summer home range), movements are restricted to rather small areas. During July and August, spotted frogs in Jackson Hole, Wyoming moved an average of 1.5 m per day (minimum, straight-line distance) and a maximum of 45 m between the first and last capture points, with frogs showing a tendency to return toward the original point of capture (Carpenter 1954). Similarly, Turner (1960) and Patla (1997) documented spotted frogs in Yellowstone remaining at sites for extended periods during the summer. Radio-tagging at a Yellowstone study area indicated that frogs tend to occupy small areas for variable amounts of time, followed by short periods of movement; only 16 percent of the locations of 46 frogs revealed movements greater than 30 m, and nearly all movements exceeding 30 m were categorized as post-breeding or late-summer migratory movements (Patla 1997).

Late summer and movements to winter habitats

As air temperature drops and day-length shortens, spotted frogs lose weight, often become darker in dorsal coloration, and tend to remain concealed underwater when flushed from stream or pond edges (D. Patla personal observation). Frogs congregate near their over-wintering sites in August and September (Turner 1960, Pilliod et al. 2002). At small springs in Yellowstone where frogs over-winter, dozens of frogs may be found within 1 to 2 m of the spring margins in September, and some individuals may be seen into late October during warm afternoons (D. Patla personal observation).

With the evaporation of surface water at upland sites (Turner 1960), or from mid-August through September (Pilliod et al. 2002), juvenile and adult spotted frogs move from summer habitats to over-wintering sites. Recently metamorphosed frogs (i.e., young-of-the-year [YOY]) must undertake their first migration wherever breeding and suitable wintering habitats are spatially separated. Adults are not known to migrate in large groups, likely because they are quite widely dispersed in summer, but mass migrations of YOY (over 100 frogs) have been observed (Pilliod et al. 2002). Late-summer migration routes include streams and intermittent drainages (Turner 1960, Patla 1997), but migration also often involves substantial overland travel. Spotted frogs in Idaho were found crossing at least 500 m of dry forested land, taking the most direct, terrestrial route rather than following streams (Pilliod et al. 2002). Young-of-the-year also accomplish long migrations, crossing 100 m of dry land and 350 m total distance to travel from a shallow breeding pool to over-wintering sites in lakes in Idaho (Pilliod et al. 2002). In Yellowstone, YOY crossed about 300 m of dry meadow and forest to reach a seep leading to a stream flowing from a spring used as the winter site; a total distance of about 480 m between breeding and wintering sites (Patla 1997). Spotted frog adults that move far during the summer have the most arduous fall migration; Pilliod et al. (2002) reported that three to five female frogs at a high-elevation study area in Idaho were making annual round-trip migrations of at least 2,066 m. Migrations can be extremely rapid; radio-tagged frogs in Idaho completed migrations in one to two days, moving up to 700 m per day and 160 m per hour. The most rapid movements were accomplished at night, when air temperatures were between 3 and 10 °C (Pilliod et al. 2002). Fall migrations were also observed during the day and following rainfall as well as during dry periods (Pilliod et al. 2002).

Winter

In winter spotted frogs cease growth (Reaser 2000) and experience greatly reduced activity levels and metabolic rates. They can maintain anaerobic metabolism for only brief periods and therefore must have access to adequate oxygen (or dissolved oxygen in water). Radio-tagging of over-wintering spotted frogs (Bull and Hayes 2002) revealed that the frogs are not dormant; they exhibited considerable mobility in water below 3 °C, in winter habitat under the ice and banks of frozen ponds, in partially frozen ponds, and in a river. Movements between consecutive winter locations varied in distance from just a few meters at some sites, to an average of 30 m at one ice-covered pond, to 500 m downstream. Such winter mobility allows frogs to avoid the risks of freezing, anoxic conditions, scouring, and predation (Bull and Hayes 2002).

Site fidelity

Although movement patterns vary and mobility may increase in years with abundant rainfall, Columbia spotted frogs exhibit strong site fidelity (Ross et al. 1999, Reaser and Pilliod 2005). Turner (1960, p. 274) reported "in many cases it was found that frogs occupied the same area year after year, their cyclic migration sometimes bringing them to the same spot they occupied exactly a year before". Fidelity to breeding and wintering sites is pronounced; a number of breeding and wintering sites used by spotted frogs at Turner's Lake Lodge study area in the 1950s are still being used (Turner 1960, Patla 1997, Patla 2002). Strong fidelity to particular winter sites was reported for spotted frogs in Idaho, with frogs returning to their winter sites even where winter sites used by other frogs in the vicinity were closer and more accessible (Pilliod et al. 2002). Pilliod et al. (2002) also found that both sexes show strong fidelity to breeding sites, but only females tended to return to the same summer habitats. Pre-reproductive spotted frogs show the least tendency to stay in their natal area. In northwestern Montana, a mark-recapture study (>10,000 frogs uniquely marked) found that 14 percent of the recaptured juveniles moved 1,000 m or further, compared to only 2 percent of the adults (Funk et al. 2005b). Nearly all frogs that moved to a new location 200 m or further (recaptured yet again in a subsequent year) remained at their new location, thus indicating permanent dispersal rather than temporary migration (Funk et al. 2005b).

Connectivity

Information about the spatial extent of spotted frog populations and connectivity among populations is becoming more precise and detailed due to modern molecular genetic techniques, coupled with intensive, multi-year mark-recapture efforts. Several generalizations about connectivity and spotted frogs can be made at this time:

(1) Spotted frogs in clusters of ponds are likely to be closely related genetically, due to frog movements and inter-breeding. Where multiple occupied ponds exist at similar elevations in the same watershed basin (a few to several km long), interchange among the ponds is so high that only one or two randomly-mating populations are likely to be present in the basin, based on genetic evidence (Funk et al. 2005a). Individual ponds typically correspond to single, randomly mating populations only where they are physically isolated from other populations (see below).

(2) The connectivity of spotted frog groups and populations is very strongly influenced by terrain and landscape features. Distances, mountain ridges, and elevation determine the isolation and connectivity of spotted frog populations in undisturbed settings (Funk et al. 2005a; also see Landscape section). Low elevation populations (e.g., in broad mountain valleys) of spotted frogs have high gene flow compared to high elevation or mountain populations (Funk et al. 2005a). Low elevation populations separated by large distances (e.g., 50 km) in northwestern Montana show more genetic similarity than higher elevation sites that are much closer to each other (e.g., 10 km) but separated by ridges (Funk et al. 2005a). In eastern Idaho, dry sagebrush uplands appear to inhibit all spotted frog movements between occupied drainages that are as close as 550 m; frogs in the same area move over 1 km along riparian corridors (observed in 15 of 631 recaptured frogs in a four-year study [Engle 2001]).

Movement barriers and hazards (discussed in more detail later in this report) are vital to considerations of potential connectivity or isolation, which in turn are important for population persistence (see section on Spatial characteristics).

(3) Connectivity is supported by high dispersal rates in this species. Individual Columbia spotted frogs are capable of dispersing long distances. There are many records of spotted frogs moving 1 to 6.5 km in one year or more, and frogs are able to move up steep slopes (e.g., 700 m elevation gain over 1,930 m horizontal distance) (Reaser 1996, Engle 2001, Pilliod 2002, Funk et al. 2005b). Funk et al. (2005b) quantified spotted frog dispersal rates in two mountain basins using mark-recapture of 10,000 frogs over four years. Genetic analysis of microsatellite loci in 312 frogs confirmed that the observed dispersal patterns are representative of historical patterns. The researchers characterized current and historical rates as "exceptionally high": juvenile movement probabilities up to 62 percent occurred in some years (with movement defined as between ponds in the same basin that are separated by 200 m or more). On average, 25 percent of recaptured juveniles (108 frogs) moved 200 m or further; 14 percent (60 frogs) moved 1 km or further; 9 percent (39 frogs) moved 2 km or further; and 2 percent (six frogs) moved 5 km or further. Some frogs moved up steep inclines (e.g., 36° incline over 2 km) and exhibited large elevation gains (>750 m). Despite the high dispersal rates, gene flow tends to be restricted between low and high elevation sites (with low elevation defined as less than 1,400 m in northwestern Montana); this suggests that low survival or lack of mating success can act to restrict gene flow, or that the observed high dispersal rates described above are unusual (Funk et al. 2005a, Funk et al. 2005b).

(4) The high dispersal rates and connectivity of populations observed in relatively undisturbed habitats have implications for management and conservation. The ability to disperse successfully likely has an important role in population dynamics and the persistence or extinction of populations (Sjogren 1991, Funk et al. 2005b). We will further examine these topics under Landscape context in the Habitat section and Spatial characteristics under the Demography section.

The Bighorn National Forest spotted frogs are totally isolated from all other spotted frogs in North America, with terrain and distance too extreme to allow for possible connections with populations to the west. Based on distance considerations alone, two of the three known breeding populations in the Bighorns (located about 2.6 km apart) have the potential for connectivity. The third breeding site (at over 7 km distance) is above the maximum dispersal movements on record for this species, and it should be considered isolated unless additional occupied or breeding sites are found in the intervening area.

On the Shoshone National Forest, the pattern of existing observational data (**Figure 10**) suggests a potential for connectivity in the central part of the forest, where there are multiple records in clustered areas. More data are needed to determine the number, distribution, and potential connectivity of breeding populations within and among watersheds of the national forest and to spotted frog populations in Yellowstone National Park and the B-TNF.

Habitat

General requirements

Columbia spotted frogs inhabit a variety of vegetation communities, including coniferous or mixed forests, grasslands, and riparian areas of sage-juniper brush-lands. Elevation range for the species is reported up to 3,036 m, with frogs ranging up to 2,890 m in the GYE (Reaser and Pilliod 2005) and 2,947 m in Montana (Maxell et al. 2003). Dumas (1964) reported that relative humidity of 65 percent at 25 °C is lethal to adult spotted frogs in approximately two hours; this would restrict spotted frogs to higher elevations or moist riparian zones in arid western landscapes. Because both breeding and over-wintering occur at aquatic sites (see below), populations are located in the general vicinity of ponds, lakes, springs, and/or streams. The examination of movement distances (see above) suggests that breeding and wintering sites are generally less than 600 m apart although adults are capable of moving longer distances. Surveys for amphibians in Yellowstone National Park during 2000-2001 found a strong association of Columbia spotted frogs with particular National Wetland Inventory (NWI) classifications (Cowardin et al. 1979): 69 percent of 116 wetland sites occupied by spotted frogs had the classifications palustrine and emergent; 19

percent were classed palustrine and aquatic bottom (the remaining 12 percent were at other types of wetlands or in unclassified areas). With regards to water regime, the majority (54 percent) were in seasonally flooded areas; 22 percent were in semi-permanently flooded areas; and 16 percent were in saturated areas (remainder unclassified) (Patla and Peterson unpublished data). A study in arid southwestern Idaho (Munger et al. 1998) found that adult spotted frogs were associated with palustrine, shrub-scrub, seasonally flooded sites, or with intermittent riverine, streambed, seasonally flooded sites. Frogs were also associated with vegetation indicative of permanent water sources (i.e., willows and submerged aquatic plants rather than emergent vegetation such as sedges) and vegetation that provides hiding and thermal cover (e.g., willows). Investigating NWI classification as predictors of spotted frog (and Pacific treefrog) occurrence, Munger et al. (1998) found only modest predictive power and suggested that habitat variables (e.g., slow-moving water) or fine-scale habitat models could provide better tools than NWI for locating frogs. Development of wetland habitat models as tools for predicting amphibian presence and habitat use is in progress for Yellowstone National Park as a research effort of USGS Earth Resources Observation Systems Data Center (USGS-EROS) and collaborators (e.g., Paul Bartelt, Waldorf College) (see edc2.usgs.gov/armi/nmd/research.asp).

Breeding and larval habitat

Characteristics of the water body, vegetation, and water temperature are important aspects of breeding and larval habitat. Breeding and egg deposition take place in stagnant or slow-moving water, including permanent and temporary ponds, marshes, stream oxbows, small springs, the edges of lakes and slow-flowing streams, and man-made bodies of water (**Figure 11**; Monello and Wright 1999). Shallow water must be available; e.g., Maxell (2000) reported eggs deposition in water 10 to 15 cm deep, and Reaser and Pilliod (2005) reported egg deposition in water 10 to 20 cm deep. Emergent vegetation (e.g., sedge) is usually present at breeding sites (Maxell 2000; Reaser and Pilliod 2005; Patla and Peterson unpublished data), but egg deposition occurs soon after snowmelt and thus prior to significant seasonal growth by most emergent and aquatic vegetation. Morris and Tanner (1969) report that eggs are never deposited among cattails, however; spotted frog tadpoles use tall stands of emergent vegetation (e.g., cattail and bulrush) following dispersal from the site of egg deposition (D. Patla personal observation). Sources differ with regards to the importance of aquatic vegetation. Reaser and Pilliod (2005) report frequent associations of egg deposition with floating vegetation while Morris and Tanner (1969) describe an avoidance of floating *Spirogyra*. Bull and Hayes (2001) note that

Figure 11. A Columbia spotted frog breeding site in eastern Yellowstone National Park (M. Chatfield, Idaho State University and USGS).

spotted frog breeding sites are dominated by submerged vegetation (pondweed and buttercup), while non-breeding sites to which frogs move had a predominance of emergent vegetation. However, amphibian surveys in the GYE in 2001 indicated a stronger association of breeding sites with emergent vegetation than with aquatic submerged or floating vegetation: 26 of 41 sites (63 percent) occupied by spotted frog eggs or larvae had no more than 10 percent aquatic vegetation cover, while 27 of the sites (66 percent) had >50 percent cover with emergent vegetation (mostly sedges) (Patla and Peterson unpublished data).

Spotted frogs tolerate a broad temperature range but prefer water exposed to sunlight that allows for daily warming. Breeding activities and egg deposition often occur in the portion of the water body with high exposure to morning sunlight (i.e., on the west side) (Morris and Tanner 1969), or on the north side, where snow melts most quickly in spring. However, oviposition locations are variable and depend on inlets, outlets, surrounding tree heights, and surrounding horizon. Eggs are normally deposited in water at temperatures of approximately 14 °C (Morris and Tanner 1969). Water temperatures after egg deposition fluctuates, increasing on sunny afternoons, falling sharply at night, and generally increasing as the season advances toward the summer solstice, unless the site has a geo-thermal influence. Embryos at the upper surface of egg masses suffer high mortality due to freezing temperatures at night and/or during spring cold spells. Larval development to metamorphosis requires periods of warm temperatures. Water bodies fed continuously by cold-water springs or otherwise prevented from warming during the day are unlikely to serve as spotted frog breeding sites. Water temperatures measured at 67 sites with spotted frog larvae in Yellowstone during the years 2001 and 2002 averaged 17.8 °C (se 0.59, range 5 °C to 29 °C; Patla and Peterson, unpublished data).

Foraging habitat

Foraging habitat includes ephemeral pools in forests and meadows, streams (permanent and intermittent) and river edges, riparian zones, temporary and permanent ponds, lake margins, and marshes (**Figure 12**). Summer foraging may occur at the same body of water used for breeding and over-wintering, but in many cases frogs move to other areas that may have more food resources and/or fewer predators and competitors (Bull and Hayes 2001). Pilliod (2001) found that female frogs migrating to adjacent wetlands for summer foraging were significantly larger than non-migratory females.

Sites used exclusively for summer foraging may be shallower, less vegetated, and more ephemeral than breeding sites, with less forest or shrub cover along shorelines (Pilliod et al. 2002). Patla (1997) found that "spotted frogs demonstrate considerable plasticity in summer foraging habitat, making use of small wet or damp areas in forest and meadows, including water-filled tire tracks, stream edges, and marshes", and she surmised that the location of such sites, en route

Figure 12. A wet meadow used by Columbia spotted frogs for foraging, Grand Teton National Park (D. Patla, Idaho State University and USGS).

between breeding and wintering sites, was an essential aspect of their use by frogs. By contrast, water bodies that provide summer foraging as well as breeding and hibernacula host diverse habitat features, including deep water sections. For example, one such year-round site in the mountains of central Idaho was characterized by emergent vegetation, perennial outlets and inlets or springs, and some deep-water habitat (up to 3 m) (Pilliod et al. 2002). A pond in northeast Oregon used for both breeding and summer foraging contained emergent vegetation (cattails and spike-rush) as well as aquatic vegetation (pondweed), and was relatively large (28,500 m^2) and deep (3 m) (Bull and Hayes 2001).

Winter habitat

Frogs of the genus *Rana* generally over-winter underwater in permanent water bodies, or terrestrially, depending on physiological tolerances for chilling and hypoxia. Columbia spotted frogs over-winter in or immediately adjacent to aquatic sites, where they can avoid the threat of freezing or oxygen depletion (Bull and Hayes 2002). Winter habitat may include ponds, streams, undercut stream banks, springs, beaver dams, and underground areas (associated with water bodies), but all such sites must have above-freezing temperatures, be moist or wet, and be well-oxygenated. The most detailed information on spotted frog wintering habitats was obtained by radio-tagging 66 frogs in northeastern Oregon, at elevations of 915 to 1,800 m where air temperatures remained below freezing from December through February and plunged to as low as -30 °C (Bull and Hayes 2002). In this study, 29 frogs over-wintered in seven ice-covered ponds. In the larger ponds, frogs moved under the ice, but most stayed within 1 m of shore and in water <1 m deep. At other ponds, frogs remained hidden under logs in water <30 cm deep and within 50 cm of the shore, or over-wintered in hollow chambers under banks along the pond edges, with entrances at or below the water surface. Some frogs (19 of 66) over-wintered in ponds with partially-frozen surfaces resulting from the up-welling of warmer water from springs; frogs remained in the ice-free sections. Frogs also over-wintered under river banks, under logs in flowing creeks, in backwaters, and in a seep under the root wad of a fallen tree.

Spotted frogs are also known to over-winter in holes or pits filled with water from underground sources in springs, and beneath the undercut banks of streams (Turner 1958a; Reaser and Pilliod 2005). Two radio-tagged frogs in Yellowstone NP entered a small spring in early October (**Figure 13**), where they apparently moved underground away from the

Figure 13. A small spring where Columbia spotted frogs overwinter, located in the sedges immediately to the right of the person (Janice Engle), Yellowstone National Park. Wintering areas can be very inconspicuous but may be detected by observations of spotted frog congregations near such areas in September or October (D. Patla, Idaho State University).

spring mouth (Patla 1997); the congregation of frogs at the mouth of this spring every year in September indicates continuous use as a hibernaculum (D. Patla personal observations, 1994-2003). Another radio-tagged frog in the same study entered an under-bank cavity formed by tree roots, adjacent to a spring-fed, perennial stream. In southwestern Idaho, spotted frogs are known to over-winter in spring-fed ponds with willows (Engle 2001). Beaver dams also serve as spotted frog winter habitat (Reaser and Pilliod 2005, D. Patla personal observation).

Area requirements

The preceding section on Activity and movement patterns discusses the nature and scale of movements of Columbia spotted frogs among habitat components. This section describes what is known about the total size of the inhabited area. The concept of "activity range" is used to refer to the area containing breeding, foraging, and wintering areas, and includes the seasonal or migratory movements among these areas. It differs from home range, which is more narrowly concerned with the area occupied by an animal in its normal daily activities and thus excludes migrations to breeding or winter habitat (Turner 1960). Turner (1960) assessed the size of the activity range for spotted frogs in Yellowstone National Park by connecting the points of capture (five or more captures, distributed throughout the active season) and then determining the area of the space so defined (minimum complex polygon). Activity ranges varied from 2,500 to 357,000 square feet (0.023 to 3.3 ha), with no significant differences among males and females, or adults and juveniles (Turner 1960). In Idaho, female frogs (five or more captures over one year) exhibited activity ranges of 0.14 to 26.3 ha, with a median of 2.5 ha (Pilliod 2001). Given the limitations of capture methods, these activity areas are likely to be underestimates.

The size of activity ranges is correlated with geography and habitat components. For example, in Yellowstone National Park, the smallest activity ranges occurred in an area where springs and wetlands provided wintering, breeding, and foraging habitat in close proximity; the largest ranges occurred where frogs used a meadow for breeding and summer foraging and then migrated to a permanent stream for over-wintering (Turner 1960, Patla 1997). A generalization about the size of the area used by individual spotted frogs throughout their lifetime escapes definition due to the small number of studies examining this aspect of the species' life history.

Because the size and configuration of activity ranges depends on local features, activity ranges change if the environment is altered. Replication of Turner's study in the 1990s, subsequent to modification of the study area by roads and residential development, indicated that activity ranges changed in configuration and size (Patla 1997; Patla and Peterson in prep). Weather is also a factor that complicates assessment of the size and configuration of activity ranges; drought or unusually wet conditions can cause some frogs to shift their movement patterns and thus alter the size of their activity ranges (Patla 1997, Reaser and Pilliod 2005).

Landscape context

Landscape context has important implications for the connectivity of spotted frog populations. As discussed earlier, the type of terrain separating groups of spotted frogs is more relevant than the distance. Landscape context is also important in understanding the metapopulation dynamics of the species (see Spatial characteristics section below), given that it determines the potential spatial structuring of breeding populations and the degree of their isolation.

In general, landscapes providing suitable spotted frog habitat must include pooled water (in the form of ponds, lakes with shallow edges, ephemeral pools, oxbows, beaver ponds, etc.) for breeding habitat, and perennial streams, springs, spring-fed lakes, or other permanent water bodies where frogs can over-winter. In selecting watersheds for spotted frog surveys in Oregon, Bull and Hayes (2000) used these landscape features as identifying criteria: presence of a perennial stream with quiet water in the form of ponds, marshes, and backwaters nearby; and streams within a wide valley bottom (<10 percent gradient) and in open meadows adjacent to coniferous forests. In northwest Wyoming, spotted frogs occur in areas with few or no trees (e.g., Hayden Valley in Yellowstone NP and the Flat Creek drainage of the National Elk Refuge), but spotted frogs and breeding sites appear to be less abundant than in forested areas (D. Patla, unpublished data).

Predicting spotted frog occurrence can be difficult because of the fine scale of habitats used by frogs. Ephemeral ponds and springs may be too small to be included in National Wetland Inventory classifications, for example. Seasonal wetlands and intermittent streams that are important as stepping stones among habitat patches, as foraging habitat, or as migration routes may not be mapped. Beaver ponds may have been created (or disappeared) since the last topographic map or wetland inventory.

The influence of landscape structure on population dynamics was assessed by Pilliod (2001) in his study of Columbia spotted frogs in the mountains of central Idaho. This study found that:

1) breeding populations are smaller as distance to over-wintering site increases

2) the physical size of the breeding site is not correlated with frog abundance

3) ponds greater than 600 m from the nearest breeding site tend to be unoccupied

4) the area of fishless habitat more strongly influences frog abundance than the total area of habitat.

These results indicate the value of assessing both the spatial arrangement of habitat components and local habitat conditions as key aspects of understanding the landscape context for spotted frogs.

Landscape structure also strongly affects population structure, as demonstrated by Funk et al.'s (2005a) investigation of genetic variation, using microsatellite loci in spotted frogs collected from 28 breeding ponds in western Montana and Idaho. The researchers describe a "valley-mountain model of population structure" for this species. Mountain ridges and elevation restrict gene flow, and genetic variation is negatively correlated with elevation. High elevation populations have small effective population sizes and a lower level of among-population gene flow, compared to low elevation populations. These findings have important implications for considering how landscape context relates to the conservation of this species:

1) high elevation populations may be particularly susceptible to extinction

2) the extinction of low elevation populations can reduce the persistence of high elevation populations, because low elevation populations may be the only source of immigrants to high elevation populations

3) low elevation populations that are affected by habitat loss and habitat fragmentation can lose their historical connectivity, with remaining populations becoming isolated and more prone to extinction.

Funk et al. (2005a) point out that upper elevation populations are like "islands" in relation to the low elevation "mainland". These are highly relevant issues considering that National Forest System lands in Region 2 consist of the higher elevation areas while the mountain valleys are often privately owned and are becoming increasingly developed or urbanized. For example, if spotted frog populations are decimated in a mountain drainage due to management activities or natural events, the chance that frogs will return to the area is limited by the extent to which habitat is lost and fragmented on the lower elevation, non-USFS lands. Furthermore, development of National Forest System lands (e.g., recreation facilities, oil-gas development) that spurs population growth and private development in the adjacent valleys can contribute to long-term frog declines.

Food habits

Spotted frogs feed mainly during the day, probably because low night temperatures in mountainous areas limit activity of frogs and their prey (Turner 1959a). Frogs may travel short distances away from water during foraging; Turner (1959a) observed a frog consuming a moth about 12 m from a stream edge. However, in a study of the diets of leopard frogs, spotted frogs, and toads in western Montana, Miller (1978) observed that spotted frogs were generally not more than 10 m from the edge of the water, with juveniles foraging farther away from the water than adults.

Like many other amphibians, Columbia spotted frogs are opportunistic and flexible predators. Variation in diet relates to prey availability and ecological conditions; thus snails and water striders are found in the diets of frogs inhabiting lakes and backwaters while the strawberry crown-girdler (*Brachyrhinus ovatus*) is consumed by frogs in areas where strawberries grow (Turner 1959a). Spotted frogs occasionally exhibit cannibalism; e.g., an adult frog was observed consuming a metamorphosing spotted frog tadpole (Pilliod 1999). Presumably, spotted frog adults would also consume other amphibian species of the right size. Captive spotted frogs will eat newborn mice, suggesting that even young small mammals may serve as prey in the wild if encountered by foraging adult frogs.

The food habits of the spotted frog are described in detail by Turner (1959a), who collected and analyzed the gut contents of 178 frogs from the central portion of Yellowstone National Park, elevation 2,380 m.

Seventy-nine to 90 percent of all food items were spiders and representatives of four orders of insects: Hemiptera (bugs), Coleoptera (beetles), Diptera (flies), and Hymenoptera (ants, wasps, and bees). Six families of insects (Carabidae, Chrysomelidae, Cordiluridae, Curculionidae, Formicidae, and Gerridae) accounted for 55 percent of all food items. Spotted frogs also consumed mollusks and earthworms.

The time of year influenced species composition of the spotted frog's diet (Turner 1959a). The greatest diversity of prey items occurred in mid to late summer (July 15 to August 31). Caddis fly larvae were consumed only in early summer, which Turner attributed to the fact that frogs were more restricted to water at that time. Spiders and ants were available throughout the active season.

Turner (1959a) found that the feeding habits of male and female spotted frogs were similar. However, differences related to body size of frogs were apparent. Small frogs (<31 mm in length) consumed small prey (2 to 9.5 mm, maximum dimension) while large frogs (>50 mm) consumed both small and large prey (2 to 18+ mm). The vast majority of prey (66 percent) was within the size range of 4 to 9.5 mm.

Little is known about the specific diets of spotted frog tadpoles. In general, anuran larvae are opportunistic omnivores or detritivores, obtaining green algae or planktonic material by filtering or scraping material from sediments and vegetation surfaces. Spotted frog tadpoles have been observed grazing on water starwort (*Callitriche palustris*) and *Spirogyra* (Turner 1959a); lodgepole pine (*Pinus contorta*) pollen (D. Patla personal observation); and conspecific dead or dying tadpoles (Morris and Tanner 1969, D. Patla personal observation). Bacteria, viruses, and dissolved nutrients may also serve as food, but the contribution of such small items has not been sufficiently studied (Hoff et al. 1999). Turner (1959a) speculated that bacteria might serve as a food source when vegetation is depleted or absent.

Whether or not food resources constitute an important factor in population regulation is a complex issue for larval amphibians because climate, predation, and competition have variable importance as regulating factors, even in adjacent ponds (Duellman and Trueb 1986). Investigating *Rana pretiosa*, Licht (1974) asserted that food shortages are highly unlikely to be a cause of significant tadpole mortality, because (1) tadpoles have flexible diets that include materials likely to be abundant in ponds (i.e., detritus, rotting organic material, and algae); and (2) tadpoles in lab tests survived several weeks of starvation. Tadpoles can survive temporary food shortages and will move to new feeding zones in a pond or marsh when a food resource becomes depleted. The conclusion that food is seldom an important factor for larval populations is reasonable for Columbia spotted frogs, with the qualification noted by Berven (1990) that starvation or adverse effects on development can occur where larval densities are very high.

Similarly, post-metamorphic populations of spotted frogs may seldom be limited by food shortages in the terrestrial environment because of the abundance of invertebrate prey, the species' flexible diet, its mobility to seek foraging sites, and the ability of adults to endure long periods of starvation or very minimal food (Licht 1974). As food availability declines in the fall, spotted frogs cease feeding and enter hibernacula, with no food requirements until emergence the following spring (Turner 1960). However, under adverse conditions, such as low rainfall and humidity in the summer, the survival of adult ranid frogs can be reduced due to desiccation and starvation, and the fecundity of some amphibians has been shown to decline where population density is high, presumably because of food shortages (Berven 1990). From this, we may infer that food shortages could become an important limiting factor for adult and juvenile spotted frog populations during drought years, in areas where chemical pesticides severely reduce insect prey, or where human-caused or natural factors reduce vegetation and the moist conditions that support high invertebrate density.

Breeding biology

Columbia spotted frogs in mountainous areas usually begin breeding activities while patches of snow still remain on the ground; breeding sites may be partially covered with snow and ice. Adult frogs gather at breeding sites early in the season while non-breeding frogs may still be in or near the wintering site (Turner 1958a, Morris and Tanner 1969). Males arrive first and may be present three or four days before females (Morris and Tanner 1969). They outnumber females at breeding sites and remain there longer (Turner 1958a).

Males vocalize weakly and sporadically from ponds, mostly at night but occasionally during the day (Turner 1958a). They may call from either above or below the water surface (Morris and Tanner 1969). Vocalization may be related to the density of frogs. Turner (1957) describes much more persistent calling at his Lake Lodge study area in the 1950s than was observed at the same area in the 1990s, by which time the population had undergone a reduction of 80 percent (Patla and Peterson 1999 and unpublished data). Vocalization is too sporadic and faint (i.e., the sound carries only 25 m or less) to be a useful or reliable tool for human observers to find finding breeding sites (Turner 1959a).

Mating commences as soon as females arrive at the breeding site (Morris and Tanner 1969). Males use their front feet to grasp females behind their forelimbs (axcillary amplexus) in an embrace that may last for several days (Turner 1959a, Engle 2001) and until the female deposits eggs. Eggs are fertilized externally by the amplexed male during egg deposition. Females move about while in amplexus, apparently not greatly hindered by the usually smaller males clinging to their backs (Engle 2001). Amplexed pairs are very vulnerable to predation during this time, particularly the male frog, which remains visible at or near the water surface while the female is concealed in the pond substrate (D. Patla personal observation).

In the GYE, egg masses are deposited between late April (elevation 1908 m, National Elk Refuge) and before the middle of June at upper elevation sites (D. Patla unpublished data). The dates of egg deposition at any given site vary among years, depending on temperatures and snowmelt. Over 14 consecutive years (1991-2004) of monitoring at a pool in a forested area of Yellowstone National Park, at an elevation of 2,380 m, the earliest date of first egg deposition was May 4 and the latest was June 6 (D. Patla unpublished data).

As noted previously, this species shows a strong fidelity for breeding sites. Females deposit eggs in the same small area year after year, but they will shift locations if necessary (e.g., if the pool becomes too small due to drought, or if the shallow-water section shifts [D. Patla personal observation]).

Eggs are held by globular mass of gelatin that initially sinks to the pond bottom, and then rises and floats on the surface. Wind may blow the clusters around in larger pools, moving them away from the deposition site (Turner 1958a). Females using a common breeding site often deposit their clutches in close proximity to one another; Turner (1958a) surmised that after the first pair deposits eggs, other pairs are attracted to the same area for oviposition. This can result in large clusters of egg masses. Up to 45 eggs masses have been observed at a single site in the GYE (Koch and Peterson 1995). While counting egg masses provides a method of monitoring reproductive effort, sometimes egg masses are so coalesced that individual egg masses cannot be distinguished and precisely counted.

No parental care of egg masses or tadpoles is provided. Females depart breeding sites soon after depositing eggs. Males are often found lingering near egg masses, probably awaiting other potential mates.

Time to hatching is highly variable. Turner (1958a) reported 12 to 21 days in Yellowstone; Maxell (2000) reported 5 to 21 days in Montana. Hatching and developmental time depends on local conditions, including water temperature, fluctuations in air temperatures, and the amount of cloud cover that reduces solar radiation (Morris and Tanner 1969). Time to metamorphosis also varies among sites and has been reported as 80 to 85 days in Yellowstone (Turner 1958a), 56 to 112 days in Montana (Maxell 2000), and 122 to 209 days in Utah (Morris and Tanner 1969).

The number of larvae and metamorphosing young is extremely variable, both among breeding sites and among different years at the same breeding site. Except at ponds or wetlands where breeding, rearing, and over-wintering occur within the same water body, successfully metamorphosed young must emerge from the breeding pools and travel to suitable over-wintering sites.

Demography

Summary

Columbia spotted frogs of mountainous areas are slow-growing, requiring four to six years to reach sexual maturity. Although spotted frogs are capable of a large reproductive effort (e.g., several hundred eggs per clutch), reproduction is limited by the inability of females to breed every year, the occasional total loss of embryos due to freezing or desiccation, and the high variability of larval survival due to the interaction of many factors at the breeding site (e.g., rainfall, evaporation, food, predation, crowding, disease, and pollution) (Turner 1962b). In many areas, successfully metamorphosed young must migrate across dry land to reach suitable wintering areas, possibly experiencing high mortality. Survival of the young is among the most important demographic factors. The long lives of adults make it possible for populations to sustain several years of null or low recruitment rates. Successive years of reproductive failures can lead to local extirpation within less than a decade if no immigration from other populations takes place, with extirpation accelerated if adult mortality rates are high due to natural or anthropogenic factors (discussed below).

Considering the large variations in local population sizes and in year-to-year reproductive performance, in addition to uncertainties about the frequency of breeding in females, the modeling of population dynamics based on information from other regions may be of limited value as a tool for local conservation management. We recommend using local information on the ecology and distribution of spotted frogs in Region 2 to build population models whenever possible.

Fecundity and larval survivorship

Egg masses are variously reported to contain about 200 to 800 eggs in Yellowstone National Park (Turner 1958a), 300 to 2400 eggs at low elevation sites in northwestern Montana (Maxell 2000), 150 to 1160 eggs in Utah (Morris and Tanner 1969), and 700 to 1500 eggs in the Pacific Northwest (Nussbaum et al. 1983). Probably most relevant for Region 2 are Turner's (1958a) findings, using an index based on the number of eggs per volume of egg mass in egg masses one to three days old; data from Yellowstone National Park yield a mean of approximately 540 eggs per mass (n = 16 egg masses, SE = 42). Morris and Tanner (1969) report that ova numbers in dissected gravid females vary widely, suggesting that the large variation in the number of eggs per clutch does not result from females depositing a small number of eggs in one location and then producing others later. They also report that female body size does not reliably correlate to egg numbers. Although the number of egg masses produced per female and per reproductive season remains unverified for this species, it may be safe to assume that each egg mass generally represents a single female's effort. One researcher reports that palpation of female spotted frogs just after egg-laying indicated no eggs remaining in the abdominal cavity; this would suggest that a single clutch is produced (B. Maxell personal communication 2002). The Conservation Strategy for spotted frogs in Utah assumes that each clutch represents one female (and one male frog) in the population but admits uncertainty on this point (Perkins and Lentsch 1998).

No precise information is available on survivorship of embryos for Columbia spotted frog, It probably is extremely variable among years. Stranding of egg masses and subsequent total mortality can occur at breeding sites with ephemeral water. For *Rana pretiosa* in southwestern British Columbia, Licht (1974) reported 68 to 74 percent embryonic survival in one year, and a probable 0 percent survival the following year when water levels dropped at the breeding sites (eggs were moved by the author to safer locations). Turner (1958a) notes that the upper layer of the floating egg masses is usually exposed to air, and eggs at the surface often do not develop due to exposure and freezing (Turner 1958a).

A review of tadpole mortality indicates that ranid frogs typically have a relatively constant mortality rate of 5 to 37.5 percent over the larval development period (Alford 1999). This assumes that ponds do not prematurely evaporate, which leads to much higher mortality. There is little specific information on *Rana luteiventris* tadpole survival rates. Turner (1960 and 1962b) reports that 800 larvae survived to late August-early September from 25,000 eggs deposited at three sites (3.2 percent survival); survival varied from 0 to 8.5 percent among sites. He cautioned, however, that these data might bear little relationship to survival in other years at the same sites. Licht (1974) reported less than 1 percent survival for *R. pretiosa* from hatching to metamorphosis in marshes in British Columbia. Total mortality occurred at ponds that dried up prior to tadpole metamorphosis. This may occur quite frequently given that spotted frogs often use ephemeral pools for breeding.

Age at first reproduction

Turner (1960) concluded on the basis of mark-recapture and growth rates in Yellowstone National Park that male spotted frogs breed for the first time in their fourth year of life (i.e., 3 years and 9 months after hatching), at about 47 mm in length. Females, on the other hand, first breed in their fifth or sixth year, at 50 to 60 mm in length. At lower elevations with longer growing seasons, much younger or smaller spotted frogs are capable of reproduction. Using skeletochronology to determine age, Reaser (2000) and Reaser and Pilliod (2005) found that male spotted frogs in central Nevada reach reproductive maturity after one to two winters (at 35 mm minimum length), and females one to two years later.

Spotted frogs of Region 2 presumably more closely resemble the Yellowstone frogs than those in Nevada, which are at the southern boundary of the species' range. However, it should be noted that relating the size of frogs to their age is problematic; the time required to reach adult size and sexual maturity is a function of growth rate, which is strongly influenced by local conditions and the length of the seasonal activity period (Duellman and Trueb 1986). Turner's study area in Yellowstone National Park was located at nearly 2,400 m in elevation, with a mean annual temperature of only 0.1 °C, an environment he described as "marginal" for spotted frogs (Turner 1960). Growth rates may be greater and age at first reproduction earlier for more favorable sites (e.g., sites with warmer temperatures and a longer growing season) in Region 2. Age at first reproduction in Region 2 is likely somewhere between the extremes presented here.

Proportion of the population breeding

Adult males are probably capable of breeding every year (Turner 1958a and 1960). Females, however, apparently breed less frequently. Based on his research in Yellowstone National Park, Turner thought that spotted frog females produce eggs every two or three years or even less often (Turner 1958a and 1960). This finding is not highly unusual; Duellman and Trueb (1986) report that although annual reproduction by female anurans is most common in temperate regions, females of populations in extremely cold environments may not produce eggs every year. Turner (1958a) points to other anuran species females that do not breed annually and attributes this to the considerable amount of energy necessary for egg development, a process that might require several seasons. However, recent work in a high elevation basin in Idaho suggests that at least some females of this species can and do breed every year at elevations similar to those of Turner's study area in Yellowstone (Pilliod unpublished data). Turner's opinion on female breeding frequency was based on the absence of marked females breeding in successive years during a 3-year study; it is possible that breeding females eluded capture and were not marked or recaptured, taking into consideration that females, unlike males, do not linger at breeding sites. A reasonable conclusion from available information is that some females in spotted frog populations of Region 2 may breed annually (possibly depending on conditions), but the majority probably do not. A more definitive answer must await further life history studies of this species.

Spotted frog populations typically have higher proportions of adult females than males. (Note: the preponderance of males at breeding sites, described above, relates to behavior and not to actual sex ratios in the population.) Turner (1960) reported that 65 percent of the adult population at his study area was female; Patla (1997) found a similar 66 percent of the adult population to be female at the same study area 40 years later. Reaser (2000) found that four of seven study sites in Nevada had more females than males; 57 to 67 percent of the adult frogs caught at these sites were female. Turner (1962b) reported as a generalization for spotted frog populations that older females consistently outnumber older males by about 3.5 to 1, while smaller frogs show an equal sex ratio.

Post-metamorphic survivorship and longevity

Survivorship data for amphibians in the wild are scarce, and existing data are highly variable (Duellman and Trueb 1986). Annual adult survivorship of the closely related *Rana pretiosa* (the Oregon spotted frog, closely related to *R. luteiventris*) was estimated at 45 percent for males and 67 percent for females (Licht 1974). Turner (1960 and 1962b) estimated one-year survival at about 60 percent for juvenile and adult (at least one year old) spotted frogs in Yellowstone National Park.

Based on growth rates, the maximum longevity of spotted frogs in Yellowstone National Park has been estimated at 12 to 13 years for females and 10 years for males, with the shorter life-span of males possibly reflecting higher levels of metabolic activity associated with annual breeding (Turner 1960). More recent (1993-2001) investigations at Turner's study area found that a few female spotted frogs lived at least 11 years (D. Patla unpublished data). Using skeletochronology to age spotted frogs in the mountains of central Idaho produced results consistent with Turner's (1960) estimates of longevity. In a study of 354 females and 235 males in Nevada, however, the technique revealed a maximum age of seven years for females and of three years for males (Reaser 2000, Reaser and Pilliod 2005). Frogs dwelling in colder areas with short growing seasons are expected to have longer life spans, due to lower metabolic rates (Turner 1962b).

Spatial characteristics and metapopulations

Previous sections (Activity and movements patterns, Habitat) discussed the importance of spatial characteristics for spotted frog biology (e.g., migrations and movements) and habitat occupancy (e.g., connectivity and landscape context). Extinction probability is positively correlated with both population isolation (Sjogren 1991) and small effective population size (Funk et al. 2005a and references therein). Because the persistence of frog populations may depend on spatially-governed linkages to other populations, consideration of spatial factors is an essential aspect of demography, and is strongly relevant to conservation and management.

Genetic data indicate that single ponds or lakes do not correspond to Columbia spotted frog "populations" (i.e., groups of frogs that interbreed or randomly mate, also called demes), except in cases where the water body is very isolated (see Connectivity section) (Funk et al. 2005a). Where clusters of ponds exist, drainage basins of a few to several km long consist of one or two frog populations, leading the researchers to point out that basins appear to be the appropriate geographic unit for management of this species (Funk et al. 2005a). In an investigation of wood frogs, Petranka et al. (2004) also found that clusters of ponds are not demographically independent and suggested that pond populations within 400 m of each other should be treated as a single, local population. In addition, frogs switch habitats as conditions change, indicating that a local "extinction" cannot be confirmed until all potential habitat in the area is checked.

Metapopulation theory seeks to describe the dynamics of collections of discrete, unstable, local populations, governed by local extinctions (parallel to "deaths" in a single population) and establishment of new populations ("births"). While local population units are subject to extinction, they can be "rescued" by migrants from other populations, or eventually recolonized if extinction occurs. Metapopulations can expand, as previously uninhabited areas are colonized, or contract or even disappear as local populations "wink out" and are not recolonized. Continuing and more recent development of metapopulation concepts have clarified the effects of patch area and isolation, and the dynamics of "sources" and "sinks" (see below) (Hanski and Gilpin 1991, Hanski 1998). Metapopulation dynamics explain how species living in patchy environments can persist in a region over time, or alternatively, why they vanish. Human or natural factors that decrease the size of populations (thus increase the potential for extinction) and/or that increase the isolation of populations either by distance or by diminished potential for successful dispersal and colonization of habitat patches are of critical interest for the conservation of amphibians and the management of their habitat.

Metapopulation theory is thought, at least until recently, to be highly relevant to amphibian populations of the north temperate zones. Metapopulation dynamics have been the focus of a number of studies (e.g., Gill 1978, Berven and Grudzien 1990, Sjogren 1991, Sinsch 1992, Sjogren-Gulve 1994, Hecnar and M'Closkey 1996, Skelly et al. 1999), and the topic is frequently cited in literature regarding amphibian declines and conservation (e.g, Bradford et al. 1993, Blaustein et al. 1994, Alford and Richards 1999, Semlitsch 2000). However, some researchers state that metapopulation dynamics are poorly resolved for pond-breeding amphibians and urge caution with applying the concept (Marsh and Trenham 2001, Petanka et al. 2004). For example, it is questionable whether breeding aggregations of frogs signify populations within a metapopulation, as amphibian metapopulation studies commonly assume (Marsh and Trenham 2001). Risks include mistaking perceived absence at the breeding site as extinction, when it is in fact due to other factors such as sampling error or habitat switching as described above; misidentifying isolation; and ignoring the importance of terrestrial habitats in population dynamics. Marsh and Trenham (2001) urge managers to balance metapopulation considerations with careful attention to site-specific habitat quality, and to see pond isolation as a concern primarily in disturbed environments that have movement barriers to amphibian dispersal such as roads and developed areas.

To "rescue" or colonize uninhabited areas, frogs must disperse from their natal sites. In the context of the potential for dispersal and colonization of suitable habitats, Engle (2001) and Munger et al. (2002) discuss barriers to spotted frog dispersal in southwestern Idaho: dry upland habitat; intermittent streams after they become dry; heavily grazed riparian corridors; canyons, ponds, and reservoirs stocked with fish; and severely eroded gullies. In Engle's study, movements occurred exclusively along watercourses, in contrast to the findings of Pilliod et al. (2002) (see Late summer and movements to winter habitats section, above). As discussed previously, adult spotted frogs have strong breeding site fidelity (Engle 2001) while juveniles can show high rates of dispersal (Munger et al. 2002, Funk et al. 2005b). The combined study of movements, genetics, and landscape factors, such as published by Funk et al. (2005a and b), is providing important insights about how demography is influenced by spatial characteristics. New approaches and understanding can be expected from the growing field of conservation genetics, which will help to refine the utility of the metapopulation concept. Funk et al. (2005 a and b) do not mention metapopulations at all.

A corollary of the metapopulation concept is the idea that population units can operate as "sinks", where mortality exceeds recruitment, or "sources", where frogs breed successfully and the reproductive surplus disperses to other areas, including sinks. This concept has been applied to Columbia spotted frogs. For his assessment of the influence of landscape structure, Pilliod (2001, p. 78) provides working definitions of source and sink habitat patches: source patches are breeding sites that contain 1-year-old juvenile frogs or breeding sites where 1-year-old frogs were found in adjacent habitats within 300 m; sink patches are breeding sites without 1-year-old juvenile frogs within 300 m, and all non-breeding habitats. Pilliod and Peterson (2001) regard lakes stocked with fish as probable sinks, where frogs only persist because of immigration. Reaser (2000) suggests that trout and excessive cattle grazing may cause some spotted frog breeding sites to operate as sinks in Nevada. She concludes that her study area in the Toiyabe Range, where drainages that formerly may have allowed for dispersal are now either stocked with fish or partially dry, is "at best a contracting metapopulation". Temporal and spatial variation in breeding success may be common, however, and multi-year mark-recapture studies are needed to better elucidate population dynamics (Reaser 2000).

Metapopulation models can be daunting due to their complexity and the amount of detailed information needed, including genetics and movements. However, whether or not spotted frog populations of Region 2 are organized as some type of metapopulation conforming to the models, knowledge of the spatial structure of populations is an important tool for conservation. For example, the loss of a source population (one that consistently produces recruits) due to management actions may have an irrevocable effect, but managers may assume mistakenly that the presence of frogs at other sites in the locale signifies that the loss of any single site is inconsequential. Furthermore, currently unoccupied habitat patches may be critically important for long-term persistence (Hanski 1998). Understanding the effects of spatial characteristics on the persistence of spotted frog populations in Region 2 is hampered by the lack of data about distribution and abundance. At the coarse scale, knowledge is needed about the distribution, number, and relative isolation of populations. At finer scales, information is needed about dispersal capabilities and conditions, movement barriers, and the frequency and causes of local population declines or extinctions.

Genetic concerns

Spotted frogs of the Bighorn National Forest have no possibility of genetic exchange with other populations due to the 100 km of dry and lower-elevation land extending between the Bighorn Range and the eastern margin of the main population's range in the Absaroka Mountains. Although identified as belonging to the Rocky Mountain clade, the Bighorn population is genetically distinct, separated by a few mutational steps from the nearest populations to the west (Bos and Sites 2001). This is thought to reflect a more recent separation from the main population than the separation among some of the Utah disjunct populations, which were likely fragmented from the main population during the Pleistocene (Bos and Sites 2001). Peripherally isolated populations may have retained or acquired types of variation not found elsewhere in the species; thus they can be important sources of evolutionary novelty or speciation potential (Bos and Sites 2001 and references therein).

Spotted frogs of the Shoshone National Forest are less likely to be genetically distinct given their much closer proximity to other spotted frogs populations within the Rocky Mountain clade (i.e., Yellowstone and the Tetons). However, no genetic samples were collected on the Shoshone National Forest for the investigation by Bos and Sites (2001). Given the small number of documented records for most of the Shoshone National Forest (**Figure 10**), it is possible that some populations are isolated (e.g., in northern, eastern, or southern portions of the Forest), which could allow them to diverge genetically.

Concerns about inbreeding and reduced heterozygosity from genetic isolation are infrequently expressed in recent amphibian decline literature (but were stressed by the Conservation Strategy for spotted frogs in Utah, see paragraph below). This apparently reflects the view that demographic factors, habitat problems, and various anthropogenic agents are much more likely to cause declines and extirpations than genetic factors, and/or the lack of data on the role of inbreeding depression in the extinction of natural populations in general (Sjogren 1991). Potentially, populations lose fitness and are more likely to go extinct when they are genetically isolated and become inbred. Reh and Seitz (1990) found that subpopulations of a ranid species (*Rana temporaria*) isolated by roads and railways had reduced heterozygosity and appeared to be highly inbred, noting that this genetic effect occurred within 30 years, or in about 10 to 12 frog generations. However, the investigators did not report any deleterious effects.

Maintaining genetic variability, such that populations can respond to changing environmental pressures while reducing the chance loss of genetic variability through drift, is considered central to the Conservation Strategy for spotted frogs in Utah (Perkins and Lentsch 1998). The Strategy thus has an emphasis on maintaining sufficient effective population size, or "the number of breeding individuals that contribute genes to the next generation" (Perkins and Lentsch 1998, p.

10) (Note: this is a highly simplified application of the term "effective population size", which is normally used by population biologists to refer to the size of the ideal population [i.e., not subject to natural selection, mutation, immigration, and other deterministic evolutionary forces] that would undergo the same amount of random genetic drift as the actual population [Lande and Barrowclough 1987]). The Conservation Strategy adopts 1000 as an acceptable effective population size within geographical management units. The empirical basis for this recommendation is lacking, however, and it is unclear whether deleterious genetic consequences of small populations are likely to be realized in spotted frogs.

*Matrix life history model**

A matrix model examining the intrinsic factors of population dynamics was developed to depict the most important or vulnerable points in the spotted frog life cycle. The model is illustrated in **Appendix A**. From the model's assessment of sensitivity (effect of changes in vital rates on population growth rate), we conclude that spotted frog populations are disproportionately susceptible to factors that affect survival to the end of their first year (i.e., from egg to the following breeding season) when compared to any other single life stage. This suggests that factors influencing survival of young are more important to manage than factors influencing the number of eggs. Moreover, the high sensitivity of population growth rate to changes in first-year survival is likely a good indication that in "good" years the response of the population will be largely determined by high survival resulting in a wave of new recruits.

In contrast, the elasticity analysis (sensitivity of population growth rate to proportional changes in the vital rates) emphasizes the importance of survival of later stages in the face of small proportional changes (+1 percent, -0.8 percent). Further, the peak female reproductive value occurs at life stage 5 (female breeders in their "on" year). In "normal" years, or years of decline, the high elasticity of population growth rate to changes in adult survival is likely the best guide to population dynamics.

Examining the effects of stochastic variation in vital rates suggested that altering the survival rates had a much more dramatic effect on population growth rate than did altering the fertilities. In fact, population growth rate was much more sensitive and elastic to variability in P_{21} alone (i.e., first-year survival) than it was to variability in the entire set of fertilities, F_i. These results suggest that populations of spotted frogs are relatively tolerant to stochastic fluctuations in production of eggs (for example, due to annual climatic change or to human disturbance), but they are extremely vulnerable to variations in the survival of adult stages.

Interpretation of the analysis (**Appendix A**), requires an evaluation of the different results from sensitivity analysis, elasticity analysis, and stochastic analysis. Based on these results, especially the analysis of stochasticity and elasticity analysis, we conclude that management of factors influencing survival, after the first year, may be most important in the conservation the Columbia spotted frog.

Community ecology

Envirograms, based on Andrewartha and Birch (1984), are provided for Columbia spotted frog larvae and post-metamorphic life stages in **Figure 14** and **Figure 15**, respectively. The envirogram is a graphic depiction of a species' community ecology (i.e., the elements of the environment that influence the survival and reproduction of an organism). It is comprised of a centrum and a web of branching chains. The centrum is the set of components that directly act on the animal and are the proximate causes of its condition: resources such as food and water, malentities (non-predatory hazards) that kill or harm the animal, predators (including disease organisms), and mates. The web depicts the elements and pathways that explain the existence of or influence the centrum's components, thus showing the distal causes of the animal's condition. Envirograms help to guide research questions and experimentation and are intended to provide a "plausible summary of the ecology of a species" (Andrewartha and Birch 1984, p. 19). We prepared two envirograms (for larvae and adult forms) because of the substantial differences between the conditions of these two life stages.

Predators and competitors

The most common predator of spotted frogs is probably the garter snake (*Thamnophis* sp.), which frequents areas in and near waters that are also inhabited by spotted frogs and tadpoles. Koch and Peterson (1995) report finding spotted frog tadpoles, juveniles, and adults in the stomachs of wandering garter snakes (*T. elegans vagrans*). Reaser (2000)

*This model was compiled by Dave McDonald and Takeshi Ise, with input by Doug Keinath and Matt McGee. The lead author was not associated with this effort except in a review capacity. Questions regarding the model should be directed to Dr. McDonald.

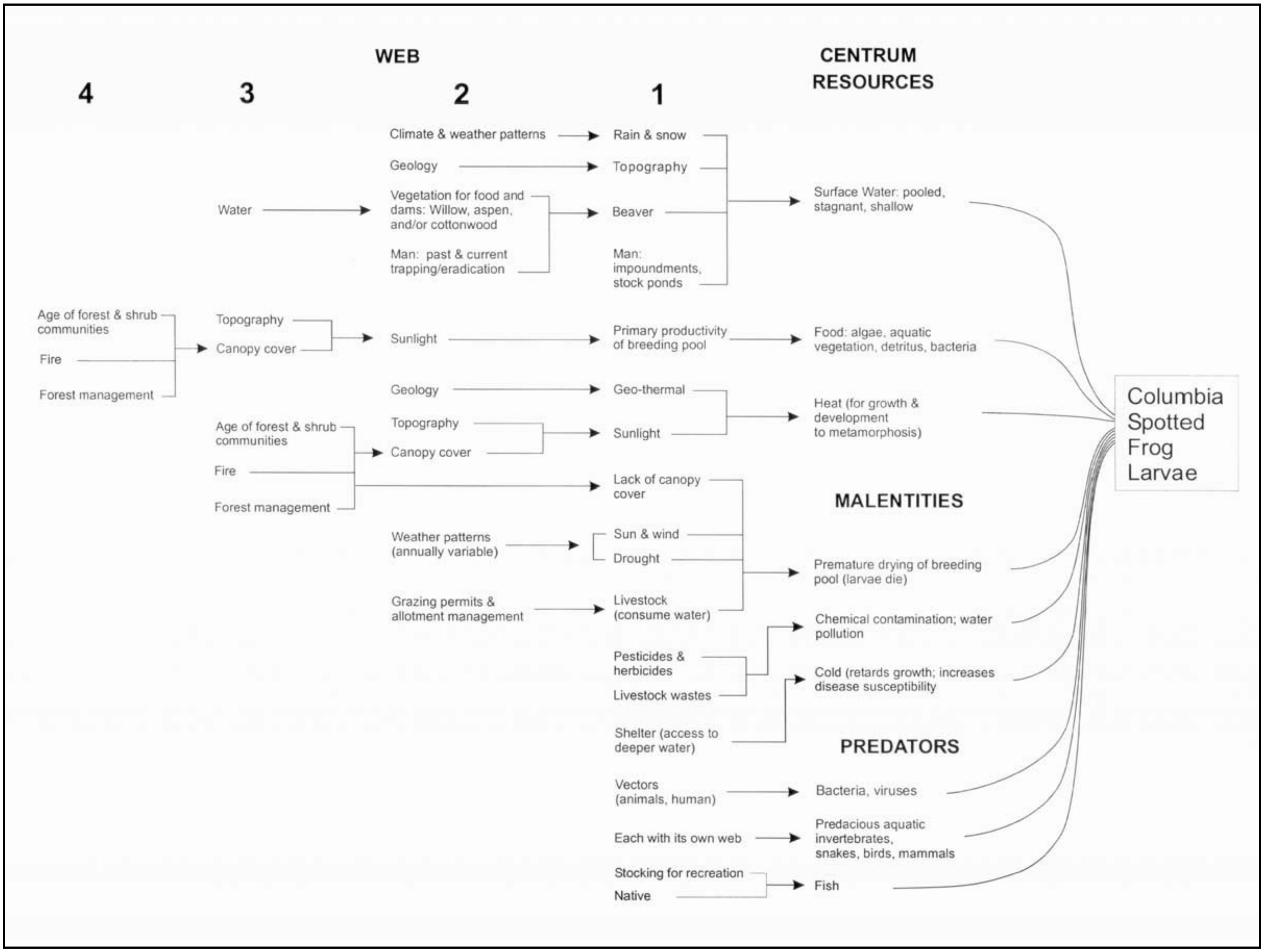

Figure 14. Envirogram (Andrewartha and Birch 1984) illustrating the ecological relationships of the larvae life stage of the Columbia spotted frog.

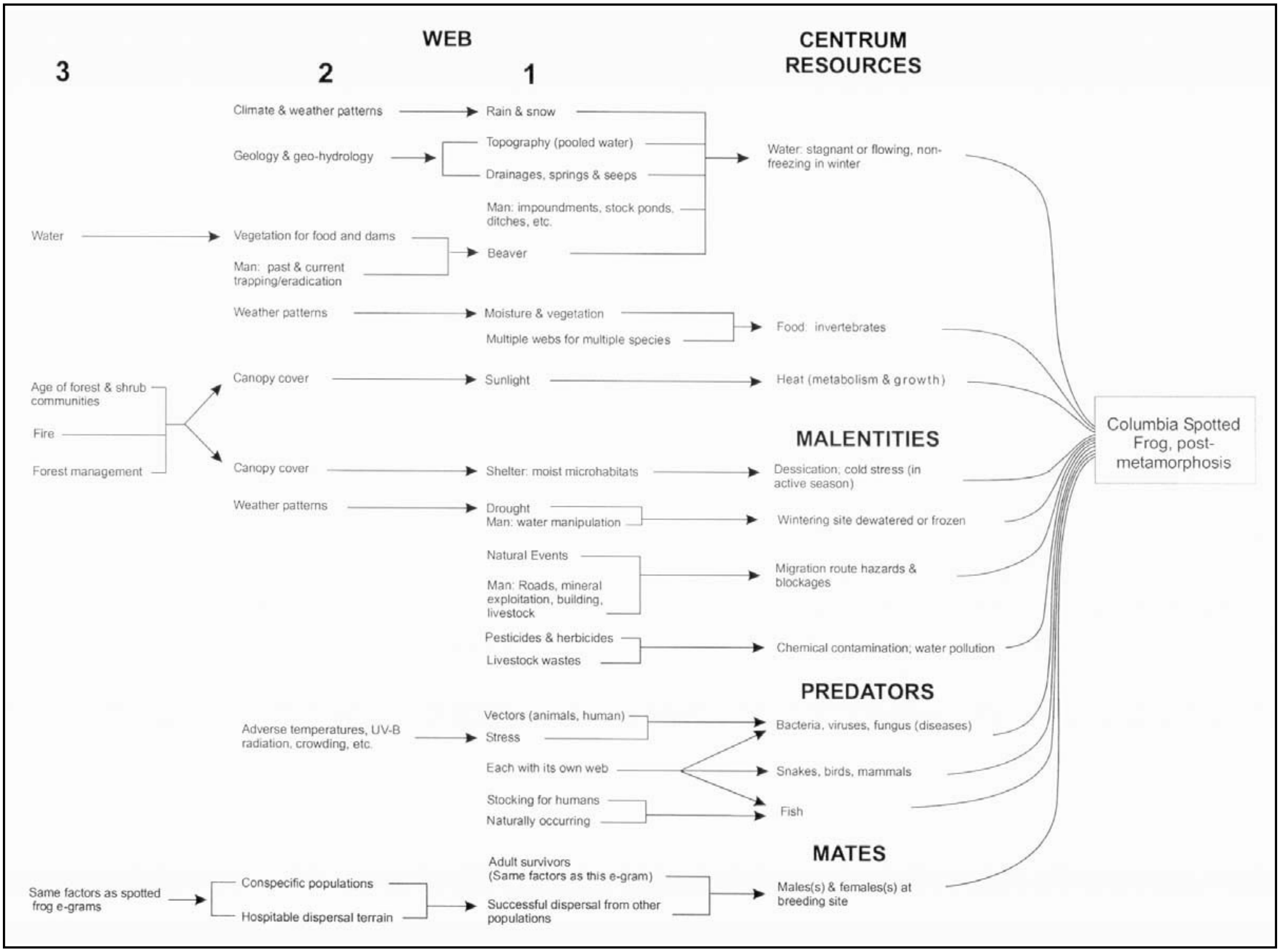

Figure 15. Envirogram (Andrewartha and Birch 1984) illustrating the ecological relationships of the adult life stage of the Columbia spotted frog.

asserts that garter snakes are a common cause of natural mortality in spotted frogs, with tadpoles and male frogs more likely to be consumed than adult females, due to their smaller size.

Amphibians, including spotted frogs, are less likely to exist or successfully breed in lakes with predatory fish. The embryonic and larval life stages of spotted frogs are particularly vulnerable to some fish species (Munger et al. 1997, Pilliod and Peterson 2000, Pilliod and Peterson 2001). In addition to the direct effects of predation, female amphibians avoid depositing eggs at sites with predatory fish (Pilliod and Peterson 2001).

Game fish populations (e.g., brook trout [*Salvelinus fontinalis*], cutthroat trout [*Oncorhynchus clarkii*], rainbow trout [*O. mykiss*], and carp [*Cyprinus carpio*]) introduced into naturally fishless waters can negatively affect amphibian populations and are a recent topic of concern among amphibian biologists (see discussion in the Threats section of this report) (Pilliod and Peterson 2001, Reaser and Pilliod 2005). Introduced predatory fish are capable of affecting the abundance and distribution of spotted frogs, as well as the long-term persistence of populations in montane basins where source populations are extirpated or key wintering habitat is occupied by fish (Pilliod and Peterson 2001).

A large variety of other animals also prey on spotted frogs. Tadpoles and metamorphosing young are preyed on by some aquatic insects, particularly dystiscid (diving) beetle larvae, and by adult amphibians, including con-specifics (Pilliod 1999) and tiger salamanders (*Ambystoma tigrinum*). Many avian species prey on spotted frogs, including herons and cranes, gulls, waterfowl, hawks and owls, ravens and other corvids (Turner 1960, Koch and Peterson 1995, Pilliod 2002, Reaser and Pilliod 2005). Some smaller birds, such as blackbirds and robins, consume spotted frog tadpoles; Turner (1960) surmised that predation on tadpoles could only affect population levels if metamorphosis occurred coincident with desiccation of breeding pools. A number of mammals are known or thought to be predators of spotted frogs, including badgers (*Taxidea taxus)*, weasels (*Mustela* sp.), minks (*M. vison*), and river otters (*Lutra canadensis*) (Koch and Peterson 1995, Roberts 1997, Pilliod 2001), and bears (*Ursus* sp.) and coyotes (*Canis latrans*) (Turner 1960). Another potential mammalian predator, the raccoon, appears to be invading formerly uninhabited areas in northwestern Wyoming (e.g., Jackson Hole and Yellowstone National Park).

Among the large number and variety of potential predators, only introduced predatory fish have been identified as capable of reducing the abundance and distribution of spotted frogs. There appears to be no information available on how predation by native wildlife, including garter snakes, affects spotted frog demographics and habitat use. On the other hand, investigators frequently point out that amphibians are an important part of the food web, providing energy transfer from invertebrates to predatory animals higher in the food chain and possibly influencing their occurrence or abundance (e.g., Koch and Peterson 1995, Stebbins and Cohen 1995, Reaser 2000). Frog populations may lack vulnerability to native predators because these predators are generalists that also feed on many other small-bodied organisms in the habitats occupied by frogs, coupled with low rates of energy expenditure for bodily maintenance by amphibians relative to other vertebrates (i.e., they can remain inactive for long periods when danger is present), and a suite of effective predator-defense mechanisms (Stebbins and Cohen 1995).

The primary defenses of spotted frogs to predation are to remain motionless and concealed whether on land or in water, to dive into water from the banks or edges of streams and ponds, and to sink below the water surface (Patla and Peterson 1997, Reaser and Pilliod 2005). Tadpoles swim to deeper water or hide within aquatic vegetation when startled at the shallow water edges of breeding pools. Behavioral responses of spotted frogs are apparently affected by the presence of certain predators. For example, in lakes with predatory fish, frogs encountered and startled by humans are more likely to return immediately to shore than in fishless lakes (Reaser and Pilliod 2005). Spotted frogs may thrash wildly and sometimes scream when caught by predators (Reaser and Pilliod 2005). Adults and juveniles produce a mild skin toxin; researchers observe a milky or frothy exudate on frightened, captured frogs and experience dry and irritated skin from frequent handling of spotted frogs, suggesting that the excretion is also an irritant to predators (Reaser and Pilliod 2005, D. Patla personal observation).

Little is known about competition between spotted frogs and other amphibians. Reaser and Pilliod (2005) report that there is little evidence that other species of native amphibians compete for habitat with spotted frogs. Theoretically, spotted frog tadpoles compete with the larvae of other amphibians present in the breeding pools, with the intensity of competition depending on resource (food and space) abundance and the degree of preferred resource overlap (Alford 1999).

Investigations of tadpole interactions (of species other than spotted frogs) found that both interference and exploitation competition occur, and that competition is lesser within groups of siblings than within groups of unrelated tadpoles (Alford 1999). Amphibians that potentially co-occur with spotted frogs in Region 2 include tiger salamanders, boreal toads, boreal chorus frogs (*Pseudacris maculata*), northern leopard frogs, and wood frogs. In Yellowstone and Grand Teton national parks, spotted frogs frequently inhabit sites that are also occupied by chorus frogs, tiger salamanders, and boreal toads (Patla and Peterson unpublished data). Differences in over-wintering strategies and habitats and the flexibility that spotted frogs exhibit in use of foraging habitats suggest that competition, if it occurs, would be most likely at breeding sites shared with other amphibian species. Dunlap (1977) speculated that competition between wood frogs and spotted frogs would be limited by ecological differences in breeding dates and habitat use between the two species.

One study investigated possible competition between spotted frogs and leopard frogs. Dumas (1964) conducted an experiment in northeastern Oregon, in an area where spotted frogs and leopard frogs co-occurred but were found breeding mostly in separate ponds. He seined two ponds of all tadpoles and placed 200 spotted frog tadpoles and 200 leopard frog tadpoles together in each of the two ponds. Seining the ponds nine weeks later, he found much higher apparent mortality rates in spotted frog tadpoles (74 to 81 percent) than in leopard frog tadpoles (53 to 57 percent), compared to 56 percent mortality of spotted frog tadpoles in a pond without leopard frog tadpoles. Furthermore, when he returned to the area three years later, nearly all of the spotted frogs were gone while leopard frogs and their larvae were numerous. The author speculated that spotted frogs could be sensitive to growth-inhibiting factors released by leopard frog tadpoles, and that leopard frogs can replace spotted frogs due to this differential mortality combined with leopard frogs' greater dispersal rates and greater tolerance of high temperatures and low humidity. However, it is unlikely that leopard frogs are currently replacing spotted frogs, given the small area of range overlap and the widespread declines of leopard frogs throughout much of their western range (Stebbins and Cohen 1995, Weller and Green 1997).

Parasites

Factors influencing the occurrence of internal parasites and the vulnerability of spotted frogs to parasitism have not been identified. Reaser and Pilliod (2005) summarized findings on parasitism in Columbia spotted frogs, listing a large variety of organisms known to parasitize the lungs and other internal organs. Spotted frog specimens collected in Yellowstone National Park in the 1950s hosted helminthic parasites including nematodes and lung flukes, with the heaviest infections occurring in large adult frogs (Turner 1958b). Spotted frog specimens collected in Yellowstone National Park in 1994 and 2000-2002 were diagnosed as hosting a variety of protozoan, myxozoan, and helminthic parasites in the blood, kidneys, bladder, and intestines; none of these were considered to be serious or pathological (Green 1996 and 2004). Similarly, Dumas (1964) found heavy internal parasite infestations in some spotted frogs but said the parasites appeared to be generally benign in their effects.

Intestinal trematodes (flukes) can be serious because they may cause anemia and secondary infections in frog hosts (Green 1996). Infection by trematodes (genus *Ribeiroia*) also causes deformities in frogs, particularly in the limbs and digits (Johnson et al. 2002). *Ribeiroia* has a complex life cycle, parasitizing snails as the first host and tadpoles as the second intermediate host. In tadpoles, trematodes form cyst-like metacercaria that interfere with a developing limb bud and cause deformities that become apparent as the tadpole metamorphoses. Recent investigations link *Ribeiroia* prevalence to the eutrophication of frog breeding ponds, which is often caused by an excess of nutrients from farms or intensive cattle operations (Johnson and Chase 2004). Spotted frogs in northern Idaho were found to host trematodes (14 to 51 percent of 59 frogs collected from five ponds), with large adult frogs hosting the largest infections (Russell and Wallace 1992 as reported in Reaser and Pilliod 2005). Low rates of infection by trematodes (*R. ondatrae*) and few individuals with limb deformities were reported by Johnson et al. (2002) in Columbia spotted frogs from southwestern Idaho. Encysted metacercaria (immature flukes, family Diplostomatidae) caused swelling and ulceration in the tail bud area of nearly all the recently metamorphosed spotted frogs at a site in Yellowstone National Park in 2003 (Patla and Peterson 2004); abnormally few juveniles and young-of-the-year were present the following year, suggesting that the parasitism may have lethal and on-going effects (D. Patla unpublished data).

Another common parasite is the leach, which sometimes occurs at great densities in ponds occupied by spotted frogs. Leaches have been found clinging to larval, juvenile, and adult spotted frogs, and they may also prey on eggs (Carpenter 1953, Licht 1969a, Reaser and Pilliod 2005, D. Patla personal observation).

Leaches may be also vectors of blood-borne diseases in amphibians (Green 1996).

Disease

Amphibian diseases have been linked to bacterial, fungal, and viral agents. Many diseases or afflictions go undiagnosed. For example, Reaser and Pilliod (2005) report a "wasting disease" of spotted frogs from Nevada and central Idaho, with symptoms of emaciation, lesions of the skin and eyes, ulcerations of the toes and tarsus, and prolapsed bladder; the cause is unknown. Of particular concern to amphibian researchers are two emerging infectious diseases: chytridiomycosis and ranavirus, both of which have been documented in species of the genus *Rana* (Daszak et al. 1999).

Chytridiomycosis is caused by a microscopic, parasitic fungus (*Batrachochytrium dendrobatidis*) that attacks the keratin in the skin of metamorphosed amphibians. This disease is thought to pose a serious threat to wild amphibians. Declines attributed to it have been documented in Australia, Panama, and Rocky Mountain National Park (Carey et al. 2003). Chytrid fungus was confirmed in sickly Columbia spotted frogs at a pond in the Owyhees of southwestern Idaho in 2001 (Munger et al. 2002), indicating that *Rana luteiventris* is a host species (Green 2001). Chytrid disease is also known to be present in northwestern Wyoming; it was diagnosed on dead and sick boreal toads in Jackson Hole in 2000 (Patla 2000b), and on dead spotted frogs from two locations in Yellowstone National Park in 2001 and 2002 (Green 2004). Further discussion of this disease is provided in the Threats section of this report.

Recent research suggests that ranavirus complex is an emergent amphibian pathogen, meaning that it recently evolved, has recently expanded in geographic range or host species, or has been newly introduced to areas with previously unexposed populations (Collins 2003). Ranavirus has also been identified in spotted frogs collected at six sites in Yellowstone National Park, including both larval and adult specimens. This disease is usually associated with mass mortality events of larval populations, but a die-off of adult spotted frogs attributed to ranavirus was documented along a stream in Yellowstone National Park in 2002 (Green 2004). The deaths of some adult spotted frogs in Grand Teton National Park in 2004 may also be attributed to ranavirus (S. Wolff personal communication 2004).

The fungus *Saprolegnia ferax* has been associated with embryonic die-offs of amphibian populations in the Cascade Mountains of Oregon. The disease it causes (Saprolegniasis) is common in fish, especially those reared in hatcheries, and transferable from fish to frogs (Kiesecker et al. 2001a). An ongoing investigation of spotted frog eggs in Idaho and Montana found *S. ferax* and other members of the water mold order Saprolegniales to be common (Pilliod et al. unpublished data). The saprophytic vs. parasitic nature of these water molds and the source of these organisms (possibly carried by hatchery fish) is uncertain. The interaction of disease with habitat conditions was demonstrated by a study that found that reduction in water depth due to global climate change (El Niño and oscillation cycles warming the Pacific and altering precipitation levels) caused greater exposure of embryos to harmful UV-B radiation, making them more susceptible to Saprolegnia infections (Kiesecker et al. 2001b).

Although concern about diseases is high and an increasing number of disease-killed specimens have been collected in northwest Wyoming in recent years, relatively little is known about disease types and disease prevalence in wild Columbia spotted frogs. The USGS National Wildlife Health Center is investigating submitted specimens from sites where two or more dead amphibians are found. Results of these pathological exams, several field studies in progress under the auspices of USGS (Amphibian Research and Monitoring Initiative), and graduate student research projects investigating amphibian disease are likely to result in much useful information in the coming years.

Interactions

Frogs are important components in native ecosystems, providing transfer of invertebrate energy (e.g., invertebrates) to predators further up the food web. As ectothermic animals, amphibians are very efficient in converting food into biomass (Stebbins and Cohen 1995). Unique among vertebrates due to their biphasic life cycle, amphibians also serve to transfer the high primary productivity of ponds to the terrestrial environment, as herbivorous larvae metamorphose, emerge, and disperse away from ponds, where they can be consumed by other animals. Tadpole grazing of algae and other aquatic vegetation may have important effects on the aquatic ecosystem and its inhabitants. Tadpoles can alter algal species composition and influence nutrient cycling; tadpole feces may be an important source of organic matter for detritivores of many taxa (Alford 1999). A wide variety of parasites (see above) infect frogs and their larvae as hosts. Mutualistic relationships among spotted frogs and other organisms have not been identified. Beavers provide important benefits for spotted frogs by creating, improving, and enhancing habitat. This is a commensal relationship, as beavers receive no apparent benefit from frogs.

Conservation

Threats

Anthropogenic and natural threats

Biologists have identified multiple factors that threaten amphibians and contribute to population declines, including habitat loss and modification, habitat fragmentation, disease, acid precipitation, chemical contaminants, exposure to high levels of UV-B radiation, adverse climate and weather patterns, exploitation for human uses (food, pets, research), and introduced predators and competitors (Corn 2000, Mattoon 2001). Most of these factors have direct anthropogenic sources. Natural causes of declines may be exacerbated by human-caused environmental perturbations. For example, the effects of naturally-caused drought or floods may be magnified by water diversions or watershed disturbances. Chemical exposure may render animals more susceptible to predators or naturally occurring disease organisms. As discussed below in the section on Intrinsic vulnerability, some characteristics of amphibian biology and ecology (and of spotted frogs in particular) render them particularly sensitive to such environmental changes (Stebbins and Cohen 1995).

Management actions and natural events that appear most likely to threaten spotted frogs of Region 2 are listed and prioritized in **Table 3**. Prioritization (severity of threats) was assigned with the following considerations: (1) spotted frogs in Region 2 exist as a small, isolated population on the Bighorn National Forest and possibly on portions of the Shoshone National Forest, rendering them more vulnerable than spotted frogs in areas where populations are widespread and numerous; (2) areas occupied by spotted frogs in Region 2 are relatively far from large urban centers and agricultural areas, lessening the potential for large-scale habitat conversion, and agrochemical or pesticide exposure. Several authors have investigated and summarized threats to Columbia spotted frogs (Gomez 1994, Perkins and Lentsch 1998, Maxell 2000, Munger et al. 2002, U.S. Fish and Wildlife Service 2002), and this existing work formed the basis for this assessment of threats, adjusted as considered necessary for Region 2.

Habitat effects (**Table 3**) are considered in terms of loss, degradation, and fragmentation. "Loss" refers to destruction of breeding, foraging, and wintering habitat components, or changes that render these areas permanently uninhabitable by spotted frogs. "Degradation" refers to changes in habitat components that cause them to be less suitable for frogs (in terms of frog growth, survival, and reproduction), or that reduce the size of habitat components. "Fragmentation" refers to the increased separation of frog habitat components due to movement barriers or uninhabitable conditions. This can occur at two scales: (1) among or between breeding, foraging, and wintering sites used by a local group of frogs; (2) among or between subpopulations and suitable habitat patches in a region, preventing interchange between subpopulations and/or the colonization of unoccupied habitat.

Direct effects are considered in terms of factors that can cause spotted frog mortality. Mass mortality is most likely to occur when frogs are congregated, such as at breeding and wintering sites or when metamorphs are emerging en masse from breeding ponds and dispersing to wintering sites.

Threats considered to be most significant for spotted frogs in Region 2 are discussed below, including a general description of the problems that the threat poses for amphibians and their habitat, and information (if any) about how these threats may affect spotted frogs. The topical sections on threats are followed by a brief summary about these threats with regards to spotted frogs in Region 2.

Drought and climate change

Periods of drought are natural events that can threaten amphibians by reducing survival and reproduction rates. The decreases in size and connectivity of local populations associated with drought increase the likelihood of local extirpations and long-term effects on a regional population. Droughts also exacerbate the threats to spotted frogs from livestock grazing, water manipulation, loss of beaver ponds, roads, reservoir and recreation development, disease, and introduced fish (Munger et al. 2002). Drought has been identified as a contributing factor to spotted frog declines in Nevada (Turner 1962a), southeastern Oregon and possibly southwestern Idaho (Munger et al. 2002).

Because climate so strongly influences the survival and reproductive success of amphibians, climate change is consistently cited as one of the main potential causes of amphibian population declines (e.g., Alford and Richards 1999, Matoon 2001). It was

Table 3. Potential threats to Columbia spotted frogs and their habitat in USDA Forest Service Region 2. Severity of potential threat is rated on a scale of 1 to 3, with 1 most severe.

Threat	Severity of threat in R2	Rationale	Habitat effects (loss, degradation, or fragmentation)	Direct effects (sources of mortality)
Disease	1	Potential for rapid population decline if diseases are introduced	N/A	Die-offs
Drought	1	Effects could be exacerbated by human activities and land use	Degradation, fragmentation	Reduced reproduction and survival rates
Road construction and improvements	1	New roads, widened roads, or increased traffic could affect populations, particularly if populations are small and vulnerable	Loss (wetland fill), degradation (run-off, noise), and fragmentation	Roadkill
Introduction of non-native fish	1	Successfully introduced (or repeated introductions of) predatory fish can reduce or eliminate frog populations	Loss (frogs may avoid stocked areas), fragmentation	Predation, introduction of diseases
Heavy livestock use of occupied frog habitat	1	Local impacts on small populations could be severe, especially during drought. Potential impacts may be mitigated through management	Degradation of wetland and moist habitats and water quality	Trampling, desiccation at sites of extreme vegetation loss
Water manipulation: diversions, dams, spring development	1	Existing and future water projects probably not evaluated for their impacts on frogs	Loss, degradation, and fragmentation	Dewatering of breeding and wintering sites leading to mass mortality
Wildfire and prescribed fire	2	Fire suppression; timing of prescribed fire may alter habitat	Degradation, fragmentation	Heat and exposure, chemicals in fire retardants, potential mechanical damage to wetlands.
Timber harvest and hazard fuel reduction	2	Threat minimized if environmental effects of logging on microhabitats are assessed and mitigated	Degradation, fragmentation	Crushing, desiccation
Eradication of beaver	2	Cumulative losses of breeding and wintering habitat	Loss, degradation	Loss of mechanism for wetland maintenance
Contaminants (pesticides, herbicides)	2 (?)	What chemicals are applied in R2? Are forests subject to chemical drift from other areas?	Reduced or contaminated prey	Lethal and sub-lethal effects
Oil and gas development, mining	2	Surface disturbance, hydrological effects, contamination	Loss, degradation, fragmentation	Crushing by equipment, exposure to toxicants
Recreation	2	Will environmental effects of developments and recreation use be assessed and mitigated?	Loss, degradation, and fragmentation	Crushing by vehicles, disease introduction, capture and handling
Ultraviolet radiation	3	Spotted frogs not very vulnerable	N/A	N/A
Human utilization (collection)	3	Probably unlikely to occur at significant levels	N/A	Collection for pet trade, food, bait, scientific uses

cited as one of two likely factors contributing to global amphibian population declines in areas where habitat remains intact (the other factor was disease) (Stuart et al. 2004). Normal variation in weather patterns and minor shifts in climate do not represent a threat to amphibians, but climate changes could be occurring at a rate faster than to which amphibians can adjust phenotypically (Ovaska 1997). Understanding the magnitude of the climate change threat for amphibians is complicated by regional differences as well as the many uncertainties about the combined effects of warming and the shifts in precipitation patterns, which are difficult to predict. The indirect and subtle effects of climate change (such as multiple and interacting changes in habitat and the biotic community) may have a significant but hard-to-measure impact on amphibians (Ovaksa 1997, Corn 2000, AmphibiaWeb 2003). While changes in temperature patterns and the amount and seasonality of precipitation likely affect the distribution and abundance of amphibians (Boone et al. 2003), demonstrating that such changes affect population size is difficult (McCarty 2001, Boone et al. 2003). Frog populations of some areas may benefit from climate change; for example, Ovaska's (1997) assessment of vulnerability found that many amphibian species in Canada may not only tolerate predicted climate changes, some species that are currently limited by low temperatures and a short growing season (e.g., high elevations) could experience benefits that exceed costs (Ovaska 1997).

In the western United States, temperatures have increased 0.8 ºC since the 1950s (Service 2004). In response to these rising temperatures, snowpack and snow water equivalents in the western mountain ranges have declined (15 to 30 percent in the northern Rockies), and snow is melting earlier in the spring. Temperatures are forecast to rise between 2º and 7 ºC in the western United States in the next century, and snowpack in the Rockies is expected to decline by 30 percent (Service 2004). Forecasts for trends in precipitation are highly uncertain since climate models produce disparate results (Service 2004). However, warming alone will produce large hydrological changes, as western snowpacks melt sooner and are lost to earlier runoff.

Direct effects on spotted frogs in Region 2 stemming from climate change may include earlier reproduction and more rapid development of larvae (beneficial if this results in higher recruitment), decreased mobility due to hotter and drier conditions (probably adverse, especially where frogs must migrate to winter habitats), and shorter hibernation periods (beneficial if growth/survival are enhanced). Earlier breeding and an extended growing season could boost reproductive output where breeding sites remain flooded but could also have adverse consequences for adults subjected to drier conditions at foraging and wintering sites. Reproductive failures could become more common with climate warming for two reasons: (1) high summer temperatures result in increased evaporation rates, with ponds drying up prior to metamorphosis; and (2) frogs may breed early in response to warm spring temperatures, with subsequent episodes of cold weather and freezing resulting in high egg mortality. Climate changes may also cause frogs to experience increased physiological stress and decreased immune system function, leading to disease outbreaks. Corn (2003) hypothesized that montane amphibian populations at lower elevations will show changes in phenology before those at higher elevations, because high elevation sites retain snow longer.

Disease

As discussed above (Parasites and disease section), native amphibians are hosts to a variety of parasitic, bacterial, viral, and fungal diseases. Concern about amphibian disease has escalated sharply in the past few years with the recognition that new or previously unknown diseases are causing amphibian die-offs and population declines around the world. A recent global assessment of amphibians found unprecedented levels of "enigmatic decline" (decline not due to habitat loss) of amphibian species relative to other kinds of wildlife, with diseases and climate change cited as the most likely causes (Stuart et al. 2004). Mass deaths of amphibians due to disease outbreaks in diverse geographic locations (including the Rocky Mountains) suggest that disease may be an important factor in population declines (Daszak et al. 1999, Livo 2000, Mattoon 2001). Mass mortality events involving the genus *Rana* are reported to have started in the 1970s in the mountains of the western U.S. (Carey 2000).

Chytridiomycosis (in particular) and ranavirus are emergent, contagious diseases that are most frequently cited as posing a threat to amphibian populations. Both of these diseases have been found in Columbia spotted frog populations and other native amphibians of northwestern Wyoming (see Parasites and disease section). David Earl Green, the USGS pathologist who first diagnosed the presence of the amphibian pathogen chytrid fungus (*Batrachochytrium dendrobatidis*) in Jackson Hole, WY, warned that the finding had potentially dire implications for all species of frogs and toads in western Wyoming, given the virulence of the disease and the apparent inability of affected populations to recover (Patla 2000b). He reiterated his concern based on additional occurrences of chytrid disease 2000-2002 in Yellowstone National Park, stating that some adult spotted frogs may survive with chytrid infections for months or years while other individuals die immediately (Green 2004). Ranaviral infections have also been found in spotted frogs in Yellowstone, co-occurring with chytrid disease at two locations. At one of these locations, the largest die-off of adult spotted frogs (>20 dead frogs discovered) documented in northwestern Wyoming occurred over a number of weeks in summer, with ranavirus suspected as the immediate cause of death for most individuals (Green 2004).

These occurrences of lethal amphibian diseases in northwestern Wyoming suggest that spotted frog populations of the Shoshone and Bighorn national forests are at risk, particularly where populations are small and recolonization via immigration after a die-off is unlikely due to isolation. While amphibian researchers working in the national parks are vigilant in following biosafety measures (disinfecting waders and field equipment), other potential vectors for disease are numerous: waterfowl, wildlife, livestock, amphibians dispersing from infected sites, the use of these amphibians as bait, and the footwear and boats of anglers and other recreationists. The potentially interacting roles of new pathogens, environmental stressors, and the failure of amphibian immune responses are under investigation but remain poorly understood (Carey et al. 1999, Carey et al. 2003). Unless spotted frog sites are monitored and dead or diseased animals are collected and submitted to an expert for analysis, a catastrophic disease outbreak among spotted frogs in Region 2 is unlikely to be detected or recognized.

Grazing

Livestock grazing can pose a variety of problems for amphibians (Maxell 2000). Applied research on this topic is scant, and documentation of impacts is primarily anecdotal (Monti 2003). Direct mortality due to trampling has been observed, and in one published account this amounted to the death of thousands of recently metamorphosed toads (Bartelt 1998, Maxell 2000). For the most part, however, the effects of livestock grazing are indirect and relate to adverse changes in water quality and the condition of plants and soils (Munger et al. 2002). The effect of wild ungulates has not been identified as a concern in the amphibian habitat and conservation literature, probably because wild grazers typically occur at much lower densities than domestic stock (except under conditions imposed by management, e.g., see remarks below concerning the National Elk Refuge) and are less prone to congregate in wetland or riparian areas in spring and summer.

Livestock waste contributes to nitrogen pollution of water bodies. Eutrophic conditions can lead to increased numbers of snails hosting the type of parasites that cause amphibian malformations (Johnson et al. 1999, Johnson and Chase 2004). Veterinary products released into ponds and streams by the urine and manure of livestock may negatively affect amphibian health and survival (Bishop et al. 2003).

Grazing can have long-term negative effects on amphibian habitat due to changes in the composition and structure of vegetation, resulting in the reduction of willows, rushes, and sedges that otherwise stabilize the banks of water bodies (Munger et al. 2002). Intensive browsing by wild ungulates can also result in the degradation and loss of woody plants, such as the cottonwood, willow, aspen, and associated shrub communities of the National Elk Refuge in Jackson Hole, Wyoming, with subsequent probable declines in the quality of amphibian habitat (Smith et al. 2004). Alteration of riparian vegetation by livestock is considered by some researchers as an important factor in the decline of ranid frogs in Califorinia (Jennings 1988, cited in Corn 1994). The extirpation of beaver populations in heavily browsed areas compounds the negative effects on amphibians (Smith et al. 2004; see section on beaver eradication, below).

Other negative effects from grazing include changes in bank structure, such as the collapse of overhanging banks that shelter amphibians in both summer and winter; and in soil compaction, resulting in loss of burrows that also provide shelter for amphibians. Changes in hydrology from long-term grazing can result in channel down-cutting and lowered water tables, resulting in less pooled surface water for amphibians (Maxell 2000 and sources therein; Munger et al. 2002).

Grazing may also have beneficial effects for amphibians, including the opening of basking areas, an increase in larval food resources due to eutrophication, and creation of habitat through water impounded for livestock (Maxell 2000 and sources therein). Retaining vegetation in early successional stages through livestock grazing may benefit some species of amphibians (Monti 2003).

All the available summaries of threats faced by spotted frogs list livestock grazing as a major concern (Gomez 1994; Perkins and Lentsch 1998; Maxell 2000;

USFWS 2002; Munger et al. 2002). Spotted frogs of all life stages can be negatively affected by factors including trampling, water quality degradation, water reduction (particularly at sites with tadpoles), prey reduction and microhabitat loss due to vegetation removal, and reduced availability of over-wintering sites where cattle trample spring openings and stream banks or cause reduced oxygen content of water (Munger et al. 2002). Where cattle make extensive, prolonged use of riparian and other moist areas used by spotted frogs, there is potential for substantial impact (Munger et al. 2002). Cattle are most often mentioned as a threat to spotted frog habitat, but pastured horses can also adversely affect pond and stream habitat (Patla 1997) (**Figure 16**). Site-specific effects depend on and vary with the timing, duration, and intensity of grazing.

Bull and Hayes (2000) reported no negative effects on Columbia spotted frog reproduction and recruitment from beef cattle grazing in northeastern Oregon, but the study did not consider grazing intensity and timing, and it possibly confounded the effects of cattle and elevation (Munger et al. 2002). Considerable caution is needed in trying to interpret results of grazing studies conducted in different habitat types (Munger et al. 2002).

Figure 16. A spotted frog breeding pool in Yellowstone National Park, showing premature drying, and trampling due to horses. This is one of the breeding sites identified by Fred Turner's spotted frog research in the 1950s (Turner 1960). The pond was fenced after this photo was taken to exclude horses and protect the site. Fencing allows the pool to last longer and retain vegetation, and it provides safety for the emerging metamorphs from trampling. (D. Patla, Idaho State University.)

Water manipulation

Because of their dependence on aquatic sites, amphibians are highly vulnerable to projects that remove water (e.g., diversions for agriculture or developments), move water, or store water (e.g., spring development for livestock). Given that historic water rights have precedence over wildlife issues or in-stream flow requirements, amphibians and their habitat are unlikely to receive consideration and are particularly vulnerable in drought years.

As mentioned previously (Parasites and disease section), reductions in water depth (resulting from diversions or other water manipulations) may lead to greater exposure to UV-B radiation and higher susceptibility to disease (Kiesecker et al. 2001b).

Breeding and wintering habitat of spotted frogs can be lost or degraded by water diversions. Spring excavation and development (such as with pipes, boxes, and troughs) can make over-wintering sites unusable or inaccessible, or trap frogs that are seeking passage into underground springs (Munger et al. 2002). Ponds formed by spring development may benefit frogs in some situations, but may also cause adverse changes in hydrology or cause frogs to be concentrated in smaller areas (Munger et al. 2002). Water impoundments can have a variety of negative effects:

- ❖ deep-water flooding of desirable shallow-water habitat
- ❖ fluctuations in water levels that destroy eggs and larvae
- ❖ lower water temperatures
- ❖ increased numbers of predators (those that prefer more permanent water bodies versus ephemeral water bodies)
- ❖ increased livestock and native ungulate presence
- ❖ concentrated waterfowl causing water quality degradation and loss of wetland vegetation (Maxell 2000).

The consequences of specific proposals should be evaluated in the context of the site specific alterations expected from the management.

Roads

Amphibians can be killed as they attempt to disperse or migrate across roads. Mortality rates can be high; a recent literature review of the effects of roads on amphibians (Jochimsen et al. 2004) lists numerous cases documenting scores to hundreds of frogs and toads killed during a single night on road sections. The chance of an amphibian safely crossing a road is related to traffic volume, and mortality can be particularly high when amphibian activity patterns, such as spring or fall migrations, coincide with heavy traffic.

Indirect effects of roads include habitat loss (e.g., wetland fill), multiple kinds of habitat degradation (including changes in hydrology and surface features, pollution from water runoff and exhaust, lights, noise), and habitat fragmentation. The adverse ecological effects of roads (on soils, water, and the biotic community) extend outward from the road edge for 100 m or more, based on quantitative studies investigating the "road-effect zone" (Jochimsen et al. 2004 and sources therein). Road maintenance activities (e.g., chemicals applied for dust control, melting ice, and weed eradication) also may adversely affect amphibians and their habitat.

Fragmenting natural habitats, roads can impede amphibian movements, and:

- ❖ alter amphibian behavior and movement patterns, causing disruption of breeding activities and migration (examples and sources in Jochimsen et al. 2004)
- ❖ prevent individuals from reaching habitat components needed for breeding, foraging, and over-wintering
- ❖ reduce the chance of colonization of unoccupied or new habitats, and a higher risk of local extirpation
- ❖ isolate populations from each other, resulting in lower chances of successful interchange of individuals and a higher risk of local extirpation (Vos and Chardon 1998).

Direct mortality, indirect habitat effects, habitat fragmentation, and population isolation probably have cumulative, adverse effects on roadside amphibian populations. Reduced anuran density and population abundance (Fahrig et al.1995; Carr & Fahrig 2001), lower probabilities of occurrence (Vos & Chardon 1998), and reduction in genetic polymorphism and heterozygosity (Reh & Seitz 1990) have been attributed to roads. However, long-term, site-specific studies of how roads affect local amphibian populations are rare.

A study of Columbia spotted frogs in Yellowstone National Park documented a population decline of approximately 80 percent between the 1950s (when the population was initially studied) and the 1990s, declining from about 1500 frogs to 300 frogs. Road construction was identified as one of the most likely causes of the local decline (Patla 1997, Patla and Peterson 1999, Patla and Peterson in prep). The road, which was constructed during the interval between the two studies, separated a breeding site from an over-wintering habitat. Thirty years after road construction occurred, the frog population was concentrated in habitat areas clustered on one side of the road, and the migration pattern documented in the 1950s across the area subsequently bisected by the new road was nearly abandoned. Spotted frogs ceased to attempt breeding at the pond nearest the road after 1994, suggesting, as other researchers have noted, that the negative effects of roads on species occurrence may take decades to realize (Patla 1997, Findlay and Bourdages 2000). Munger et al. (2002) summarize threats of roads posed to Columbia spotted frogs as direct habitat loss, disturbance of habitat areas near roads from construction activities, pollution from run-off, and habitat fragmentation.

Introduced fish

Introduced fish species have been documented as the cause of local declines of amphibian populations worldwide (Bradford 1989, Bradford et al. 1993, Bronmark and Endenhamn 1994, Brana et al. 1996, Hecnar and M'Closkey 1997, Knapp and Matthews 2000). Estimates suggest that 95 percent of mountain lakes in the western United States were naturally fishless (Bahls 1992). Therefore, the introduction of game fish (e.g., salmonids) likely caused a significant change in amphibian habitat quality and population distributions during the last century. All life stages of amphibians are subject to predation by introduced fishes (Licht 1969a, Semlitsch and Gibbons 1988, Liss and Larson 1991). Indirect effects of predation include adult avoidance of egg deposition sites where predators are present (Resetarits and Wilbur 1989, Hopey and Petranka 1994), decreased larval foraging and growth rates as a result of staying in refuges to avoid predators (Figiel and Semlitsch 1990, Skelly 1992, Kiesecker and Blaustein 1998, Tyler et al. 1998), and decreased adult foraging, growth rates, and over-winter survival as a result of avoiding areas with fishes (Bradford et al. 1983).

Columbia spotted frogs are palatable to fish; tadpoles and metamorphs of this species have been found in trout stomachs (Pilliod 2001). Spotted frog populations are negatively affected by introduced predatory fish (Munger et al. 1997, Monello and Wright 1999, Pilliod and Peterson 2000 and 2001, Munger et al. 2002). A study of Columbia spotted frogs and fish stocking in the mountains of central Idaho found that the abundance of spotted frogs at all life stages was significantly lower in lakes with fish than in fishless sites, even when accounting for differences in habitat (Pilliod and Peterson 2001). In comparing frog populations among mountain basins with varying amounts of fish and fishless habitat, the authors found that densities of older life stages (>1 year old) of frogs decreased with increases in proportion of habitat occupied by trout, suggesting lower frog survival in basins lacking sufficient deep, fishless habitat. Tadpole survival, juvenile recruitment, and frog abundance were lower in heavily stocked basins compared to basins with less habitat occupied by trout. The authors of this study also observed that deep-water, fishless sites allowed the highest over-winter survival of frogs. They postulated that the majority of high-quality over-wintering habitat had been lost due to fish introductions and warned that this loss, coupled with six to eight years of reproductive failures (as shown in the age structure), could result in the imminent disappearance of spotted frogs from some of the fish-dominated mountain basins.

Fire

Wildfire and prescribed fire can act directly (e.g., fire-related mortality) or indirectly (e.g., habitat alterations) to have positive and negative impacts on amphibians. A recent literature review of the effects of fire and fuels management on amphibians and their aquatic habitats found that amphibian responses to fire and the associated habitat changes are species-specific, incompletely understood, and variable among habitats and regions (Pilliod et al. 2003). Studies involving various ranid species revealed a large variety of fire effects, including some cases of direct mortality. An important indirect and negative effect of fire is the elimination of cover through the combustion of woody debris, litter, and duff, where amphibians normally find moist retreats. Such a loss of microhabitat could result in physiological stress, elevated predation rates, reduced foraging and dispersal capabilities, and changes to prey species dynamics. The habitat effects of fire can be long term; in the slow-growing conifer forests (e.g. in the Rocky Mountains), large woody debris takes many decades to replace and the recruitment of down woody debris may not peak for as many as 80 years after a fire (Bragg et al. 2000). On the other hand, fires can benefit amphibians by increasing the amount of solar radiation that reaches the ground or water, by enhancing nutrient cycling and aquatic productivity, and by increasing the amounts of standing surface water and ephemeral water-providing habitat (Pilliod et al. 2003).

Understanding how fire affects amphibian populations in western forests is complicated by the dynamic nature of fire across the landscape; severity and scale are determined by many factors including management activities, forest structure and composition, and prior fire history. For example, livestock grazing can affect forest fire intensity and frequency by removing understory grasses and sedges that would otherwise compete with conifer seedlings (resulting in dense tree recruitment and vulnerability to fires), and by reducing the fine fuels that would otherwise carry low-intensity fires and prevent the buildup of fuels (Belsky and Blumenthal 1997). Grazing can also result in an increase in annual, fire-prone grasses such as cheatgrass (*Bromus tectorum*) (Munger et al. 2002). Decades of fire suppression and forest disease outbreaks may contribute to catastrophic fire events. Studies investigating fire effects on amphibians across the range of burn severities are needed (Pilliod et al. 2003).

Wildland and prescribed fires can have different effects on amphibians because of differences in timing. Wildfires are most common when conditions are at their driest, and amphibians are likely to inhabit areas close to water. Prescribed fires, often implemented in spring or late fall when conditions are moist, may catch amphibians during active periods of breeding or migrating when they would be more vulnerable to fire-related mortality (Pilliod et al. 2003). As prescribed fire plans are devised, knowledge of the phenology of amphibian populations can aid in evaluating potential positive and negative impacts.

Efforts to suppress forest fires can have detrimental effects on amphibians. The application of fire retardant and suppressant chemicals may pose a risk for amphibians due to the formation of ammonium compounds that are toxic or hazardous to aquatic life (Pilliod et al. 2003). Sodium ferrocyanide, an ingredient of fire retardants and suppressants used to inhibit equipment corrosion, oxidizes in the presence of natural solar ultraviolet radiation and releases cyanide. It is known to be highly toxic to fish and amphibians (including leopard frogs) at very dilute concentrations, particularly with exposure to sunlight (Little and Calfee 2000). Also, byproducts of fire-retardant foams and cyanide can bioaccumulate in amphibian prey and in the bodies of amphibian larvae (Pilliod et al. 2003).

Another potential threat to amphibians is the firebreaks constructed by firefighters and bulldozers, which could damage sites used by frogs for breeding, foraging, over-wintering, or migrating. Ruts and ditches created by firebreak construction can fill with water and attract amphibians, where they can be tempted to breed unsuccessfully or be crushed by vehicles. New routes constructed for fire fighting can have some of the negative effects discussed above under Roads.No studies are available on the effects of fire on Columbia spotted frogs and their habitat in Region 2. The potential for extensive wildfires (and strenuous efforts to suppress them) in the spotted frog's range in Region 2 is indicated by extensive mortality of conifers on the Shoshone National Forest (USDA Forest Service 2000), and prolonged drought in northwestern Wyoming. Amphibian inventory results in Yellowstone National Park suggest that the 1988 fires were not a catastrophe for this species; the Columbia spotted frog is the most widely distributed amphibian in the Park, present in wetlands of all 19 randomly-selected catchments (sub-watersheds) that were surveyed 2000 to 2003 (Patla and Peterson 2004). However, we lack sufficient data to know if population declines occurred after the 1988 fires, or if burned areas now show differences in occupancy related to post-fire effects. Whether fires will benefit or harm spotted frogs in Region 2 is a complex question, depending on temporal scale evaluated, the particular characteristics of the affected watersheds (e.g., vegetation, topography, and hydrology), characteristics of the fire events (e.g., intensity, patchiness, and timing), and the abundance and distribution of spotted frog breeding populations. Given the isolation and restricted distribution of spotted frogs on the Bighorn National Forest, locally severe fires and intensive fire-fighting activities could pose a particular threat for the population.

Timber harvest

Similar to fire, the effects of timber management on amphibians are variable. The potential for negative effects from timber removal and other forest management activities depends on the methods used, as well as the spatial extent, location, and timing of projects. A thorough review of forest management and amphibian ecology (deMaynadier and Hunter 1995) found that clearcut harvesting has negative short-term impacts on local amphibian populations as evidenced by declines in abundance, but the long-term effects relating to forest succession are variable. Site preparation practices (e.g., stump removal, roller chopping, prescribed fire, herbicide application, and/or machine planting) largely determine how severe the impacts of timber harvest activities are to amphibian microhabitats. Amphibians are adversely affected where harvested stands lose residual structural components and suffer reductions in the abundance and distribution of microhabitat features including uncompacted litter, coarse woody debris of various sizes and ages, and patches of canopy shade (deMaynadier and Hunter 1995). Temporary pools and ponds can be adversely affected by logging practices that alter soil and water temperature, pond evaporation rates, volume and rate of import of leaf and woody material, and local topography and water-holding capacity, or that disrupt migration routes surrounding the pool (deMaynadier and Hunter 1995).

Mechanical fuel reduction and forest thinning projects to prevent or reduce potential wildfires are increasingly being implemented in western forests, but no studies are available assessing the direct effects of these practices on amphibians (Pilliod et al. 2003). As in timber harvest, the severity of impacts (negative and positive) to frogs from thinning and fuel reduction most strongly relate to how much microhabitat remains following treatment, and how the treatment influences local hydrology. Areas managed to remain sanitized of potential fuel (such as in urban interface zones) could be degraded in terms of frog habitat if cool, moist shelter zones are lost, if forest wetlands and migration routes are negatively affected, or if stands become drier and colder due to more air circulation. Given the slow growth of trees in the mountains of northern Region 2 and the slow rate of coarse woody debris production, these detrimental site-specific effects could be long term.

No studies of Columbia spotted frog responses to forest management have been conducted. Timber harvest has not been noted by other assessments as a threat to the species, probably because spotted frog populations of concern in southwestern Idaho, Utah, and Nevada do not occur in areas with marketable or wildfire-prone conifer forests. At a long-term spotted frog monitoring study site in Yellowstone National Park, hazard fuel reduction activities in 1999 resulted in surface area disturbance (e.g., skid road, log skidding and piling, slash piles and burning of piles, removal of coarse woody debris) around a breeding pool and within a migration corridor between the breeding and wintering site. This lead to concerns about possible frog mortality, disruption of late-summer migration, and habitat degradation (Patla 1999). The number of juveniles in the population (indicating recruitment from the previous one to three years) plummeted after 2000 (2001 through 2003), but it is difficult to separate the possibly interacting effects of drought and habitat disturbances (Patla and Peterson 2004).

Beaver reduction or eradication

Beavers play important roles in creating, maintaining, and enhancing habitats used by frogs. Through dam construction, beavers create breeding habitat (ponded water); elevate water tables, which leads to enhanced riparian vegetation; and reduce stream flow velocity, which leads to more frog habitat along stream edges. Stored water behind dams is available as habitat for frogs during droughts when isolated and temporary ponds dry up. Also, dams provide wintering sites for spotted frogs.

Olson and Hubert (1994) estimate that beavers occupy approximately one third of their original range in Wyoming (reported in Munger et al. 2002). Past and current beaver trapping/removal has led to vast reductions in the numbers and distribution of beaver. Also, elk and livestock grazing can reduce willows to the point that beavers become extirpated due to lack of food and building materials for dams and lodges (Smith et al. 2004).

Munger et al. (2002) state that loss of beaver in Idaho likely caused a substantial decrease in breeding and hibernating habitat available for Columbia spotted frogs. Dam repair and beaver reintroduction at a site in southwestern Idaho, where spotted frogs had declined, rapidly led to increased numbers of spotted frogs and re-establishment of frog breeding in the subsequent year (Munger et al. 2002).

The severity of beaver eradication and the effects of current beaver harvest levels in portions of Region 2 inhabited by spotted frogs are unknown. Potentially, protection and reintroduction of beavers could mitigate for threats posed by management activities or natural events.

Pesticides, herbicides, and environmental contaminants

Amphibians are exposed to chemical hazards through direct uptake from water or by ingestion of contaminants in soils, sediments, and food items (Sparling et al. 2000). They are thought to be highly vulnerable to contaminants because of their permeable skin and because their occupation of both terrestrial and aquatic environments may expose them to many kinds of chemicals that are either locally applied or introduced from elsewhere.

Wetlands and ponds occupied by amphibians can accumulate pollutants from the surrounding lands, including pesticides, herbicides, fertilizers, and animal wastes. Aquatic habitats may also be contaminated by wastewater and unintended releases of sewage, fuels, solvents and other chemicals used for maintenance or construction, and heavy metals (e.g., lead, zinc, and cadmium) that may be washed into drainages from mine operations (Lefcort et al. 1998). Some chemicals can have detrimental effects long after they are used. Russel et al. (1995) detected toxic levels of DDT in tissues of spring peepers *(Pseudacris crucifer*) at Point Pelee National Park, Ontario even though DDT had not been used in the area for 26 years. Thus, early stages (eggs and larvae) of pond-breeding amphibians, which are critical in development, may be exposed to various combinations of harmful contaminants. Tadpoles in particular are at risk given their habit of feeding off both the substrate and algae, and their processing of water for respiration (Lefcort et al. 1998).

While there is little evidence that contaminants have caused range-wide declines of widely distributed amphibian species (Corn 2000 and references therein), there is increasing evidence of a variety of effects that could lead to declines of local populations. Many insecticides, fungicides, herbicides, and piscicides contain active and inactive ingredients that are either directly lethal (Harfenist et al. 1989, Sparling et al. 2000) or have a variety of sub-lethal effects (Corn 2000). While they have not been investigated in standard toxicity, sub-lethal effects that are of increasing interest to biologists include depressed disease resistance and compromised immune systems, inhibition of growth and development, decreased reproduction, decreased thermal tolerance, inhibition of predator avoidance behaviors, and morphological abnormalities (Johnson and Prine 1976, Cooke 1981, Hall and Henry 1992, Berrill et al. 1993, Berrill et al. 1994, Boyer and Grue 1995, Carey and Bryant 1995, Lefcort et al. 1998, Sparling et al. 2000). Toxins can bioaccumulate in insects and become concentrated in the bodies of frogs. Furthermore, some man-made chemicals (e.g., DDT compounds, PCBs, synthetic steroids) interact with cell receptors or block intercellular communication, working to break down, mimic, or interfere with naturally occurring hormones and the endocrine system (Stebbins and Cohen 1995, Crump 2001). These endocrine effects can be severe given the crucial role that hormones play in development and reproduction. For amphibians, skewed sex ratios, hermaphroditism, malformations, and accelerated rates of metamorphosis have been associated with endocrine-disrupting chemicals (Crump 2001). A recent study found that the widespread herbicide Atrazine causes gonadal abnormalities (feminization) of male leopard frogs, and that most water sources in the United States, including rain, have more Atrazine than the doses found to affect frogs in laboratory studies (Hayes et al. 2002).

Airborne dispersal of contaminants far from their source has been postulated as an important contributing factor to amphibian declines in protected areas of the western United States (Stebbins and Cohen 1995, Drost and Fellers 1996). The decline patterns of the California red-legged frog (*Rana aurora*) appear to be related to the amount of upwind agriculture (Davidson et al. 2001). Sparling et al. (2001) found that frogs in Yosemite and Sequoia national parks and at sites near Lake Tahoe had detectable concentrations of pesticides (chlorpyrifos, diazinon, endosulfans, and DDTs) and depressed ChE indicating exposure to organophosphates pesticides.

Chemical pest eradication treatments may affect prey availability and frog survival. Of particular concern are malathion applications that target wetland areas to reduce mosquito populations but also kill many other kinds of insects. Piscicides such as rotenone are very toxic to aquatic invertebrates (Wilson and McCranie 1994) and thus have the potential to negatively affect frogs by reducing prey populations.

Information specific to spotted frogs and chemicals is limited. Concerns about mosquito control spraying programs as a potential threat to spotted frogs in Utah were expressed by Perkins and Lentsch (1998), who reported that no studies had been conducted to evaluate the effects of chemical toxins on the spotted frog or its environment in Utah. Mortality of spotted frogs at a pond in Oregon due to DDT application was documented by Kirk (1988). DDT in solvent and fuel oil was applied over 173,000 ha of forest in Oregon, Washington, and Idaho for control of the Douglas-fir tussock moth in June 1974, 20 dead frogs were found around the pond three weeks later. In Idaho, Lefcort et al (1998) found detrimental effects from heavy metals on Columbia spotted frog tadpole growth, development, and survival to metamorphosis, plus reduced avoidance behavior in the presence of a predator (rainbow trout).

Because of their unique physiology and life histories (e.g., permeable skin and protracted development in aquatic environment), amphibians may be unusually susceptible to toxicants, and environmental guidelines developed from fish and invertebrates are not likely to provide sufficient protection (Burkhart et al. 2003). According to a memo from Region 1 of USFS (Ulmer 2001), when analyzing the potential effects to amphibian populations of proposed herbicide/pesticide treatments managers should consider the decomposition rate of the toxicant, its sublethal effects, and the timing of the proposed application. Because chemical applications on USFS lands can have more severe effects on frogs than land managers may realize, they should also consider the following:

1) chemicals intended for and applied to upland areas can be transported into aquatic systems

2) chemicals can interact in complex and unknown ways to increase their toxicity

3) many chemicals approved for use have not been tested on amphibians and may pose higher risks than known or that are listed on the label.

Oil/Gas development and mining

Potential threats to amphibians and their habitat from oil/gas development and mineral extraction have not been formally assessed, to our knowledge. Threats from minerals management to the boreal toad were identified by the Boreal Toad Recovery Team (Loeffler 2001) and probably also apply to spotted frogs. These threats include environmental contaminants produced by tailings, released groundwater, mining/transport accidents, acid drainage, and leaching of additional metals from stream and soil substrates. Contaminated settling ponds can be used by toads (and presumably by frogs), exposing them to accumulated heavy metals, some of which (e.g., copper) are acutely toxic to tadpoles (Loeffler 2001). Lefcourt et al. (1998) describe the dramatic impact of heavy metals on the terrestrial and aquatic environment in northern Idaho, where soils, rivers, and lakes have high levels of metals. They report that "only remnant, nonrecruiting populations of anurans" occur in the upper reaches of the contaminated Silver Valley.

Lefcourt et al. (1998) tested the effects of heavy metals (i.e., lead, zinc, cadmium, and combinations) on spotted frog tadpoles and found that they reduced the survival, growth, and fright response of tadpoles. Munger et al. (2002) reported that high elevation historic mining habitat near Silver City in southwestern Idaho was not found to support spotted frogs although the area was well within the species' range. As pointed out by the Boreal Toad Recovery Plan, the construction of roads and buildings associated with mineral activities can cause direct loss of amphibian habitat, and have indirect effects such as pond/stream sedimentation, reduced food availability, and topographic disturbances (e.g., subsidence) (Loeffler 2001). The effects of oil/gas development on amphibians can be assumed to be detrimental to spotted frogs to the extent that habitat is lost or degraded, including aquatic/wetland habitat used for breeding and over-wintering, and terrestrial habitats used for foraging and migration. One unknown effect is the extent to which mineral extraction activities create potential habitat (e.g., ponds) and the risks or benefits of such created habitat. Also unknown is the extent to which restoration activities following mineral exploration and development benefit or harm spotted frogs.

Recreation

Recreation has been cited as a potentially significant threat to boreal toads in the southern Rocky Mountains (Loeffler 2001). Presumably, similar recreation-related problems threaten spotted frogs. These threats come from multiple dispersed and concentrated uses in frog habitat (e.g., hiking, biking, off-road vehicles, camping) and result in the destruction of riparian areas, the trampling and crushing of frogs by feet and vehicles, stream bank degradation, fecal contamination, and the spread of pathogens (Loeffler 2001). Recreationists visiting aquatic sites for fishing or boating can potentially transport amphibian diseases among sites on vehicles and waders. Development of recreation sites can threaten amphibians and their habitat, depending on location. For example, a parking lot could separate breeding and over-wintering sites, fragmenting habitat and leading to increased mortality of migrating frogs. Maxell (2000) stated that amphibian populations in or near recreation facilities are at risk due to handling and killing by humans and by their pets. Some predators of amphibians (e.g., ravens, raccoons, skunks, foxes, coyotes) inhabit human-influence areas in high numbers due to food sources or the absence of larger predators. Ravens were observed depredating 20 percent of the western toads gathered at a breeding site near a recreation facility in Oregon (Olson 1989). Artificial night lighting around facilities may disrupt breeding and foraging (Buchanan 1993)

Other potential threats

Introduced American bullfrogs (*Rana catesbeiana*) (native to eastern and central North America) have been implicated in declines of native frogs, including *R. pretiosa* west of the Cascades in Oregon and elsewhere in the Pacific Northwest, and several other ranid species (Dumas 1966, Nussbaum et al. 1983, Corn 1994). Bullfrogs can negatively affect native amphibians via predation and competition (particularly predator-naïve native amphibians in the tadpole stage), or by transmitting pathogens (Kiesecker and Blaustein 1997). Bullfrogs occur in Wyoming, but usually at lower elevations than spotted frogs. One exception is a long-established bullfrog population in a warm spring in Jackson Hole (1,980 m elevation) (Koch and Peterson 1995), indicating that this species can survive at high elevations under certain, unusual conditions. Although naturally warm waters and waters warmed due to land uses could host bullfrogs, the potential for bullfrogs surviving and spreading into spotted frog habitats of Region 2 forests appears to be low at this time given that bullfrogs have not been found in Yellowstone National Park or on the B-TNF. Any reported occurrence of bullfrogs in the vicinity of the Shoshone and Bighorn national forests warrants attention.

Some researchers consider ultra-violet (UV) radiation (especially UV-B) and its interactions with contaminants, climate, and disease to be of great concern for amphibian populations (Corn and Muths 2004). However, some researchers argue that although UV-B levels are increasing at higher latitudes (Herman et al. 1999 cited in Boone et al. 2003), amphibians have a suite of natural defenses against damage from UV-B (Froglog 2004). Exposure to UV-B radiation (increased due to atmospheric pollution) does not appear to be a direct threat to Columbia spotted frogs, based on research indicating that this species has high levels of photolyase enzyme activity, which allows for repair and resistance to solar radiation in embryos. Eggs and developing embryos were not affected by ambient levels of UV-B in field experiments (Blaustein et al. 1999). The authors concluded that resistance to UV-B evolved under strong selection pressure, given the species' habit of depositing egg masses in shallow, sunlit water where they are only partially submerged. Despite the lack of direct threat, continuing research on UV-B effects may yet reveal threats to spotted frogs. UV-B/chemical interaction is thought likely to be a contributing factor to amphibian declines at many locations, because of the way in which UV-B breaks down chemicals in the environment (sometimes producing more toxic substances) as well as its ability to affect the sensitivity of exposed animals (Carey et al. 2001, Burkhart et al. 2003).

Acid precipitation has not been identified as a problem for spotted frogs by other assessments. Acid deposition is said to be unlikely to be involved in population declines of amphibians at high elevations in the Rocky Mountains or the Sierra Nevada (reviewed in Alford and Richards 1999).

Specific Region 2 locations

Shoshone National Forest: Determination of how the threats listed above may have altered spotted frog distribution and abundance and frog habitat on the Shoshone National Forest can only be speculative at this time given the paucity of available information on spotted frogs. Human or management activities that may negatively affect spotted frogs and their habitat on the Shoshone National Forest include all the above listed threats, particularly road building (e.g., highway along the North Fork Shoshone, forest roads to access timber), fish stocking in naturally fishless lakes and streams, timber management, livestock grazing, and oil and gas exploration/development. Natural events that may affect spotted frogs include drought, wildfire, and range expansion of predators such as raccoons. Also, the occurrence of amphibian disease and mortality events elsewhere in northwestern Wyoming suggests a high likelihood for spotted frog populations of the Shoshone National Forest to be affected eventually, if not currently, by the diseases chytridiomycosis and ranavirus.

Bighorn National Forest: Given the small population size, limited distribution, and isolation of spotted frogs on the Bighorn National Forest, this population is more vulnerable to the threats from ongoing management activities listed above, particularly recreation, cattle grazing, and fish stocking. Of the three known spotted frog breeding sites on this forest, two were reported to be heavily impacted by cattle grazing, and the third was impacted by recreation (i.e., dogs and children) (Golden 2001). One breeding/foraging site was stocked with fish likely to prey on frogs (i.e., cutthroat, rainbow, and brown trout) (H. Golden personal communication 2002). Roads and traffic may be affecting the frogs in terms of elevated mortality and habitat fragmentation; frogs at one breeding site are known to cross the highway to reach a summer foraging area (H. Golden personal communication 2002). Natural events that may affect spotted frogs are the same as those listed for the Shoshone National Forest: drought, wildfire, and range expansion by predators, with the potential importance of these threats magnified by the small population size and its isolation. Given the vulnerability of the Bighorn National Forest population, disease outbreaks are also of particular concern. Spotted frog wintering sites have not been identified for this population. Human or natural events negatively affecting the suitability of wintering sites (e.g., dewatered springs), or disturbing the sites while frogs are congregated, could have a devastating effect on this small population.

Conservation Status of the Columbia Spotted Frog in Region 2

Abundance and distribution trends

Information is insufficient to determine if Columbia spotted frogs are declining in Region 2 (see Distribution and abundance and Population trends sections of this report). Survey, monitoring, and research efforts for spotted frogs on National Forest System lands in Region 2 lag behind efforts on federal lands in other portions of the species' range, such as the national parks and refuges of Montana and northwestern Wyoming, BLM lands in southwestern Idaho, and national forests in Idaho (Munger et al. 2002, Patla and Peterson 2004). This lack of attention from agencies and researchers is at odds with the biological importance and vulnerability of spotted frog populations in Region 2. Spotted frogs on the Bighorn National Forest are geographically isolated and genetically distinct (Dunlap 1977, Bos and Sites 2001), and they exist (based on available information) as a few, small breeding populations within a restricted area. The Bighorn spotted frog population appears to represent a distinct biological unit similar in importance to the Wasatch Front, West Desert, or Great Basin populations, which were considered for listing under the Endangered Species Act in 1993 (see Federal Endangered Species Act section of this report). Spotted frogs of the Shoshone National Forest do not constitute a disjunct population, and their status is less vulnerable due to the existence of populations to the west in Yellowstone and Grand Teton national parks and portions of the B-TNF. However, their position on the edge of the core range of the species identifies them as important; it is here that range contractions or expansions might be evident and provide important insights about changes in the status of this species (Green 1997).

Habitat trends

Large portions of Wyoming have experienced several years of drought, beginning sporadically in the late 1990s and increasing in extent and severity (National Oceanic and Atmospheric Administration 2003). During the summers of 2000 – 2002, nearly every county in Wyoming experienced severe to extreme drought conditions. Such prolonged and severe drought conditions likely reduced the number and quality of breeding, foraging, and wintering sites for amphibians in Wyoming, but monitoring efforts prior to and during this time are insufficient to corroborate this anecdotal assessment. Given that drought effects can be exacerbated by land uses (see Threats section), habitat quality has potentially suffered a substantial decline in recent years. Site-specific information from occupied and previously occupied areas is needed to determine actual declines in frog habitat.

Human or forest management activities may be affecting the quantity and quality of suitable spotted frog habitat in Region 2. As discussed in the Threats section of this report, a number of activities commonly occurring on National Forest System lands may negatively affect amphibians. These include livestock grazing, water manipulation, roads, game fish introductions, beaver eradication, timber management, chemical use, oil/gas and mineral extraction, and recreation development and activities. A common thread among these activities is their potential for eliminating, reducing, or degrading ponds, lakes, wetlands (including temporary wetlands), and springs. In addition, these activities may negatively impact the terrestrial zones that spotted frogs occupy in summer or migrate through in spring or late summer. Furthermore, human activities may result in the isolation of populations and prevent the interchanges necessary to sustain populations across the region.

To determine if the anthropogenic and natural factors listed above (or other factors) have resulted in spotted frog habitat trends in Region 2, assessment by interdisciplinary specialists (e.g., biologist, hydrologist, geologist, GIS expert, silviculturist, plant ecologist, climatologist) of landscape and biotic characteristics (e.g., geological and hydrological processes, hydrological features, vegetation types, fish distribution) is necessary.

Intrinsic vulnerability

Amphibians have a suite of characteristics that might make them more sensitive to environmental changes than other major groups of vertebrates. Their complex life cycle requires both aquatic and terrestrial habitats. They have strong fidelity to breeding and wintering sites and naturally fragmented distributions. Some characteristics make them unusually sensitive to air and water contaminants, such as skin that is permeable to gases and liquids, shell-less eggs, feeding habits that expose them to pesticides and other chemicals accumulated in ponds and in the bodies of insect prey, and dependence on sequestered fat reserves during hibernation or aestivation (Stebbins and Cohen

1995). The complex process of metamorphosis renders them particularly vulnerable to hormone mimics or chemicals that interfere with hormones. Species that bask in sunlight or use clear, shallow waters for breeding may be vulnerable to the harmful effects of increased ultraviolet light levels.

Columbia spotted frogs are further vulnerable to disturbance and stochastic environmental fluctuations leading to population declines due to their dependence on specific habitat patches for survival and reproduction, and demographic factors including high variability in annual recruitment rates, long time period to reach reproductive age (four years in males and five to six years in females for some populations), tendency of females to breed every other year or less, and the likelihood that some populations act as "sinks", sustaining annual or intermittent breeding efforts but producing few if any recruits. Other characteristics that make spotted frogs vulnerable to declines are their attractiveness as prey for a large number of animals, and the potential for mass mortality due to disease outbreaks or habitat catastrophes when frogs are congregated at breeding or wintering sites. Exceptionally high rates of dispersal by juveniles suggests that isolation of populations through habitat fragmentation (e.g., roads, clear-cutting, and urbanization) may increase local extinction rates (Funk et al. 2005). In the event of repeated reproductive failures (which may be common in the highly variable conditions of mountain environments), high levels of adult mortality (or simply reaching the limits of longevity) will lead to local population extinctions within a decade or much shorter time frame if recolonization cannot occur. While spotted frogs have demonstrated an ability to travel long distances (e.g., 6 km), some historical or current populations may be beyond the range of "rescue" in the mountainous landscapes of Region 2, with natural isolation exacerbated by human-caused habitat fragmentation, drought, and non-native fish introduction.

Within the life history pattern of the spotted frog, there are several stages when the frogs are most vulnerable. At wintering sites, frogs may congregate in large numbers, rendering the population vulnerable to catastrophic decline if conditions become unsuitable or if an outbreak of infectious disease occurs. Adults also congregate at breeding sites soon after snowmelt, where they are vulnerable to predation, infectious diseases, or other causes of mass mortality. Eggs are deposited communally, and thus an entire year's reproductive effort can be lost if water levels decline before the eggs hatch or if eggs become infected with a parasitic fungus. Tadpoles are confined within the aquatic breeding site, and premature drying of the breeding pool can lead to complete mortality of a tadpole cohort. Furthermore, pollution, crowding, food depletion, and predation at the breeding pool can greatly reduce or eliminate the larval population. Emerging metamorphs are highly vulnerable to a variety of factors and must migrate to suitable wintering sites in mid or late summer. Juvenile and adult frogs also must migrate from foraging to winter habitat in many situations, exposing themselves to multiple dangers, such as terrestrial predators or road crossings. Life history modeling (**Appendix A**) indicates that spotted frogs are relatively tolerant to stochastic fluctuations in production of eggs but extremely vulnerable to variations in survival, particularly in the long, five-year pre-reproductive phase.

Paradoxically, many of the vulnerabilities cited above also relate to factors explaining the success of amphibians as a stunningly diverse, ancient (in existence for at least 360 million years), and widespread class of vertebrates exploiting an extremely wide range of habitats (Halliday and Adler 1986). As ectothermal vertebrates, they have a number of physiological advantages; for example, they require low rates of energy for metabolism, can withstand long periods of inactivity when conditions are hostile or resources are minimal, and are highly efficient in converting food into growth. The ability to reproduce explosively when conditions are favorable allows populations to increase dramatically and thus withstand periods of decline. Nevertheless, the recent finding that amphibians are more threatened and declining more rapidly than birds and mammals (Stuart et al. 2004) suggests that characteristics contributing to amphibian success are inadequate for the challenges posed by recent environmental changes including habitat loss and fragmentation, climate change, the unprecedented spread of new diseases, and pollution.

Management of the Columbia Spotted Frog in Region 2

Conservation elements and management approaches

Although spotted frogs occur on only a small portion of National Forest Lands in Region 2, their status and fate in there has important implications in the context of amphibian population declines in North America. Loss of the Bighorn National Forest spotted frog population, should it occur, would represent a significant reduction in the distribution of the northern population of Columbia spotted frog and a change in the historical range of spotted frogs in North America. Changes in the spatial distribution and abundance of spotted frog breeding populations on the Shoshone National Forest could indicate how the northern population is faring at the southeastern edge of its range; is the occupied range expanding or contracting? The answer to this question would be of interest to the scientific community and an important guide to the management of spotted frogs and their habitat within Region 2 and adjacent areas (e.g., B-TNF in Region 4 USFS).

Conservation elements for this species are outlined below. These elements are presented as approaches to consider and are not meant to represent specific recommendations although the concise presentation may appear otherwise. The previous section on Threats provides the ecological and biological foundation for the management approaches listed here. These approaches are those that have been used or suggested for conservation management of spotted frogs in other areas or described by the scientific literature.

1. Distribution of breeding populations. Documentation of occupied habitat can serve as the basis for monitoring, and provides the basic information necessary to target management (see Inventory and monitoring section below).

2. Critical habitats and sites
    a. Assign priorities to populations or areas for protection and monitoring (Munger et al. 1997).
    b. Determine the location of breeding sites and potential breeding sites, foraging areas, over-wintering sites, and movement corridors at high-priority sites; evaluate each in light of current management context (Pilliod et al. 2002).
    c. Protect permanent ponds and river and stream habitat within 500 m of breeding ponds from pollution, structural damage, significant vegetation removal, and water depletion (Bull and Hayes 2001).
    d. Identify and protect critical terrestrial habitats (e.g., movement zones, seasonally wet areas that are not identified as "wetlands") as well as breeding sites (Marsh and Trenham 2001, Pilliod et al. 2002).

3. Habitat protection and maintenance
    a. Conduct surveys prior to any activities that could significantly impact spotted frog habitat (Munger et al. 1997); when loss or deterioration of breeding, foraging, wintering, or migration habitat is unavoidable, devise and implement mitigation measures (Maxell 2000).
    b. Manage livestock allotments
        i. Fence critical breeding, foraging, and over-wintering habitat (e.g., ponds, springs, riparian areas) and movement corridors between breeding and wintering sites (Patla 1997, Perkins and Lentsch 1998, Maxell 2000, Engle 2001, Munger et al. 2002); where fencing is not feasible, enforce utilization levels that maintain or improve habitat conditions for frogs (Engle 2001); remove livestock from known hibernation sites (Engle 2001).
        ii. Design and implement Allotment Management Plans that protect spotted frog habitat considering the local situations; enforce sustainable grazing practices, evaluate drought threats, and apply livestock closures as needed (Perkins and Lentsch 1998, Munger et al. 2002).
        iii. Manage grazing on stream habitat to avoid compaction, late season vegetative loss, willow damage, stream channelization, and down-cutting (Engle 2001, Munger et al. 2002); evaluate prescribed burning in riparian areas in light of the potential for frog mortality and how changes in vegetation could affect spotted frog habitat. (Engle 2001).
    c. Water projects
        i. Maintain and restore natural hydrological characteristics (Perkins and Lentsch 1998), or evaluate how human-caused changes to hydrology may affect frog breeding, foraging, and wintering habitat; consider how the hydroperiods of modified or constructed water bodies could affect frogs by increasing/reducing habitat or by attracting/sustaining predators (e.g., fish, bullfrogs)

(Maxell 2000); consider how existing or new projects (such as water diversions) could negatively affect water tables in riparian corridors (Munger et al. 1997, Engle 2001).

ii. Protect springs that may be important for spotted frogs (Munger et al. 1997); avoid developing springs that are used as frog hibernation areas, including the outflow streams, which serve as movement corridors (Engle 2001); where spring development exists or cannot be avoided in an area important for frogs, consider measures that could help to mitigate impacts, such as fencing a portion of the spring to exclude cattle or allowing for pooled surface water and unobstructed access to a spring mouth.

d. Roads

i. Allow no new road development within 100 feet of known spotted frog habitat (Munger 1997); at distances over 100 feet, evaluate potential spotted frog movement patterns when determining road placement.

ii. Minimize motorized traffic near breeding sites (Semlitsch 2000); close routes to vehicle use during peak migration periods (Maxell 2000).

iii. Use culverts or tunnels under roads to direct amphibian movements at known concentration points (Semlitsch 2000); where roads cross areas connecting critical habitat components, use bridges, oversize culverts, underpasses, or overpasses that attract frog use (Patla 1997, Jochimsen et al. 2004); install tunnels between upland habitat and wetland breeding areas (Jochimsen et al. 2004).

e. Fish and bullfrog introductions

i. Do not introduce fish into previously fishless waters in the range of the spotted frog; terminate stocking in lakes with suitable frog habitat that have been stocked in the past but in which fish cannot successfully reproduce (Munger et al. 1997, Pilliod and Peterson 2000).

ii. Remove introduced fishes if this will open key sites for occupation by spotted frogs (Munger et al. 1997 Pilliod and Peterson 2000); establish protocols and eradicate or control targeted populations of non-native fish where feasible and in areas that are key habitats for survival of local sets of populations (Perkins and Lentsch 1998, Maxell 2000, Pilliod and Peterson 2000); during fish eradication, avoid methods that will kill amphibians; try to mitigate effects of piscicides on amphibians through timing, dosage, and methods of application.

iii. Do not allow fish stocking by non-professionals; ensure that any mistakes in stocking by agencies are rectified by the responsible agency (Munger et al. 1997).

iv. Prohibit introductions of bullfrogs; eradicate or prevent further spread of bullfrog populations in areas of overlap with spotted frogs (Munger et al. 1997, Maxell 2000).

f. Fire

i. Restrict use of fire retardants around aquatic sites (Semlitsch 2000).

ii. Prescribed burns should not be conducted at times when amphibians are widely present in the habitat to be burned, particularly if the population in the area is isolated from other populations and thus at risk of extirpation if mortality is high (Maxell 2000).

g. Timber management and oil/gas development

i. Minimize practices that degrade terrestrial habitat near breeding sites (e.g., surface disturbance, road construction, reduction of ground cover and moist areas) (Semlitsch 2000); use harvest practices that minimize the immediate and long-term differences in abundance and distribution of moist microhabitats (e.g., woody debris) between harvested and unmanaged areas (deMaynadier and Hunter 1995, Maxell 2000); avoid skidding or

piling logs in occupied frog habitat (USDI National Park Service 2002); conduct timber management activities after amphibians have entered their over-wintering sites (i.e., after mid-October) (USDI National Park Service 2002); avoid operating machinery in areas likely to host amphibians (e.g., moist swales, snowmelt pools) (USDI National Park Service 2002).
   - ii. Maintain natural vegetation buffer zones around ponds; Semlitsch (2000) proposes 160 m from the edge of wetlands and 30 to 100 m along streams, adjusted for stream width, slope, and site use; the size of buffer widths needed for spotted frogs has not been specified, but a relatively intact buffer around breeding pools is recommended to provide cover for migrating adults and habitat for dispersing young-of-the-year frogs (deMaynadier and Hunter 1999); within this buffer, protect natural vegetation and ground cover, and avoid surface disturbance.
   - iii. Maintain a diversity of terrestrial habitats around ponds (Semlitsch 2000); outside the buffer zone, or where a buffer zone is not implemented, provide corridors of natural vegetation among wetlands that can facilitate frog movements and survival during migrations; if vegetation corridors cannot be maintained, protect or restore small wetlands that could serve as stepping stones for amphibian movements (Semlitsch 2000).
- h. Recreation
   - i. Avoid degradation of wetlands and direct mortality of amphibians by restricting off-road vehicle and other motorized use to designated roads, trails, or pit areas (Maxell 2000).
   - ii. New recreational facilities should not be located within 300 m of key breeding, foraging, or over-wintering habitats (Maxell 2000).
   - iii. Provide educational signs or pamphlets about spotted frogs and how they might be impacted by humans and their pets at recreational facilities that are near documented population centers (Maxell 2000)
- i. Chemical use
   - i. Restrict herbicide and insecticide use near ponds, ditches, and ponds where runoff can move into wetlands (Semlitsch 2000); do not apply fertilizers, herbicides, and pesticides within 100 m of water bodies and wetlands until lethal and sublethal impacts on frogs are known (Maxell 2000).
   - ii. Analyze effects of treatment chemicals to amphibian populations (i.e., decomposition rates of the toxicant, sub-lethal effects, and timing of application) (Ulmer 2001).

4. Habitat restoration and enhancement
   - a. Manage harvest of beaver to prevent decline or loss of beaver populations; reintroduce beavers in areas where a need for dam-building activities of beavers has been identified (Munger et al. 1997).
   - b. Stabilize stream banks (Perkins and Lentsch 1998).
   - c. Restore springs; modify existing spring development to allow passage of frogs and to restore habitat (Munger et al. 1997).

Tools and practices

Inventory and monitoring

In the context of amphibian management, inventory refers to the documentation of species occurrence within an administrative unit or a defined geographic region. The presence-absence data produced by an inventory can be used for basic documentation, to establish geographic or ecological distributions, or to document changes in distribution and habitat use (Chapter 3 in Heyer et al. 1994). Basic inventory for the Columbia spotted frog is complete at the level of National Forest units in Region 2; the species has been documented on the national forests within its known and expected geographic range. Inventory may be desirable at finer scales within the each forest (e.g., ranger districts, sub-watershed units or drainage catchments, wilderness areas, suitable timber zones, project areas). If monitoring programs (see below) are not established, repeated inventory (e.g., every 10 or 15 years) could reveal if the species persists, or is undergoing changes in distribution. Changes in status for some amphibian species in the western United States since the 1970s (e.g., leopard frogs and boreal toads in Rocky Mountain National Park, CO) present strong evidence that the persistence of widespread amphibian species in protected areas cannot be assumed (Corn et al. 1997). Documenting the presence of spotted frogs is most reliably achieved by searching for tadpoles in temporary or permanent ponds; other life stages may be present but are easier to miss because of their ability to disperse among upland habitats (see Survey techniques section, below). If two or more surveys of potential habitat units are conducted during the time frame when tadpoles should be present (e.g., between mid June and late July in a given year), detection probabilities can be calculated, providing an estimate of how often the species is likely to be missed during surveys (MacKenzie et al. 2002).

Monitoring efforts aim at determining changes in species abundance (number of individuals or population units per species) at one or more sites through time (Heyer et al. 1994). The design of amphibian surveys for extensive monitoring (or inventory) at a scale relevant to large management units has received much attention in recent years. Compilations of approaches are provided by Heyer et al. (1994) and Olson et al. (1997). The USGS-ARMI has developed a conceptual model, strategy, methods, and national database for assessing status and trends of amphibians (http://edc2.usgs.gov/armi/ and http://www.fort.usgs.gov/research/rarmi/rarmi_intro.asp). Because ARMI integrates expertise of herpetologists, statisticians, mapping specialists, water quality scientists, database experts, and managers, it provides the best available, scientific approach for monitoring amphibians on large blocks of public land. ARMI has implemented its approach on Department of Interior (DOI) lands across the United States and hopes to develop a national program by extending the effort to non-DOI agencies through partnerships (USGS Amphibian Research and Monitoring Initiative Task Force 2001, Corn et al. 2005b). Another source of monitoring expertise resides in the National Park Service's Greater Yellowstone Network Inventory and Monitoring Program (based in Bozeman, MT), which has selected amphibian occurrence as a "Vital Sign" for monitoring in Yellowstone and Grand Teton national parks and Bighorn Canyon National Recreation Area (http://www.nature.nps.gov/im/units/gryn/index.shtml). This program will likely integrate with the USGS Rocky Mountain Region ARMI to implement long-term amphibian monitoring on DOI lands in northwestern Wyoming.

The conceptual model for monitoring employed by ARMI is a pyramid, with coarse or broad scale assessment of amphibian occurrence at the base level of the pyramid, analysis of trends within regions or management units at the mid level, and intensive research geared towards population monitoring (at selected sites) and the causes of declines at the apex (Corn et al. 2005b). The mid level is most applicable to monitoring the status and trend of the Columbia spotted frog in the national forests of Region 2. Elements of the model and procedures (sampling design, data collection, and data analysis) are listed below, with explanations of how they have been used in the GYE and could be applied to determine status and trend of the Columbia spotted frog in national forests of Region 2.

1. Sampling design (for monitoring status and trend): Define the range of statistical inference, and divide the area to be monitored (e.g., national forest) into sampling units. Select units to be sampled via a probabilistic scheme. Sampling design also entails decisions about habitat monitoring, including the determination of which characteristics (covariates) should be measured or recorded to assess wetland dynamics, habitat change, suitability, and amphibian occupancy.
   In the GYE, the two national park units (Yellowstone and Grand Teton) were defined as the range of inference for pilot studies of amphibian occupancy beginning in 2000 (Patla 2002, Patla and Peterson 2003 and 2004). GIS layers were prepared with USGS 7th-level hydrological (or similar) units. To achieve a geographical distribution of sampling areas across the parks, a grid was imposed over the parks' area, and one hydrological unit (catchment) was randomly selected from within each block of the grid. (Alternatively, coarser hydrological units [e.g., 4th level units, such as Snake River, Upper Yellowstone] could be used for the purpose of distributing sampling units.) Within the selected catchment, National Wetland Inventory (NWI) polygons with temporary or permanent surface water were identified for amphibian surveys.

   A similar approach could be applied to national forests, using available GIS tools to define watershed units and potential amphibian habitat (wetland sites) within the units.

2. Data collection: Conduct visual encounter surveys to determine occupancy rates of the Columbia spotted frog (and other pond-breeding amphibians) at wetlands within the selected units, with emphasis on documenting breeding sites. Collect habitat data for analysis of covariates (as determined during the design phase), providing the same level of effort for apparently unoccupied sites as for occupied sites. Recent scholarship has emphasized the need for assessing detection probability (detectability) when conducting occupancy monitoring (MacKenzie et al. 2002, Bailey et al. 2004, Gu and Swihart 2004). This entails conducting multiple surveys (at least two) at all or most sites within the same season, during the period when the species is likely to be present (i.e., before metamorphosis and emergence occurs).

   In the GYE, amphibian surveys (usually by two-person teams) were conducted at all potential amphibian habitat within the catchments (each containing 10 to 50 wetland units); wetlands were detected with the use of NWI and topographic maps (Patla 2002, Patla and Peterson 2004). Sites were visited multiple times to acquire data on detection probabilities. Site variables (e.g., maximum water depth, vegetation type) and sampling variables (e.g., weather, date, time of day) were recorded, and voucher photos were taken of sites and amphibians (all life stages). This was a successful method of identifying active breeding sites for the Columbia spotted frog and other pond-breeding amphibians (e.g., tiger salamanders, boreal chorus frog, and boreal toad), as well as documenting the existence of potentially suitable but apparently unoccupied habitat (Patla 2002, Corn et al. 2005a).

   This type of survey appears to be feasible for the national forests, given the similarity of Yellowstone-Tetons and the Bighorn and Shoshone national forests in terms of terrain. A benefit of this approach is that the national forests can simultaneously conduct inventory/monitoring for other pond-breeding amphibians in addition to the Columbia spotted frog.

3. Data analysis: Use the survey data to determine proportion of sites (or area) occupied (McKenzie et al. 2002). Occupancy statistical tools support the assessment of changes in site occupancy over time, which reflect trends in amphibian abundance. Because this approach provides analysis of how detectability, site variables, and sampling variables affect patterns of species presence or absence, occupancy methodology is a considerable advance over previous methods of simply enumerating changes in the number of breeding sites as a way to determine trends. Software (PRESENCE) for estimating occupancy rates and related parameters may be obtained through the USGS: http://edc2.usgs.gov/armi/PAOEstimator.asp

   Estimation of occupancy for the Columbia spotted frog, using ARMI software is in progress for the GYE. The naive occupancy rate (not corrected for detectability and with no variance calculated) estimate for spotted frog breeding sites (eggs, larvae, or metamorphs present) in the two national parks over four years (2000-2003) ranged from 14 to 22 percent per year; detection probabilities ranged from 69 to 95 percent; and adjusted occupancy ranged from 14 to 27 percent (Patla and Peterson 2003 and 2004, Corn et al. 2005a). Full implementation of long-term monitoring in the two national parks is expected to begin in 2005 or 2006. Annual surveys of the set of randomly-selected catchments and analysis of the data with occupancy statistical tools will make it possible to determine if spotted frogs are declining, remaining stable, or increasing within Yellowstone and Grand Teton national parks.

   The occupancy approach would provide Region 2 with objective, quantitative data on population trends for Columbia spotted frogs. Sampling design and the selection of habitat variables could enable assessment of how spotted frogs (and/or other amphibians) are responding to management practices (e.g., amounts of woody debris in logged areas, grazing intensity, and prescribed fire). Clarification of monitoring objectives is essential to design and the success of implementation. An effective amphibian monitoring program that meets USFS objectives could be integrated with other monitoring efforts in northwestern Wyoming, with mutually beneficial partnerships and shared resources.

More intensive monitoring of specific breeding populations (as opposed to monitoring trends across a management unit, as described above) may be necessary to determine if populations of management or conservation interest (e.g., the Bighorn spotted frog population) are persisting, declining, or increasing. The most important types of information to collect for this level of monitoring include the number of egg masses per breeding site, presence and estimated number of tadpoles and other life stages, and whether or not successful metamorphosis occurs. To determine if diseases are present, dead individuals should be counted, collected, frozen as soon as possible, and submitted for pathology diagnosis, along with notes about location, date, and relevant observations. Where multiple dead are found, some should be frozen and other fixed in ethanol. Determining the presence of eggs, tadpoles, and metamorphs frequently requires multiple visits. Amphibians are cryptic during certain kinds of weather and lighting conditions and can be missed even when abundant. The timing of visits is critical; eggs will be missed if the visit is too early, and tadpoles or metamorphs will be missed if the visit is too late (see Survey Techniques, below). Tadpoles have the longest residence of these life stages and are thus the most convenient and reliable target of annual monitoring. Relative abundance estimates are not precise and should be used with caution; mark-recapture is necessary for reliable estimates of abundance. The number of egg masses can be used to roughly estimate the size of the annual breeding female population. This is an uncertain indicator of population robustness because it does not include pre-reproductive juveniles and non-breeding females, which are crucial to the population in subsequent years, but it is the best available index of population size. Furthermore, this estimate can be accomplished at a fraction of the time and costs needed for estimating abundance through mark-recapture. Mid-summer monitoring can be used to determine the ratio of adults to juveniles, indicating if the young of the previous one to three years have survived. Late summer and fall surveys around known breeding areas can help to identify migration zones and over-wintering sites. Even when the monitoring target is a specific breeding population, the monitoring of groups of ponds in an area rather than single sites has been recommended so that local shifts in breeding activity can be recognized and expansion into new breeding sites can be detected, thus avoiding the hazard of mistakenly assuming that absence of breeding represents a true local decline (Marsh and Trenham 2001).

Habitat monitoring, at the fine scale, can be conducted simultaneously with the above population monitoring, with surveyors documenting impacts of potential threats or various activities (e.g., recreation, grazing) at breeding and foraging sites. Habitat monitoring at a coarser scale can be part of an inventory/monitoring program, described above, with data collected on habitat variables that can indicate the impacts of forest management practices and natural processes.

Survey techniques

This section applies to both inventory and monitoring efforts that seek to determine the presence/absence of spotted frogs. Surveys for spotted frogs are generally conducted during daytime hours, using visual encounter survey protocols described in Thoms et al. (1997). Adults and juvenile spotted frogs often bask on sunny days, and tadpoles use the warmest available water within the breeding pools; thus surveys along pond/lake edges or along the shores of low-gradient streams are efficacious in detecting spotted frogs. Dip-netting with a fine-mesh net on a long (1 to 5 ft.) handle is useful to detect tadpoles in areas that have aquatic vegetation or cloudy water, and dip-net transects can be conducted across shallow ponds to sample in areas of various depth. Transects (zig-zag or straight lines at intervals) are employed to survey large wetland areas. To detect active breeding sites, the time frame for surveys is restricted from egg deposition to metamorphosis, a time frame that varies with elevation and latitude. Tadpoles that have recently hatched can be difficult to detect, so it can be better to postpone surveys until a few weeks after egg deposition, unless egg-mass count data are being sought. Surveys between mid-June and late July or early August will probably be suitable for most areas in Region 2 inhabited by spotted frogs, with higher elevation areas surveyed last. Paper forms can be used to record data, or personal digital assistants (PDAs) can be used to automatically upload information into databases. A sample survey data form, previously used for NPS-USGS surveys in Yellowstone and Grand Teton National Park, is provided in Appendix B. This data sheet probably includes more fields than necessary for monitoring occupancy and would require revision based on program design.

The potential for spreading diseases through surveys and handling of amphibians is a concern among herpetologists, and protocols for minimizing this risk need to be closely followed by survey personnel. Protocols are provided by the Declining Amphibian Population Task Force (www.mpm.edu/collect/vertzo/herp/Daptf/fcode_e.html). In brief, protocols require a thorough cleaning of all boots, nets, and equipment used during surveys, followed by disinfection with ethanol or bleach. These procedures should be strictly followed whenever people working in amphibian habitat move between sites in different watershed units, or following work conducted in an area where a die-off has occurred.

Captive propagation and reintroduction

Captive propagation and introduction of Columbia spotted frogs is highly experimental and still in its infancy. Due to the potential for multiple, serious problems (e.g., disease and genetic issues) and large expense, captive breeding should only be considered in cases where few other conservation alternatives exist. An example would be rapid population decline in a distinct breeding segment of the species. The Conservation Strategy for spotted frogs in Utah (Perkins and Lentsch 1998) contains several action items with respect to captive breeding:

- ❖ determine feasibility and methodologies for augmentation and reintroduction
- ❖ develop protocols for captive propagation and rearing
- ❖ develop protocols for translocation and introduction
- ❖ identify and develop brood stock sources and potential rearing facilities
- ❖ augment populations through stocking where genetic viability may be threatened
- ❖ establish additional populations.

An experimental translocation of egg masses and adults into an unoccupied area along the Provo River was attempted to test reintroduction methodologies. The egg mass translocation effort was considered successful, but translocation of adults was not (U.S. Fish and Wildlife Service Region 6 2002). Further work in Utah may be useful in determining if introductions on the Bighorn National Forest are desirable and feasible, should a catastrophic decline occur.

Information Needs

The distribution and abundance of populations of Columbia spotted frogs on the Bighorn and Shoshone national forests are poorly understood; acquiring this information is the highest priority. On the Bighorn National Forest, documented surveys are needed to establish if the distribution of spotted frogs is as limited as it appears and to determine if any additional (or potential) breeding sites exist in the single watershed where spotted frogs currently occur on this forest. On the Shoshone National Forest, spotted frogs appear to be common in only one area. Surveys are needed here to determine:

- ❖ the distribution and abundance of populations in other watersheds of the forest
- ❖ presence/absence of spotted frogs at the southern extremes of the forest
- ❖ the edge of the species' range
- ❖ if human-caused habitat changes have influenced the boundaries of the species' range.

Previously documented breeding sites should be surveyed to determine if they remain active, and baseline surveys are needed to document new breeding sites and local populations.

The Columbia spotted frog's response to changes in habitat is only roughly known. Research into the potential threats and benefits of forest management activities (timber harvest, grazing, fire and fire management, fish stocking and management, chemical use and road, trail, recreational, and water developments) on spotted frogs or closely related species anywhere in coniferous, mountainous environments similar to Region 2 is a high priority. Controlled studies that examine the response of spotted frog populations to pre- and post-treatment conditions would be especially valuable. Livestock grazing is probably the most widespread activity on the national forests, and the one with the least amount of information in terms of impacts on amphibians. USFS Region 1's review of risk factors to amphibians in Montana (Maxell 2000) provides a comprehensive list of research needs and suggestions.

The most important habitat questions for Region 2 are listed below. Although we stress the Bighorn National Forest because of the isolated, at-risk spotted frog population there, these questions may also apply to the Shoshone National Forest, particularly where spotted frogs are uncommon or spatially isolated.

a. Roads. Are roads affecting spotted frogs on the Bighorn National Forest? Are breeding, foraging, and wintering habitat components separated by roads? Is road-kill occurring? What road improvements could benefit spotted frogs?

b. Fish introduction. Is fish stocking restricting habitat availability and frog reproduction and survival, particularly at Sibley Lake (one of the three breeding sites on the Bighorn National Forest)? Is it possible to limit fish access to frog habitat? Would removing fish from some sites allow for the expansion of frog populations?

c. Livestock grazing. Is grazing having a significant impact on the habitat or populations (occupied and potential) of spotted frogs on the Bighorn National Forest? What is the impact of grazing and different grazing regimes?

d. Contaminants. How readily do fire retardant chemicals and forest management herbicides enter streams and ponds? What are the effects of chemicals on spotted frogs at their various stages of life history?

e. Timber management and fire. How are spotted frog microhabitats affected by the removal of woody debris, canopy reduction or removal, and various kinds and intensities of timber harvest? How does wildfire (of various intensities) affect the distribution and abundance of spotted frog populations?

Research of the seasonal and daily movement patterns of spotted frogs shows that there is considerable variation among study areas, suggesting that movements are largely determined or influenced by the local environment or configuration of habitat components. This makes it difficult to evaluate the effects of habitat change at broad scales. One approach would be to collect spotted frog habitat use data at several areas within Region 2 to determine the spatial configuration and distance among the various habitat components used by the populations. This would assist in broad-scale habitat evaluations (e.g., where is the spatial separation of potential breeding and wintering sites too extreme for spotted frog populations to be supported?) The metapopulation concept has not been thoroughly researched for spotted frogs, and research is needed to determine the spatial scale at which metapopulations operate and the applicability of the source-sink population concept. For isolated and small populations of spotted frogs, determination of specific movement patterns could be vital to understanding the effects of management actions and the future of those populations.

Movement patterns and spatial relationships are not well understood; it is unknown to what degree past studies reflect typical conditions, and how much variation may occur among spotted frogs in different environmental settings. Of most urgency is the determination of conditions governing the distance and success rate of young of the year moving from natal to over-wintering sites. Also important is determination if highly migratory populations (e.g., with individuals moving more than 100 m among habitat components) are typical or uncommon, if they have lower survival rates, and what features (natural or otherwise) of the landscape influence the distance moved and the success rate of frogs attempting these movements.

There is no detailed information on how insect prey population's response to habitat changes affects spotted frogs. Frogs are opportunistic and flexible feeders, shifting prey type if one group of prey becomes locally scarce due to habitat changes. Future research could investigate how aquatic and terrestrial prey species respond to habitat changes from management actions but may be of less urgency than determining if toxic chemicals have bioaccumulated in insect prey, and if this is being passed up the food chain to spotted frogs. National forests provide valuable research opportunities for determining pesticide or herbicide drift from targeted (private lands) to non-targeted areas.

Some important demographic questions for the species remain:

❖ what are the maximum and average life spans? The reliability of skeletal chronology to determine maximum ages is in question and needs to be critically reviewed (J. Bowerman personal communication 2003).

- ❖ at what age does breeding first occur?
- ❖ how frequently does a female reproduce?
- ❖ how many times does a female reproduce over the course of a lifetime?
- ❖ how many egg masses does a female produce in a single season? It is commonly assumed that a female produces one egg mass per year. The notion that egg mass numbers provide a suitable index of population size has not been critically reviewed, but it is critically important if this parameter is to be used as an index for monitoring populations.
- ❖ do these demographic parameters vary significantly among regions or elevations?

Demographic studies are needed particularly in the Bighorns, where the population's long isolation and adaptation to local conditions may have led to differences in parameters.

The monitoring of abundance trends for amphibian species across large management units (e.g., national forests) is a work in progress, with USGS-ARMI providing a lead role in developing and testing survey design and statistical methods. Much more information is likely to be published and available within the next several years. USFS efforts to effectively monitor spotted frogs could greatly benefit by partnership with the USGS-Rocky Mountain-ARMI program.

We suggest that determining risk factors for spotted frog populations on the Bighorn National Forest, where the population is small, restricted in distribution, and geographically isolated, is a research priority. Natural history and demographic studies have never been conducted for this disjunct population. Annual and carefully documented monitoring of all known breeding sites would facilitate the detection of declines, if they occur. Additional genetic studies will clarify the relationship of this population to others and how long it has been isolated from the main population.

A second research priority involves obtaining natural history information for spotted frogs, including activity ranges, dispersal, migration patterns, and over-wintering habitats in Region 2. Particular attention should be given to those aspects of natural history that shed light on the impact of anthropogenic disturbances (e.g., livestock grazing, timber management, recreation) on breeding sites and dispersal ability.

Finally, research is needed to determine if diseases that may be causing declines of amphibians elsewhere in Region 2 (e.g., chytrid disease outbreaks in boreal toads) are affecting spotted frogs. The most important initial task is sampling to detect disease presence in spotted frog populations, making use of the techniques (e.g., PCR-based assays for fungal infections) and knowledge provided by efforts such as the boreal toad recovery project in Colorado (Loeffler 2001, Livo and Loeffler 2003). The vulnerability of spotted frogs to the emergent infectious diseases, chytrid and ranavirus, and methods to minimize the spread of the diseases should be also be investigated. Partnerships with research agencies and institutions could aid in health monitoring and sampling, assessment of risk factors, and formulation of responses to catastrophic die-offs should they occur or are deemed likely to occur.

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Appendix A

Matrix Life History Model by Dave McDonald and Takeshi Ise

Background

Matrix models are designed to examine the intrinsic life history of a species, (i.e., evolved traits affecting reproduction, or the component of population persistence that is affected by factors internal to the species) rather than external to the species (e.g., habitat availability or the impacts of disease). Although initially developed for birds (Leslie 1945, 1966) and applied extensively to plants (e.g., Menges 1990, Bierzychudek 1995, Enright et al. 1999), they are very generalizeable models that can be applied successfully to nearly any taxon, including amphibians (Biek et al. 2002). The utility of matrix models in biology are primarily to gain insight into those transitions in the life cycle that are the key to population dynamics – where are the "weak links" or vulnerable points in the life cycle? Matrix models are not necessarily the only or even the appropriate means for assessing whether populations are growing or declining, nor for assessing likelihood of extinction, nor for determining the impacts of specific habitat factors. For instance, consider that populations of an amphibian are declining due to the elimination of breeding ponds resulting from introduction of a disease (an external influence). This does not impact the structure of the model, since the intrinsic, evolved traits of the species are not altered (e.g., the remaining ponds and individuals may all have the same vital rates). The fact that specific populations may be in decline (i.e., violating the assumption of the population growth rate being approximately one, $\lambda \approx 1$) will not, by itself, change the relative importance of the different life stages. If such a decline is affecting one stage to an abnormally high degree, one can incorporate the altered vital rates (survival and fertility rates) with an adjusted model. What they **can** do is to point to particular transitions in the life cycle that are most likely to have a strong effect on population dynamics. They can, for example, tell us that changing adult survival will have much more impact on population dynamics than would a similar change in fertility.

The life history described by Turner (1958a, 1960), and matrix models of *Rana aurora* by Biek et al. (2002) provided the basis for a life cycle graph (**Figure A1**) and a matrix population analysis with a post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2001) for spotted frog. The model has two kinds of input terms: P_i describing survival rates, and m_i describing fertilities (**Table A1**). We assumed that fertility was 250 (female) eggs per female per year (Turner 1958a), that females breed only every other year, and that annual survival was constant after the first year (0.6) (Turner 1960). We assumed that first-year survival was 2 percent (slightly higher than the values used by Biek et al. 2002 for a model of *R. aurora* where embryo survival x larval

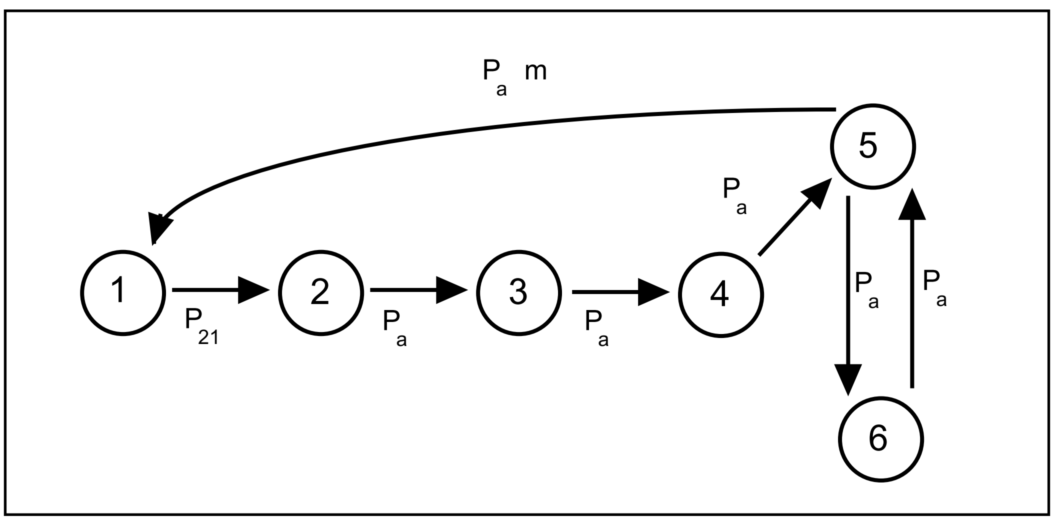

Figure A1. Life cycle graph for spotted frog. Note that the model deviates from an age-classified analysis (Leslie matrix) in that females alternate between Stage 5 ("on" year for breeding) and Stage 6 (non-breeding "off" year), resulting in stages that are heterogeneous for age (see Table 3 for the mean and SD of the ages of females in those two stages).

Table A1. Parameter values for the component terms (P_i, and m_i) that make up the vital rates in the projection matrix for spotted frogs.

Parameter	Numeric value	Interpretation
m_a	250	Number of female offspring produced by a female
P_{21}	0.02	Annual survival rate of eggs
P_a	0.60	Annual survival rate of stages after first year

survival x metamorph survival = 0.152). **Figure A2a** shows the symbolic terms in the projection matrix corresponding to the life cycle graph. **Figure A2b** gives the corresponding numeric values. The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female. λ, the population growth rate, is 1.002 based on the estimated vital rates used for the matrix. Although this suggests an essentially stationary population, the value is subject to the many assumptions used to derive the transitions and should not be interpreted as an indication of the general well-being and stability of the population. Other parts of the analysis provide a better guide for assessment.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. **Sensitivity** is the effect on population growth rate (λ) of an **absolute** change in the vital rates (a_{ij}, the arcs in the life cycle graph [**Figure A1**] and the cells in the matrix, **A** [**Figure A2**]). Sensitivity analysis provides several kinds of useful information (Caswell 2001). First, sensitivities show "how important" a given vital rate is to population growth rate (λ) or fitness. For example, one can use sensitivities to assess the relative importance of survival (P_i) and reproductive (F_i) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing the population growth (λ) of endangered species or the "weak links" in the life cycle of a pest. **Figure A3** shows the "possible sensitivities only" matrix for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible – for example, the sensitivity of λ to moving from an older reproductive stage back to an earlier pre-reproductive stage).

In general, changes that affect one type of age class or stage will also affect all similar age classes or stages. For example, any factor that changes the annual survival rate of Stage 5 females is very likely to cause similar changes in the survival rates of other "adult" reproductive females (those in Stages 2 through 7). It is, therefore, usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). For this model, the result is that the sensitivity of λ to changes in first-year survival (8.19; 87.9 percent of total) is the salient feature. The summed "adult"

A

	1	2	3	4	5	6
1					$P_a m_a$	
2	P_{21}					
3		P_a				
4			P_a			
5				P_a		P_a
6					P_a	

B

	1	2	3	4	5	6
1					150	
2	0.02					
3		0.6				
4			0.6			
5				0.6		0.6
6					0.6	

Figure A2. The input matrix of vital rates, **A** (with cells a_{ij}) corresponding to the spotted frog life cycle graph (**Figure A1**). A: Symbolic values. B: Numeric values.

	1	2	3	4	5	6
1					0.001	
2	**8.19**					
3		**0.273**				
4			**0.273**			
5				**0.273**		0.153
6					0.153	

Figure A3. Possible sensitivities only matrix, $\mathbf{S}_p$ (remaining elements correspond to zero values in the matrix **A**). The four transitions to which the λ of spotted frogs is most sensitive are highlighted: first-year survival (Cell s_{21} = 8.19), and the three subsequent survival rates ($s_{32} = s_{43} = s_{54}$ = 0.273).

survival sensitivity is 1.13 (12.1 percent of total). The spotted frog shows virtually no sensitivity to changes in fertility (the first row of the matrix in **Figure A3**). The major conclusion from the sensitivity analysis is that, in the event of absolute changes in vital rates, first-year survival (survival of eggs, emergent tadpoles and through the first winter) is the key to population growth. The circumstances under which first-year survival is likely to vary absolutely are during periods of rebound and rapid population growth following ameliorated environmental conditions. During such periods the vital rates may change sufficiently to warrant constructing new matrix models that incorporate the large changes in some of the rates.

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, a change of 0.5 in survival may be a big alteration (e.g., a change from a survival rate of 90 percent to 40 percent). On the other hand, a change of 0.5 in fertility may be a very small proportional alteration (e.g., a change from a clutch of 3,000 eggs to 2,999.5 eggs). Elasticities are the sensitivities of λ to **proportional** changes in the vital rates (a_{ij}) and thus largely avoid the problem of differences in units of measurement. The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). The elasticities provide a further tool for assessing key life history transitions and stages as well as the relative importance of reproduction (F_i) and survival (P_i) for a given species. Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). In years that are close to the average portrayed by the present model, changes are likely to be small and proportional, thereby suggesting use of the elasticities as guidelines. During periods of rapid growth, with potentially greatly heightened survival in the early stages, the changes may be absolute, thereby suggesting greater emphasis on the sensitivities as guidelines. Because these analyses assume small, near-equilibrium changes, major changes in the vital rates would warrant reanalysis of models that incorporate any greatly changed vital rates.

Elasticities for spotted frogs are shown in **Figure A4**. The λ of spotted frogs is most elastic to changes in the survival of "adult" individuals (Stages 2 to 7; summed elasticities = 67.3 percent), followed by equal values for first-year survival and the single fertility transition (both 16.4 percent). The transitions with the highest sensitivities and elasticities do not correspond in relative magnitude – the sensitivities emphasize first-year survival whereas the elasticities emphasize survival after the first year. Note, however, that the sensitivities decrease rapidly with increasing stage, whereas the four largest elasticities are of equal magnitude. The survival rates in the first four stages are therefore the data elements that warrant careful monitoring in order to refine the matrix demographic analysis. Periodic very good years are likely to result in large changes in first-year survival, violating the assumption of a small change in the parameters. The high sensitivity of λ to the first-year survival is likely a good indication that in good years the response of the population will be largely determined by high survival of a wave of new recruits. In other "normal" years, or years of decline, the high elasticities of λ to "adult" survival is likely the best guide to the population dynamics.

	1	2	3	4	5	6
1					0.001	
2	**8.19**					
3		**0.273**				
4			**0.273**			
5				**0.273**		0.153
6					0.153	

Figure A4. Elasticity matrix, **E** (blank elements are zeros). The λ of spotted frogs is equally elastic to changes in survival through the first four stages and to fertility. Note, however, that elasticities to "adult" survival rates (beyond the first-year) are likely to vary in concert and that their summed elasticities predominate (67.2 percent of the total elasticity).

Other demographic parameters

The stable (st)age distribution (SAD, **Table A2**) describes the proportion of each Stage (or Age-class) in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SAD within 20 to 100 census intervals. For spotted frog at the time of the post-breeding annual census (just after the end of the breeding season), eggs represent 95 percent of the population, because amphibians generally lay numerous eggs compared to the number of adults. Therefore, for this report, we also calculated the stage distribution excluding the first-year (egg) stage (**Table A2**). At the time of the census, 78.7 percent of the (non-egg) population consists of prereproductive stages, 12.8 percent of females are females in a breeding "on" year and 8.5 percent are females in a nonbreeding "off" year. **Reproductive values** (**Table A3**) can be thought of as describing the "value" of a stage as a seed for population growth relative to that of the first stage. The reproductive value of the first stage is always 1.0. A female individual in Stage 2 is "worth" 50.1 female eggs, and so on (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). As in many species with high clutch sizes, the peak reproductive value (233 for reproductive females in their "on" year at Stage 5) is considerably higher than that of the eggs (**Table A3**). The reproductive value result complements that of the sensitivities and elasticities. Only by increasing the survival through the first few years can one increase the number of older reproductive females that are the mainstay of the population. Stages 5 and 6 of the present model are heterogeneous for age; females may reenter the stage in subsequent years. Because the transitions contain information on the time intervals elapsed, one can calculate the means and variances of ages in multi-age stages (Cochran and Ellner 1993). **Table A4** shows the mean and standard deviation of the ages of the stages for the spotted frog model. The cohort generation time for spotted frogs is 6.1 years (SD = 1.9 years). The cohort generation time is the mean age of the parents of the offspring produced by a cohort over its lifetime, and provides a measure of the turnover time for the population.

Table A2. Stable stage distribution (right eigenvector) for females, with Stage 1 (eggs/first-year) excluded. At the census, 78.7 percent of the non-egg individuals in the population should be pre-reproductive, 12.8 percent will be breeders in an "on" year, and 8.5 percent will be non-breeders in an "off" year.

Age Class	Description	Proportion
2	Pre-reproductive	0.404
3	Pre-reproductive	0.234
4	Pre-reproductive	0.149
5	Breeders in an "on" year	0.128
6	Non-breeders in their "off" year	0.085

Table A3. Reproductive values for females. Reproductive values can be thought of as describing the "value" of an age class as a seed for population growth relative to that of the first (newborn or, in this case, right at the census, egg) stage or age-class. The reproductive value of the first stage is always 1.0. The peak reproductive value is highlighted.

Age Class	Description	Proportion
1	First-year individuals	1.000
2	Pre-reproductive	50.10
3	Pre-reproductive	83.67
4	Pre-reproductive	139.74
5	Breeders in an "on" year	**233.37**
6	Non-breeders in their "off" year	139.74

Table A4. Reproductive values and ages of the females in each stage. Reproductive values can be thought of as describing the "value" of an age class as a seed for population growth relative to that of the first (newborn or, in this case, right at the census, egg) stage or age-class. The reproductive value of the first stage is always 1.0. The peak reproductive value is highlighted. The age values are for individuals at the time of the census, which occurs at the beginning of the one-year census interval.

Stage	Description	Reproductive values	Mean age (yrs) ± SD
1	First-year individuals (eggs)	1.000	0 ± 0
2	Pre-reproductive	50.10	1 ± 0
3	Pre-reproductive	83.67	2 ± 0
4	Pre-reproductive	139.74	3 ± 0
5	Breeders in the "on" year	**233.37**	5.1 ± 1.9
6	Non-breeders in the "off" year	139.74	6.1 ± 1.9

Stochastic model

We conducted a stochastic matrix analysis for spotted frogs. We incorporated stochasticity in several ways, by varying different combinations of vital rates or by varying the amount of stochastic fluctuation (**Table A5**). Under Variant 1 we altered the fertilities (F_i). Under Variant 2 we varied only first-year survival, P_{21}. Under Variant 3 we varied the survival of all age-classes, P_i. Variant 4 combined variability in first-year survival with variability in the set of fertilities. Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the Stable Age Distribution (SAD) under the deterministic model. Beginning at the SAD helps avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). We varied the amount of fluctuation by changing the standard deviation of the random normal distribution from which the stochastic vital rates were selected. The default value was a standard deviation of one quarter of the "mean" (with this "mean" set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Variant 5 affected the same transition as Variant 3 (all the P_i) but was subjected to slightly larger variation (SD was 1 / 3.5 [= 0.286 compared to 0.25] of the mean). We calculated the stochastic growth rate, $log\lambda_S$, according to Eqn. 14.61 of Caswell (2001), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

The stochastic model (**Table A5**) produced two major results. First, altering the pre-reproductive survival rates had a much more dramatic effect on λ than did altering all the fertilities. For example, only under the variable pre-reproductive survival rates of Variant 1 did populations go extinct (30 of 100). Variant 1 had 61/70 non-extinct showing declines from the starting size, versus no declines in 100 runs of Variant 2 and three declines under Variant 3. Median ending size under Variant 1 (276) was considerably smaller than under two high-variance Variants, 2 and 3 (medians 246,554 and 233,180 respectively). Even with the reduced variability of Variant 4, pre-reproductive survival had more of an effect than did high variation in either reproductive survival (Variant 2) or fertility (Variant 3). Variant 4 showed 9/100 declines and a median ending size of 97,544. This difference in the effects of stochastic variation is predictable from the sensitivities and elasticities. λ was as elastic to variability in first-year survival, P_{21}, as it was to variability in the fertilities, F_i. Second, large-effect stochasticity has a negative effect on population dynamics. This negative effect occurs despite the fact that the average vital rates remain the

Table A5. Summary of five variants of stochastic projections for spotted frogs.

	Variant 1	Variant 2	Variant 3	Variant 4	Variant 5
Input factors:					
Affected cells	F_i	P_{21}	P_i	$F_i + P_{21}$	P_i
S.D. of random normal distribution	1/4	1/4	1/4	1/4	1/3.5
Output values:					
Deterministic λ	1.00018	1.00018	1.00018	1.00018	1.00018
# Extinctions/100 trials	0	0	23	0	53
Mean extinction time	—	—	1,582.5	—	1,479.9
# Declines/# surviving populations	29/100	71/100	73/77	69/100	42/47
Mean ending population size	14,891.4	15,010.3	8,535.4	21,309.1	4,040.3
Standard deviation	9,499.5	38,586.2	44,553.1	56,566.6	12,896.5
Median ending population size	11,925.1	4,565.28	99.01	4,557.49	64.77
Log λ_s	0.000081	-0.000385	-0.00317	-0.000349	-0.00473
λ_s	1.0001	0.9996	0.9968	0.9997	0.9953
Percent reduction in λ	0.0096	0.0562	0.334	0.0526	0.49

same as under the deterministic model – the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2001). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. The number of extinctions went from 30 in Variant 1 to 0 in Variant 4 when the magnitude of fluctuation was reduced. These results suggest that populations of spotted frogs are relatively tolerant to stochastic fluctuations in production of eggs (due, for example, to annual climatic change or to human disturbance) but extremely vulnerable to variations in survival, particularly in the long, five-year pre-reproductive phase. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. A possible concern is that anthropogenic impacts may induce variation in previously invariant vital rates (such as annual adult survival), with consequent detrimental effects on population dynamics. Further, in the case of the spotted frog, with high sensitivity of λ to changes in first-year survival, selection may be relatively ineffective in reducing variability that surely results from a host of biotic and abiotic factors.

Potential refinements of the models

Clearly, the better the data on survival rates the more accurate the resulting analysis. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of "stochastic" matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variation in vital rates. Where we varied F_i and P_i values simultaneously, we assumed that the variation was uncorrelated, based on the assumption that factors affecting reproduction and, for example, over-winter survival would occur at different seasons or be due to different and likely uncorrelated factors (e.g., predation load vs. climatic severity or water levels). Using observed correlations would improve on this assumption by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence. The present model also incorporated a simple alternation of breeding and not breeding in successive years. Further data may provide insights into latency to rebreeding, which would allow more sophisticated analysis of breeding probability. Females may for example breed in successive years in good conditions or fail to breed every other year if conditions are bad.

Spotted frog populations appear to be characterized by fluctuating population dynamics, with long periods of decline followed by occasional bursts of rapid growth and rebound. The deterministic model presented here, assumes near-equilibrium conditions that are doubtless often violated in natural populations. Nevertheless, the long term dynamics likely center around equilibrium and the sensitivities and elasticities provide a useful guide to the important transitions even in the case of deviations from equilibrium. A major refinement would be to have strong demographic data on increasing and declining populations that would allow models based specifically on those two ends of the spectrum of population levels. Separate models for those conditions would allow prediction of short-term trajectories that would help managers under the variety of conditions faced by natural populations.

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APPENDIX B

Survey Data Sheet for GYE Amphibians

Date | **Observer(s):** | **Recorder:** | **Watershed name & code:**

Site Name | **Pre-Assigned Code:** | **Locality**

UTM East | **UTM North** | **UTM EPE** | **Zone** | **Datum** | **Visit Number this year**

Begin Time | **End Time** | **Total minutes of Survey:** | **Number of persons searching:** | **Site detection** *(circle)*: NWI unit Topo Map Photo Incidental

State | **County** | **Land Owner** | **Elevation** *(from topo)* | **Topo name**

Weather: Clear Overcast Partly cloudy Fog or mist Rain Sleet or hail Snow | **Wind:** Calm Light Mod Strong

Air Temp | **Water Temp** | **Water pH** | **Cond** | **Color:** Clear Stained | **Turbidity:** Clear Cloudy

Site Description: Lake/Pond Wet Meadow Bog/Fen Spring/Seep Stream/River Oxbow/Backwater Ditch/puddle Site dry Thermal site Terrestrial Beaver Pond: Active or Inactive

Water Connectedness: Permanent Temporary Isolated | **Human Impacts:** Road Impoundment Camp/picnic site Maintenance area

Water Permanence: Permanent Semi-permanent Temporary | **Max Depth:** <1m 1-2 m >2 m

Percent of site at <50 cm depth: 0 1-25 25-50 50-75 75-100 | **Extent Water Cover:** 0% 1-5 6-25 26-50 51-75 76-100%

Site Length:______ **Site Width:**______ | **Percent of site perimeter searched:** 0 1-25 26-50 51-75 76-99 100

Primary Substrate: Silt/Mud Sand Gravel Cobble Boulder/Bedrock Other________

% of Water Body with Emergent Veg: 0 1-25 26-50 51-75 76-99 100 | **North Shoreline Characteristics:** Shallows: Present Absent Emergent Veg: Present Absent

Rank emergent veg in order of abundance: ____Sedges ____Fine rushes _____Grasses _____Bulrush _____Cattail _______Shrubs ______Pond lily _______Other (Describe):

Submerged aquatic veg %: 1-10 11-50 51-75 76-100 | **Distance (M) to Forest Edge:** _______ | **Forest Tree Species in Order of Abundance:**

Other Wildlife:

Fish Present: Yes No | **Fish species if known:**

Herpetofauna Species Information (include reptiles)

Species * for breeding	Life History Stage	Number of Individuals *(sex if known)*	Range of Sizes	Detection Method*	Photo No.	Comments (UTM for larvae or eggs, number of dead)

***Dectection Method abbreviations:** Visual only =VID Caught and handled =HC Auditory =A

Site Map

Grid Scale: ____________ Site Number: __________

Indicate where in drawing GPS point was taken and where amphibian observations occurred.

Site Photos (List: Subject, location, direction; e.g."Main pond, south shore, looking NW")

Remarks: