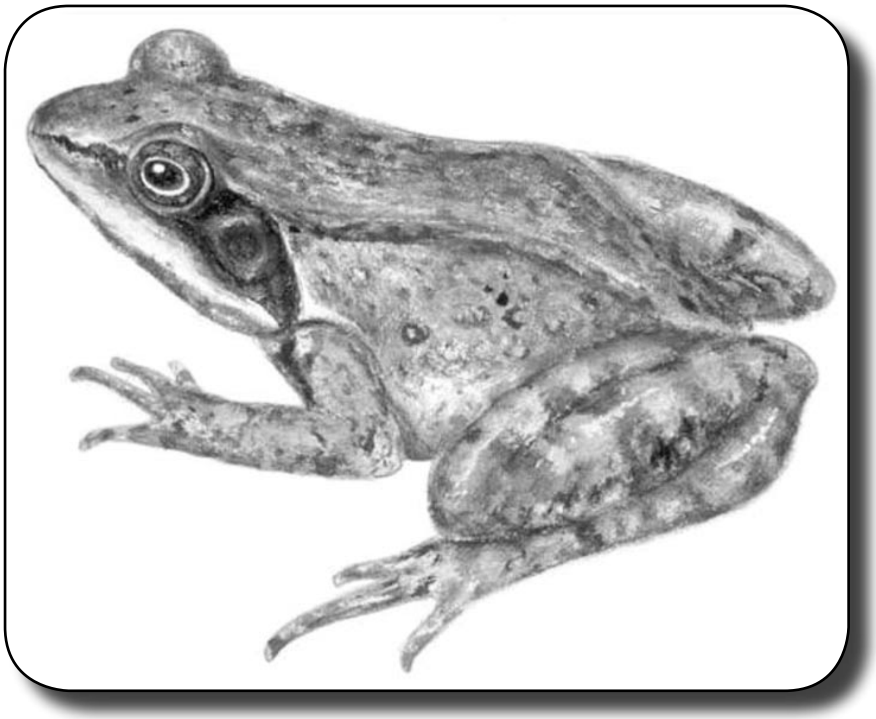
Wood Frog (*Rana sylvatica*): A Technical Conservation Assessment



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Rick Scherer is working toward a Ph.D. in Fishery and Wildlife Biology at Colorado State University. His dissertation research is focused on the spatial distribution and population dynamics of wood frogs (*Rana sylvatica*) in the Kawuneeche Valley of Rocky Mountain National Park. He has spent the last 8 years conducting research on amphibians in Colorado and is generally interested in amphibian population ecology, demographics and management. Rick earned his B.S. from Indiana University in 1988 and his M.S. (Ecology) from Colorado State University in 2004.

COVER PHOTO CREDIT

Cover illustration was produced by Summers Scholl for the Wyoming Natural Diversity Database.

Summary of Key Components for Conservation of the Wood Frog

Overall, the wood frog (*Rana sylvatica*) is ranked G5, secure throughout most of its range (NatureServe Explorer 2002). However, it is more vulnerable in some states within USDA Forest Service Region 2: S3 (vulnerable) in Colorado, S2 (imperiled) in Wyoming, and S1 (critically imperiled) in South Dakota (NatureServe Explorer 2002); there are no records for wood frogs in Kansas or Nebraska. Primary threats to wood frog populations are habitat fragmentation (loss of area, edge effects, and isolation) and habitat loss due to anthropogenic causes (e.g., wetland draining, grazing) and natural changes as habitat succession occurs.

Wood frogs are most conspicuous at breeding sites early in the spring, when snow and ice are often still present at pond margins. They tolerate freezing and hibernate terrestrially in shallow depressions, under leaf litter, grasses, logs, or rocks (Bagdonas 1968, Bellis 1961a); there are no reports of aquatic hibernation for this species (Licht 1991, Pinder et al. 1992). Wood frogs require semi-permanent and temporary pools of natural origin and adjacent wet meadows, and landscape alterations that shorten the hydroperiod of ponds can result in catastrophic tadpole mortality. Plant communities utilized by wood frogs in the Rocky Mountains are hydric to mesic and include sedge and grass meadows, willow hummocks, aspen groves, lodgepole pine forests, and woodlands with leaf litter and/or herbaceous understory (Maslin 1947, Bellis 1961a, Roberts and Lewin 1979, Haynes and Aird 1981). Wood frogs are likely to disperse into surrounding marsh and woodlands soon after oviposition (Heatwole 1961, Haynes and Aird 19891, Vasconcelos and Calhoun 2004) or remain near the waters edge (Roberts and Lewin 1979, Haynes and Aird 1981). In the early fall, wood frogs begin to seek hibernacula at or just below the ground surface, generally in upland forest habitat (Regosin et al. 2003). Licht (1991) demonstrated shelter-seeking behavior at 1.5 °C. Once they have concealed themselves for hibernation, wood frogs are very difficult to detect.

Because wood frogs use a variety of habitats and have a multiphasic life history (i.e., obligatory aquatic egg and tadpole phases plus terrestrial adult), degradation of the entire habitat or a critical piece of the habitat (e.g., breeding ponds) is likely the most critical component that managers can address. Logging, clear cuts, herbicide application, road cutting, and reservoir construction are obvious ways that amphibian habitat can be degraded. Other, less obvious mechanisms that should be considered include fish stocking, wetland draining, weed control, and road maintenance (e.g., magnesium sulfate application). There is virtually no information about how any of these less obvious, but potentially important, activities affect wood frogs. Some information is available from studies on other amphibian species (e.g., Dunham et al. 2004) such that potential or probable effects can be extrapolated.

Disease (e.g., amphibian chytridiomycosis [*Batrachochytrium dendrobatidis*]) may be important to short- and long-term amphibian population persistence, but since little is known about this environmental component, it is difficult to address beyond ascertaining its presence. Amphibian chytridiomycosis has been identified in wood frogs in Rocky Mountain National Park, Colorado (Rittmann et al. 2003, Green and Muths in press), but the impact on the populations there or on wood frogs in general has not been determined.

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INTRODUCTION

This conservation assessment is one of many being produced to support the Species Conservation Project of the USDA Forest Service (USFS), Rocky Mountain Region (Region 2). The wood frog (*Rana sylvatica*) is the focus of an assessment because it is 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 assessment addresses the biology of the wood frog throughout its range in Region 2. However, much of the ecological and physiological information available about this species is based on field work and laboratory studies accomplished in the eastern United States, and while this information generally applies to wood frogs in the Southern Rocky Mountains, it may not represent wood frogs in Region 2 precisely. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide managers, biologists, and the public with a thorough understanding of the biology, ecology, conservation status, critical conservation elements, and management of certain species based on scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and an outline of information needs. The assessment does not seek to develop prescriptive management recommendations. Rather, it provides the ecological background and a synthesis of existing knowledge upon which management must be based. It focuses on those elements that appear to be critical to the conservation of the species and on consequences of changes in the environment that result from management (i.e., management implications). The assessment cites management recommendations proposed elsewhere and examines the success of those recommendations that have been implemented.

Scope and Limitations

This assessment examines the biology, ecology, status, conservation, and management of wood frogs with specific reference to the geographic and ecological characteristics of the Rocky Mountain Region. Although a majority of the literature on the species originates from field and lab investigations outside Region 2, this document places that literature in the ecological context of the Southern Rocky Mountains. In producing the assessment, we reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on wood frogs are referenced in the assessment, nor are all published materials considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed literature is included when refereed information was unavailable, but it is regarded with greater skepticism. Unpublished data (e.g., Natural Heritage Program records) were important in estimating the geographic distribution of this species.

Little published research on wood frogs in Region 2 is available. For instance, population and trend estimates for Region 2 wood frog communities do not exist. Most of the literature evaluated for this assessment pertains to populations in the contiguous range of this species (eastern Canada, Maine, Maryland, Michigan, Virginia; **Figure 1**).

Limitations on the content and quality of information in this assessment include the limited data on wood frog occurrences in some parts of Region 2, and the general "work in progress" nature of our understanding of wood frogs in the Rocky Mountains.

Uncertainty

Science presents a rigorous, systematic approach to obtaining knowledge where competing ideas are measured against observations. However, because our observations are limited, science also focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). The geologist, T.C. Chamberlain (1897), suggested an alternative approach where multiple competing hypotheses are confronted with observation and data. Because ecological science is inherently "messy" and often must rely on observation, inference, and models (Hillborn and Mangel 1997), this alternative approach is the one that we recommend.

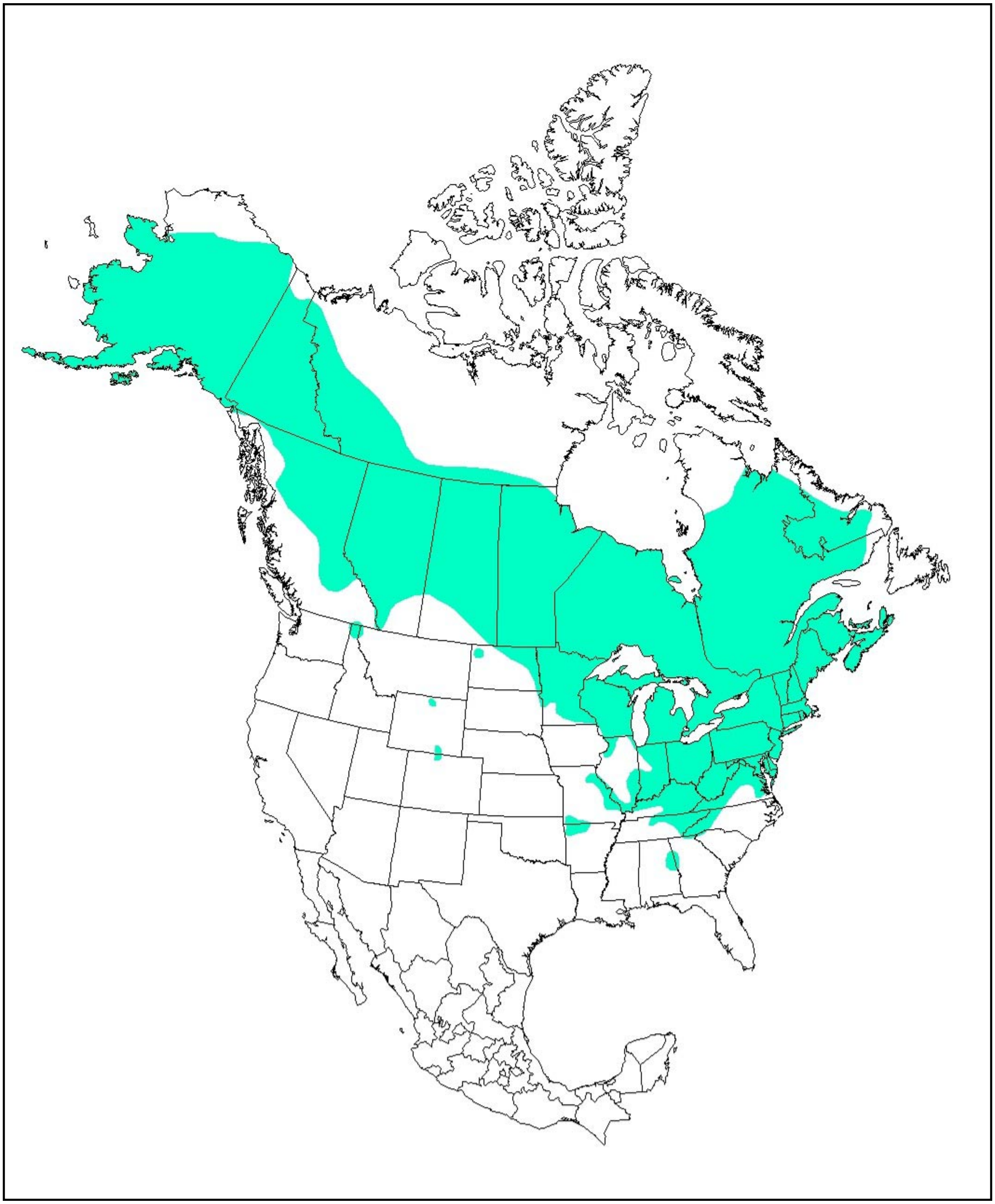

Figure. 1. North American distribution of the wood frogs (*Rana sylvatica*), adapted from Stebbins (2003).

Importantly, confronting uncertainty is not prescriptive. Successful application of this approach lies in being fully aware of the limits of the available data, and the assumptions and potential pitfalls of inference. For example, many of the studies referenced in this document are the result of research in the eastern United States. These studies should be used with caution as a guide rather than at face value as many variables are likely to be different in Region 2.

Peer Review and Publication

Recognized expert herpetologists that specialize in amphibian ecology in Region 2 states reviewed this report prior to its publication on the World Wide Web. Peer review for this assessment was administered by the Society for Conservation Biology. This conservation assessment will be published on the USFS Region 2 World Wide Web site in order to facilitate its use by USFS personnel, other agencies, and the public. A link to this publication will also be available on the Wyoming Natural Diversity Database Web site. Web publication will make this information on the wood frog accessible more rapidly than publication as a report. More importantly, it will facilitate revision of the assessment, which will be accomplished based on guidelines established by Region 2.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Federal Endangered Species Act

The wood frog is not listed under the Federal Endangered Species Act.

Bureau of Land Management

The wood frog has no special status on Bureau of Land Management lands.

USDA Forest Service

The wood frog is listed as a sensitive species in Region 2 of the USFS (USDA Forest Service 1994) but not in adjacent Regions 1, 4, or 9.

State wildlife agencies

In Colorado, the wood frog is classified as a "species of special concern". While this is not a legal designation, it does identify species at risk and directs management attention toward them (http://wildlife.state.co.us/species_cons/wildlifeindanger/howspecies.pdf). The South Dakota Natural Heritage Program ranks the wood frog as S1 (critically imperiled), but this classification does not offer the wood frog any legal protection in the state. The Wyoming Game and Fish Department classifies the wood frog as Native Species Status 3 (NSS3), on a scale of 1 to 7 where NSS1 represents critically imperiled species and NSS7 represents stable or increasing species. The NSS3 rank is based on estimates that the wood frog is widely distributed in its native range, and while extirpation is not deemed imminent, its habitat is declining or vulnerable (Oakleaf et al. 2002). Again, these ranks are designed to help biologists roughly prioritize wildlife concerns in the state, and they carry no legal, regulatory, or management weight.

Natural Heritage Program

The Natural Heritage Program network assigns range-wide and state-level ranks to species based on established evaluation criteria (e.g., Master et al. 2000). The wood frog merits a global rank of G5, which means that range-wide it is deemed secure. This is based on a synthesis of state ranks and biological evidence that suggests that the species is widespread in North America, abundant in many areas, and not of conservation concern in the majority of its range. Many local populations, however, have declined as a result of agricultural and residential development and intensive timber harvesting practices (NatureServe Explorer 2002).

A total of 49 states and Canadian provinces have given the wood frog a Heritage Rank, of which most (33) are between vulnerable (S3) and secure (S5) and seven are uncertain (S?). Four states list the wood frog as imperiled (S2) or critically imperiled (S1), and three of these states are found within Region 2. Region 2 state ranks are as follows: Colorado - S3; Kansas – not ranked; Nebraska – not ranked; South Dakota - S1; Wyoming - Bighorn Range Population – S1, Southern Rocky Mountains Population - S2 (NatureServe Explorer 2002).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

In Region 2, wood frogs occur in small, often isolated, populations that can be indirectly and directly impacted by habitat alteration, human activities, and possibly disease. Based on this information, existing state regulations, and the general paucity of detailed management plans aimed specifically at wood frogs, there is some concern that this species could be at risk in Region 2.

The wood frog is designated as critically imperiled by the South Dakota Natural Heritage Program, yet this ranking conveys no legal status. Amphibians not listed as a state endangered species are legally considered bait (South Dakota Codified Law 41-1-1), and persons in possession of a fishing license may collect up to 144 animals for non-commercial use (Backlund 1994). Data on amphibian populations and numbers collected for non-commercial use are lacking (Backlund 1994). Ninety percent of South Dakota's land is privately owned, so habitat conservation in the state emphasizes cooperative agreements with landowners.

Wyoming does not have state threatened or endangered listings for plants and animals; only plants and animals with federal status are given legal protection. State statutes exist prioritizing the protection of wetlands and critical habitat (Wyo. Stat. 11-16-103, 35-11-309, 36-12-102).

The State of Colorado listed wood frogs as threatened in 1979, due primarily to concerns regarding habitat degradation from road construction, lack of knowledge, and limited distribution (Puttmann and Kehmeier 1994). A recovery plan was produced in 1994 (Puttmann and Kehmeier), but the wood frog was removed from the Colorado list of threatened species in 1998 (Colorado Wildlife Commission Regulations 1998). The species was removed because the following recovery criteria were met: surveys detected wood frogs in >50 percent of their historic range (Colorado Division of Wildlife [http://wildlife.state.co.us/species_cons/wildlifeindanger/woodfrog.pdf] and Wilks et al. 1998); threats to habitat were perceived to be minimal, the "vast majority of *Rana sylvatica* populations and habitat is located on U.S. Forest Service lands" (Colorado Wildlife Commission Regulations 1998); and the USDA Forest Service provided assurances that wood frog breeding habitat on National Forest System land was secure for the "foreseeable future" (http://wildlife.state.co.us/species_cons/WildlifeInDanger/woodfrog.pdf). Wood frogs are designated as nongame wildlife by the state of Colorado and as such are "protected from pursuit, capture, or harvest" except by special permit (Colorado Wildlife Commission Regulations 1998).

The Colorado recovery document (Puttmann and Kehmeier 1994) lists habitat alteration, acid precipitation, climatic change, and disease/immune suppression as potential limiting factors to wood frogs. Although considered an issue at the time of preparation of the recovery plan, concurrent and subsequent investigations concluded that acid precipitation is not likely a major issue for wood frogs in Region 2 (Corn and Vertucci 1992, Vertucci and Corn 1996), except possibly at very specific sites (Muths et al. 2003b, Campbell et al. 2004). We found no evidence that wood frogs are used for bait in Colorado, but wood frogs do occur in places where fishing occurs and such use is a possibility that should be considered.

While the 1994 Colorado wood frog recovery plan (Puttmann and Kehmeier 1994) provides the rudiments for conservation and management action, it requires greater rigor and detail to be useful. Few of the actions described in the Colorado plan were undertaken, primarily because of state delisting. However, most actions were not described with appropriate statistical rigor and would not have provided defensible data had they been implemented. For example, inventory and monitoring protocols are not described clearly, and key terms such as "viable" and "stable" are not defined.

Biology and Ecology

Description and systematics

Wood frogs are medium-size frogs, with a snout-vent length of 3.2 to 8.2 cm (1.25 to 3.25 inches) (Stebbins 2003). Color variations occur within local populations as well as across the species' geographic range, and albinism has been documented in Wisconsin (Luce and Moriarty 1999). Colors include light tan to dark brown, olive, green, gray, and pink. Females may be lighter in color than males (Seale 1982, King and King 1991). A study in Indiana revealed that wood frogs are capable of changing color to match the substrate on which they are found (King and King 1991); this characteristic likely occurs throughout the range of the frog. A black or dark brown mask extends from the tip of the nose across the eye ending just past the tympanum, and a white jaw stripe is present below the mask. There are dark spots on each side of the chest at the foreleg, and a flecked, or reticulated, marking pattern is present laterally between dark dorsal and light ventral regions. Dorsolateral folds are present, and there may be as many as seven bold or indistinct leg bars. Leg bars may also be absent entirely. Webbing is absent on the front feet and complete on the rear feet (Stebbins 2003). Occurrence of the mid-dorsal stripe is greater in the north and west areas of the range, and absent in the south (Martof and Humphries 1959). In Colorado, approximately 93 percent of wood frogs have the mid-dorsal stripe (Porter 1969a). Baxter and Stone (1985) reported the dorsal stripe present in Medicine Bow (Wyoming) populations and absent in Bighorn (Wyoming) populations. Occurrence of the dorsolateral stripe in North and South Dakota is closer to 50 percent (R. Newman personal communication 2003).

Tadpole coloration is brown to gray dorsally, copper to bronze on the sides, and light with a pinkish sheen ventrally (Livo 1998a). The tail fin is high and strongly arched, and the anus is located on the right side near the tail fin (Livo 1998a). The labial tooth row formula for wood frog tadpoles can be either two anterior-three posterior or three anterior-four posterior (Hammerson 1999). Wood frog tadpoles are morphologically distinct from their conspecific, the chorus frog (*Pseudacris maculata*), by the placement of the eyes, which are lateral in the chorus frog versus dorsal in the wood frog (Livo 1998a).

Wood frog eggs are bi-colored (black above, white below) and deposited in softball-sized, globular masses of 700 to 1250 eggs (Corn and Livo 1989). The egg masses are generally laid in communal clusters and may protrude partially above the surface of the water (Hammerson 1999).

Currently, *Rana sylvatica* is the only valid designation for the wood frog, and no subspecies are recognized (Integrated Taxonomic Information System 2003). Martof and Humphries (1959) characterized five phenotypes based on variations in coloration, relative leg length (tibia to body,) presence or absence of white dorsal stripe, presence or absence of tibial bars, and other visual characteristics. South Dakota wood frogs were included inferentially in the "Midwest" phenotype based on characteristics of specimens from North Dakota and Minnesota: brown background with light sides; dorsolateral folds narrow; mid-dorsal stripe occasionally present; "diffuse" dorsal and lateral markings making a more gradual change from dark to light. Colorado and Wyoming wood frogs were assigned to the "Rocky Mountain" phenotype: coloration is tan to brown dorsally, white to clear laterally having large, reticulated lateral markings with warts; dorsolateral folds are broad and heavily pigmented; mid-dorsal stripe present, "bordered by dark tan or brownish region"; leg bars generally indistinct, though they may be distinct or absent. Porter (1969b) designated the Rocky Mountain phenotype as a new species, *R. maslini*, based on unsuccessful crossbreeding with *R. sylvatica* collected in Manitoba. However, Bagdonas and Pettus (1976) found reproductive success to be equivalent between Colorado-Manitoba hybrids and controls. *Rana maslini* is considered an invalid species (Collins 1990, Integrated Taxonomic Information System 2002).

Distribution and abundance

The wood frog is the second most widely distributed frog in North America, covering nearly 10.5 million acres and superceded only by the leopard frog (*Rana pipiens*) (Martof and Humphries 1959). The wood frog is found across Canada, from Labrador west to British Columbia, and into the Yukon Territory (**Figure 1**). In the United States, it is present throughout most of the east from Maine to Alabama. The western edge of its contiguous distribution runs through eastern Illinois, Wisconsin, Minnesota, and North Dakota with the southern edge including Bonner and Boundary Counties in extreme northern Idaho (Dumas 1957). Disjunct populations occur in Missouri, Arkansas, Oklahoma (G. Seivert personal communication 2003), Colorado, and Wyoming. It occurs in Alaska as far north as the Arctic Circle.

Wood frogs likely colonized the southern Rocky Mountains during the Wisconsonian age of the late Pleistocene period as vegetation zones shifted southward ahead of glaciers (Martof and Humphries 1959). As the glaciers receded, isolated populations persisted in the high mountain areas, where environmental conditions remained suitable (e.g., cool and wet). South Dakota, Colorado, and Wyoming are the only Region 2 states with current or historical records of wood frogs (**Figure 2**). Roberts County in northeastern South Dakota is on the western edge of the species' contiguous range, but it has not been seen in historical sites there since 1994 (D. Backlund personal communication 2003).

Wood frogs exist in Region 2 as isolated relict populations, occurring in the Medicine Bow – Routt National Forest (Albany County, Wyoming and Grand, Jackson, and Larimer counties in northern Colorado) and the Bighorn National Forest (Sheridan County, Wyoming). Some surveys have been conducted in Colorado (e.g. Colorado Division of Wildlife [http://wildlife.state.co.us/species_cons/wildlifeindanger/woodfrog.pdf] and Wilks et al. 1998), providing a rudimentary understanding of its distribution in the state. Wyoming populations in the Big Horn Mountains and Medicine Bow Range have received less attention. Where animals are found, they can be common and abundant or relatively rare, as they are at some sites in the Never Summer Range in Northern Colorado (E. Muths personal observation). While some surveys have been performed in Region 2, to our knowledge,

Figure 2. Distribution of the wood frog (*Rana sylvatica*) in relation to Region 2 national forests (light gray). (A) Green areas represent suspected distribution based on documented occurrences. Solid black dots represent confirmed sites with likely breeding activity in (B) the southern Rocky Mountains of Wyoming and Colorado and (C) the Bighorn Mountains of northern Wyoming. Crosses (X) represent sites where amphibian surveys were conducted, but where no wood frogs were found.

no statistically robust survey method has been used to provide an unbiased estimate of the number of wood frog populations across the landscape. To provide such an estimate, a survey must carefully define the area of inference and address the issue of detectability (Mackenzie et al. 2002). These methods are available and have been applied successfully to amphibian surveys and monitoring (Muths et al. in press).

Population trend

A study by Halverson (2001, unpublished data) reported no significant changes in the distribution or abundance of southern Rocky Mountain wood frog populations compared with previous surveys by Haynes and Aird (1981) and Corn et al. (1997). However, none of these studies was comprehensive in their examination of wood frogs over the entire range in the Rocky Mountains, and the rigor of the studies is questionable. Conclusions, therefore, are tentative at best.

Formerly abundant in the state, the last record of wood frogs in South Dakota was a questionable auditory identification in 1998 (D. Backlund personal communication 2003). While the South Dakota Department of Game and Fish has accepted unconfirmed auditory observations as proof of presence, the last official, visual confirmation of the species in the state was in 1927. It remains unclear whether this decline is a range contraction or a natural extirpation due to the dynamic nature of amphibian populations (Berven and Grudzien 1990, Pechmann et al. 1991).

The status of individual populations of wood frogs (e.g., effective population size, number of egg masses produced per year, survival or recruitment rate) is not known, nor is there any evaluation of the robustness of existing populations. Because of this dearth of data, it is impossible to assess relevant demographic parameters through modeling (e.g., Program MARK). One wood frog population in Rocky Mountain National Park is being monitored currently (2002 to present), but because of low capture rates and the limited time this project has been underway, the data are too scarce to run appropriate models (Muths and Scherer unpublished data).

Activity and movement patterns

Circadian

Activity of wood frogs varies among age classes and season. Adults are diurnal in the spring when average daily temperatures are cooler, but they may be active at any time of day in the warmer summer months (Hammerson 1999). In Alaska, the majority of egg masses are laid during the warmest part of the day (Herreid and Kinney 1967). Bagdonas (1968) observed most egg laying occurred at night in the Rocky Mountains. Metamorphs seek refuge under rocks during the heat of the day and migrate to wet meadows and woodlands at night when ambient temperatures are cooler (Bagdonas 1968).

Seasonal

Kessel (1965) found that "…the time of thaw in the upper layers of the ground (and about ponds)…" was the most significant factor influencing commencement of breeding behavior. Annual variations in environmental conditions, specifically temperature and snowmelt, can cause the first date of calling in Alaska to vary by as much as three weeks between years (Kessel 1965). This observation apparently applies to Rocky Mountain populations as well, where wood frogs become active in early May (Bagdonas 1968) and calling has been observed as early as April (E. Muths personal observation). Range-wide, calling behavior begins after at least four consecutive days with mean daily temperature above 0 °C (Kessel 1965). Upon emergence from hibernation, adults move directly to breeding sites. Ice may still be present on the surfaces of ponds and/or the surface may be subject to freezing overnight (Kessel 1965, Bagdonas 1968, Hammerson 1999). Breeding is a seasonal event, generally of short duration (see breeding phenology below).

Amphibians have been characterized as having poor dispersal ability (Funk et al. 2005). Consequently, amphibian populations that are separated by long distances or apparently inhospitable habitat are often assumed to be isolated both genetically and demographically. However, recent research has shown that amphibian populations may be more connected by individual movements and gene flow than previously thought. In the Shenandoah Mountains of Virginia, Berven and Grudzien (1990) found marked juvenile wood frogs at breeding ponds an average of 1,140 (± 324 [SD]; males) and 1,276 (± 435 [SD]; females) meters from their natal pond. Newman and Squire (2001) found that subtle genetic differentiation between wood frog populations in the Prairie Pothole region of North Dakota only began to emerge at distances of a few kilometers. These studies suggest that there is potential for wood frogs to disperse considerable distances. In Region 2, telemetry data from Rocky Mountain National Park indicated that wood frogs moved less than 10 m between daily sightings during the breeding season (E. Muths unpublished data), but these data do not address post-breeding movements and are based on a small sample size. More data on movements of wood frogs in Region 2 are needed before conclusions can be drawn about short or long-term movements.

Habitat

General requirements

Wood frogs utilize a broad range of aquatic and moist habitats. Breeding ponds may be permanent, semi-permanent, or temporary. Non-breeding habitat is consistently moist and humidity has been shown to be important to wood frog microhabitat selection (Bellis 1962). Microhabitat selection in wood frogs is governed by substrate structure and the moisture content of both substrate and air (Heatwole 1961, Bellis 1962, Roberts and Lewin 1979).

Plant communities utilized by wood frogs vary across their range. In the eastern and southern portion of its distribution, they are found in both deciduous (hardwood) and coniferous (spruce and tamarack) forests with herbaceous understory, preferring closed canopy conditions (Gibbs 1998a). In the western Canadian provinces and the Rocky Mountains, they are more commonly associated with sedge wetlands with adjoining grassy meadows, willow bogs, coniferous forests, and aspen groves. The importance of canopy cover in the West is unknown, but many sites that support wood frogs are characterized by only partial canopy cover or are open (Muths and Scherer personal observation). In eastern North Dakota, breeding sites are wetlands and prairie potholes surrounded by native grassland or cropland. While Murphy (1987) identified breeding sites with clumps of aspen (*Populus tremuloides*) nearby, many sites have no trees present (R. Newman personal communication 2003). Sites selected for oviposition may be little more than shallow depressions in the ground (R. Newman, personal communication). Wood frogs have been found inactive in the grasslands one month prior to breeding season/emergence, suggesting that they hibernate in close proximity to breeding locations.

Haynes and Aird (1981) conducted a study of wood frog habitat requirements in Colorado. They determined that preferred breeding ponds are usually small (less than 0.25 hectare), semi-drainage ponds of natural origin, less than 1 m deep, fish-free, with emergent vegetation. Wood frogs may also use inactive beaver ponds and man-made ponds if topographical features are suitable. For example, typical oviposition sites are shallow, unshaded north shores with emergent vegetation, and a depth of 10 to 30 cm within 3 m of shore (Haynes and Aird 1981). Wood frogs may also use anthropogenic pools such as roadside ditches or depressions and wheel ruts from forest management activities, but many such locations dry before metamorphosis is completed (Biesterfeldt et al. 1993, DiMauro and Hunter 2002). The shade-intolerant sedge, *Carex rostrata*, is an indicator species for wood frog breeding sites in Colorado, "If *C. rostrata* or its ecological equivalent did not flourish along the north shore, [wood frogs] did not breed there" (Haynes and Aird 1981). In the post-breeding season, wood frogs make extensive use of sedge-meadows, hummock-bogs, forest floor leaf litter, fallen trees, branches, and roots (Heatwole 1961, Bellis 1962, Didyk and Burt 1999).

Seasonal and life history shifts

In early spring, adult wood frogs congregate at breeding ponds, and they remain in or around the pool until breeding is completed, usually one to two weeks (Bagdonas 1968, Hammerson 1999). Beginning in late spring or early summer, adults disperse from breeding sites into surrounding moist habitats such as sedge and grass meadows, willow bogs, and damp woodlands (Herreid and Kinney 1967, Haynes and Aird 1981, Vasconcelos and Calhoun 2004). Sometimes, however, they do remain at the breeding pond (Roberts and Lewin 1979, Haynes and Aird 1981).

In the Rocky Mountains, adults and young-of-the-year become inactive in September (Bagdonas 1968) and seek appropriate refugia for hibernation. The wood frog is a freeze-tolerant species and can withstand freezing of up to 65 percent of total body water (Layne and Lee 1986). Glycogen in the liver is converted to glucose, which is thought to protect internal organs and intracellular fluids from freezing (Pinder et al. 1992). The ability to withstand freezing enables wood frogs to hibernate at or near the ground surface. Hibernacula have been described by many authors (Blanchard 1933, Wright and Wright 1949, Heatwole 1961, Hodge 1976, Schmid 1982, Licht 1991) and are always shallow depressions that may be under dead vegetation, leaves, grasses, rocks, or logs. Licht (1991) outlined preferences for hibernation refugia: 1) leaf litter, 2) moist soil, and 3) wet mud, which was only selected in a laboratory setting. This preference of sites, determined by substrate moisture level, is related to the physiology of freeze tolerance in wood frogs. Layne et al. (1990) showed that wood frogs do not freeze until the skin comes in contact with ice crystals, at which point body water turns to ice within 30 minutes. Avoidance of substrates with high water content (e.g., mud) may minimize freezing and thus demand on liver glycogen stores (Licht 1991). Aquatic hibernation by wood frogs has not been reported for adults or tadpoles; adults can survive under ice for up to 10 days with no ill effects (Licht 1991, Pinder et al. 1992). The shallow nature of hibernacula allows for periods of activity when ground surface temperatures permit (Zweifel 1989, Licht 1991). Wood frogs have demonstrated normal activity at temperatures as low as 3 to 4 °C in laboratory and field experiments (Johansen 1962, Wells and Bevier 1997).

We are not aware of any accounts of overwintering tadpoles; Licht (1991) referenced Martof and Humphries (1959) and Hodge (1976) stating "The northern distribution is limited primarily [by]…the number of days breeding ponds with developing larvae remain ice-free." Pinder et al. (1992) stated that wood frog larvae "typically" do not overwinter.

Like most amphibians, wood frogs have a complex life cycle with both aquatic and terrestrial stages. Eggs and larvae are obligately aquatic; eggs are generally attached to vegetation such as sedge or to sticks. Rocky Mountain populations require habitats that will retain water for at least 85 days (Bagdonas 1968, Baxter and Stone 1985); the larval period varies between 60-120 days across the species' range (Martof and Humphries 1959). Embryonic and larval development rates are variable, depending on ambient air and water temperatures (Herreid and Kinney 1967, Duellman and Trueb 1994). Newly hatched larvae are known to seek refuge under the jelly mass for a short period of time, and they may feed on algae present in the matrix (Haynes and Aird 1981, Thurow 1997). Once metamorphosis is completed, juveniles will often remain near the water's edge for a few days before dispersing into terrestrial habitats (Bellis 1965, Bagdonas 1968).

Area requirements

During the post-breeding season in Minnesota, Bellis (1965) determined that the mean home range of wood frogs, at least one year old, in natural habitat was 64.5 m^2 and that the average distance between captures of adults was 11.2 m (Bellis 1965). Furthermore, wood frogs exhibited familiarity with their habitat, and a tendency to remain in a restricted area, suggesting non-random spatial distribution among adults (Bellis 1965). Seale (1982) observed a similar spatial distribution among males in a breeding pond in Pennsylvania. Maximum population density reported was 19.6 animals per 1000 m^2 in northern Alberta, in a mixed community of willow, grasses, and aspen (Roberts and Lewin 1979). More recently, a field study in eastern Massachusetts reported winter densities of wood frogs as 0 to 6.3 frogs per 100 m^2 (Regosin et al. 2003).

While the studies mentioned above suggest relatively small areas used by wood frogs, the amount of habitat and the degree of connectivity necessary between habitat patches for wood frogs in Region 2 is unknown. The patchiness of appropriate habitat at high elevation sites in Region 2 and data that indicate that wood frogs do move from specific breeding sites to overwintering hibernacula should be considered in management decisions. For example, non-breeding habitats may be more than 400 m from breeding sites (Bellis 1965). Newly emerging juveniles were captured 300 m from natal ponds (Vasconcelos and Calhoun 2004) presumably in the process of immigrating to new ponds or finding appropriate hibernacula. Protecting a breeding site alone is not adequate to protect the species.

Landscape context

While wood frogs will make use of many types of water bodies for breeding, the characteristics of breeding localities are generally similar. Preferred ponds have emergent vegetation, still water, and shallow, sloping shores. Moist grassy meadows, willow bogs, or forests with moderate to thick leaf litter exist within 100 m of shore. Typical plant community composition at breeding localities in the Rocky Mountains includes sedges, grasses, willows, lodgepole pine (*Pinus ponderosa*), and aspens. Forests used by wood frogs for hibernation are characterized by fallen trees, branches, roots, mucky depressions from uprooted trees, leaf litter, and/or herbaceous understory (Bellis 1961a, Bagdonas 1968, Roberts and Lewin 1979).

Juvenile wood frogs in the East tend to move farther from their natal pond, and males tend to return more often than females to their natal pond to breed (Vasconcelos and Calhoun 2004). These data indicate that there is some immigration occurring from ponds. What this suggests is that a landscape context larger than a pond with surrounding forest may be important to a functioning wood frog population. Although research is lacking on the use of landscape by wood frogs in Region 2 and the West, we can tentatively infer that multiple ponds connected by appropriate terrestrial habitat will foster population stability, facilitate gene flow, and provide refugia if a natural disaster destroys a particular pond within a particular landscape.

Food habits

Adults and juveniles are carnivorous, feeding on arthropods such as ants, flies, beetles, and spiders (Moore and Strickland 1955). Tadpoles are omnivorous, feeding on algae, bacteria, and periphyton (single-celled organisms), but they have been shown to be opportunistic predators of amphibian eggs and hatchlings including the American toad (*Bufo americanus*), gray treefrog (*Hyla chrysoscelis*), pickerel frog (*Rana palustris*), and spotted salamander (*Ambystoma maculata*) (Morin and Johnson 1988, Petranka et al. 1994, 1998). None of these species occur in the Rocky Mountains, and a similar carnivorous habit of tadpoles is undocumented.

Breeding biology

Breeding phenology

Wood frogs breed early, often arriving just as ponds become free of ice; snow may still be present on the ground (Waldman 1982). In Colorado and Wyoming, this can be as early as April, though it is generally in May (Hammerson 1998, E. Muths personal observation). The breeding period is short, usually one to two weeks in duration in the Rocky Mountains (Hammerson 1999) and the same in the Midwest (Stebbins 1985). Several authors have observed migration of adults away from the breeding area shortly after oviposition is completed (e.g., Bellis 1962).

Males may arrive at breeding grounds before females (Banta 1914, Guttman et al. 1991, Hammerson 1999), or the sexes may arrive synchronously (Schueler and Rankin 1982, Waldman 1982). Breeding and oviposition are usually completed in 14 days or less but may last as long as 22 days, depending on temperature and other weather conditions (Herreid and Kinney 1967). Eggs hatch after approximately four to seven days (Bagdonas 1968), and metamorphosis occurs between 78 and 85 days after egg deposition (Haynes and Aird 1981).

Breeding behavior

Wood frogs breed explosively, congregating at breeding sites as soon as open water is available. Females assess breeding sites and avoid sites with fish to such an extent that avoidance behavior may be more important than strong philopatry to natal sites (Hopey and Petranka 1994). They will often remain hidden or submerged at the bottom of the pond until they are ready to mate (Banta 1914, Bagdonas 1968, Seale 1982).

Amplexus, the physical grasping of the female by the male frog, generally occurs in the water. However, terrestrial amplexus has been observed (Schueler and Rankin 1982). This unusual behavior is thought to be a result of the abrupt onset of spring-like conditions when large numbers of frogs emerge from hibernation simultaneously and competition for mates is so extreme that males may seize females before they get to water (Schueler and Rankin 1982). There are no accounts of such terrestrial breeding behavior in Region 2.

Amplexus may persist up to 84.9 hours, but oviposition and presumably sperm deposition are completed in 15 minutes or less (Howard 1980). During oviposition, female wood frogs remain close to submerged vegetation, roots, or branches and make slight forward and backward motions causing the egg string to fold back on itself and form the characteristic globular mass (Thurow 1997). A single egg mass may include between 700 and 1250 eggs (Corn and Livo 1989). Wood frogs deposit their eggs in large communal masses. Howard (1980) observed 58 egg masses in 1 m^2 of a 256 m^2 pond.

Males call from the water and actively search for mates when frog density is high (Woolbright et al. 1990). Seale (1982) observed: "The calling males in all eight ponds floated at fairly regular intervals on the surface, although distances between males shifted constantly…" and "…surface area/male frog was comparable from pond to pond (2.4 +/- 0.4 m^2)." Males do not defend a specific territory but will advertise from different locations in the pond (Seale 1982). Hopey and Petranka (1994) observed males traveling between adjacent ponds in North Carolina during the breeding season; one male visited four ponds in less than 10 minutes. Sex recognition is by trial embrace (Banta 1914, Howard 1980), and males will amplex nearly any moving object of appropriate size (Bagdonas 1968, Howard 1980). Unpaired males will attempt to dislodge males already in amplexus by clasping and kicking (Bagdonas 1968, Seale 1982, Waldman 1982), and pairs that are attacked may seek refuge at the bottom of the pond or try to swim away (Banta 1914, Howard 1980, Waldman 1982). Aggregations of unpaired males are attracted to combat, and many males may become involved in the struggle for a female, occasionally resulting in her death (Banta 1914, Howard 1980). Observations by Howard (1980) indicated that such attempts generally occur at the oviposition site and that dislocation attempts are rarely successful and unrelated to male size. Males do not feed during the breeding season, relying on liver glycogen stores for energy (Wells and Bevier 1997). There is no information available on whether or not females feed during the breeding season.

Population demography

Fecundity and survivorship

Male wood frogs reach sexual maturity before females (Bellis 1961b, Berven 1990). Howard (1980) observed males to breed in the first year after metamorphosis while female sexual maturity was delayed until their second year. Bellis (1961b) observed males breeding at two years of age, but also observed female sexual maturity delayed until age three in Minnesota. Conversely, in a seven-year study in Maryland, Berven (1990) observed up to 20 percent of females breeding in the first year after metamorphosis. Wood frogs living in colder climates (e.g., high latitude and/or altitude areas of Region 2) tend to live longer and may mature much later; in northern Quebec, males and females mature at age 4 and 6, respectively (Leclair et al. 2000). Male breeding probability is largely a function of the sex ratio (Howard 1980) with polygyny playing a secondary role in mate acquisition (Howard and Kluge 1985). The probability that a male will breed in any given breeding season varies; for example, some males do not mate at all while others may breed twice (Howard 1980).

The delayed maturation of females may provide extra time to gather adequate resources for vitellogenesis. Howard (1985) found that larger females produced up to five times as many eggs as smaller females. Younger females produce more small eggs, and older females produce fewer larger eggs (Berven 1988.) No correlation has been found between egg size and viability. Relationships between egg size, food availability, and larval densities “suggest that the relative fitness of large or small eggs may actually vary with environmental conditions” (Berven and Chadra 1988).

Fluctuations in numbers of reproductively mature adults are due largely to larval survival rates. Berven (1990) identified larval survival rates as the most critical factor in population fluctuations, with 92 to 99 percent of all mortality occurring before the onset of metamorphosis. Many factors, including higher than normal water temperatures, premature pond drying, and chemical disturbances, may affect larval survival. Herreid and Kinney (1967) observed embryonic mortality at temperatures of 7.5 °C, with cessation of development at 3.4 °C. In laboratory experiments, Bagdonas and Pettus (1976) noted significant reduction in zygote viability at temperatures greater than 27 °C.

Larger pre-metamorphic size is correlated positively with juvenile survival, and size at metamorphosis relates to adult size and age at first breeding. Larger individuals breed earlier and have higher survival rates (Berven 1990). In Berven’s (1990) study, rainfall was the only environmental factor to affect juvenile and adult survival. Increased rainfall led to greater survival (Berven 1990). An important, often overlooked, fact is the high probability and high frequency of complete reproductive failure during a season both at the level of the individual and at the level of the pond or even metapopulation. This inherent feature of amphibian reproduction - that of natural and often catastrophic reproductive failure - is one of the primary difficulties in the determination of amphibian decline (Pechmann et al. 1991).

Life history characteristics

There are no data on life history traits for Region 2 wood frogs specifically. The following information comes from studies of this species in Maryland, Michigan, Minnesota, and Virginia. Site fidelity varies but appears to be generally high. Wood frogs observed by Berven and Grudzien (1990) had a high incidence of site fidelity, with 82 percent of adults breeding in their natal pond, and breeding adults were 100 percent faithful to the pond in which they first bred. Vasconcelos and Calhoun (2004) provided estimates of breeding pool fidelity that ranged from 78 to 100 percent (mean fidelity across ponds = 98 percent) for males and from 38 to 98 percent for females (mean fidelity across ponds = 88 percent). Conversely, Hopey and Petranka (1994) suggest that the species is opportunistic and will abandon breeding sites in favor of nearby sites with lower predator densities, and Petranka et al. (2004) observed wholesale shifting of populations from a pond to adjoining ponds.

Spatial and genetic concerns

Spatial characteristics of wood frog populations in Region 2 have not been examined. There are ongoing genetic studies (A. Halverson, Yale University, PhD candidate, unpublished data) that examine the relationships between various populations within the Rocky Mountain Region, and studies that are attempting to determine how the genetics of wood frogs in this region relate to the genetics of wood frogs in other areas (J. T. Irwin, unpublished data). A small-scale, landscape-level assessment of wood frogs on the west side of Rocky Mountain National Park as part of dissertation work through Colorado State University is in progress (R. Scherer, PhD candidate; Drs. B. Noon and E. Muths, supervisors). This study is examining the population structure in the Kawuneeche Valley in Rocky Mountain National Park from a landscape and a genetic perspective, but no data are yet available. The Colorado and Wyoming populations represent the oldest genetic stock of wood frogs in the West (J. T. Irwin and D. M. Green, unpublished data). On a broad scale, the closest relatives of these wood frogs belong to another relict population in the Ozark Mountains of Arkansas and to populations of wood frogs in western Canada. These data strengthen the hypothesis that the Colorado and Wyoming populations are relicts from a relatively rapid post-glacial dispersal that reached as far north as Alaska. The South Dakota populations have not been included in this analysis, but populations from North Dakota also belong to this western lineage (J.T. Irwin and D.M. Green, unpublished data).

A study of the genetic structure of wood frogs at Lake Itasca, NY found differentiation at a distance of 5 to 6 km (Squire and Newman 2002). In an examination of North Dakota populations by Newman and Squire (2001), differentiation occurred at 2.2 to 5 km. Berven and Grudzien (1990) identified the average "genetic neighborhood" radius as 1266 m^2, further stating that size to be an overestimate given the mountainous terrain of the study area. These studies suggest that the distance necessary to affect genetic differentiation is related to topographical barriers to dispersal and not necessarily linear distance. In localities where there is a high density of suitable ponds or pools, larger distances are necessary to achieve genetic differentiation; in areas such as the Rocky Mountains where breeding sites are separated from one another by xeric woodlands or high mountain passes such differentiation may occur between populations that are relatively close to one another. Unfortunately, the information described above is not available for wood frogs in Region 2. Relevant studies are underway, but still several years away from the presentation of any definitive information. These data, when available, will be relevant to answering questions of whether or not isolated wood frog populations are fully viable, subject to long- term genetic problems, or particularly vulnerable to perturbation.

Community ecology

As outlined below and in the habitat section above, the wood frog interacts with its environment in many, complex ways through its life stages. To further clarify these ecological linkages, we have developed two envirograms: "larvae" (eggs and tadpoles) and "adults" (post metamorphosis) stages for this species (**Figure 3a** and **Figure 3b**). It is a useful tool to conceptualize how various factors might affect wood frogs, but it must be duly noted that this is not the last word in what is important to this animal's survival and reproduction. It is meant, rather, as a rough and hypothetical snapshot of what we currently believe to be the key components in its natural history, most of which are discussed in detail throughout this assessment.

Predators and competitors

Adult and juvenile wood frogs are consumed by largemouth bass (*Micropterus salmoides*, Cochran 1999), smallmouth bass (*M. dolomieui*, Bagdonas 1968), western garter snakes (*Thamnophis elegans*, Bagdonas 1968), raptors (Banta 1914), mallards (*Anas platyrhynchos*, Eaton and Eaton 2001), and whimbrels (*Numenius phaeopus*, Didyk and Burt 1999) and likely raccoons (*Procyon lotor*) and skunks (*Mephitis mephitis*). Tadpoles are preyed upon by raccoons (Thurow 1994), ambystomid salamanders (Walls and Williams 2001, Wilbur 1972) and larval dragonflies (*Anax* sp.). Waterstriders (*Gerris* sp., Eaton and Paszkowski 1999) will prey opportunistically on tadpoles trapped in shallow, drying pools. Eggs may be eaten by amphibians, snakes, fish, and invertebrates (Pough et al. 2001). Leeches (*Macrobdella* sp., Cory and Manion 1953) and caddisflies (*Limnephilus* sp., Stein 1985) are two examples of invertebrate egg predators. All of these potential predators occur in Region 2, except the whimbrel. Although we found no documentation regarding predation specifically on wood frogs, sandpipers, corvids, and foxes have been observed preying on other amphibians in Region 2. (Beiswenger 1981, Corn 1993, Devito et al. 1998, Livo 1998b).

The wood frog is an important component in determining the structure of assemblages of amphibians in the Southeast (Petranka et al. 1998). American toads, gray treefrogs, and pickerel frogs (not present in Region 2) have evolved avoidance behavior toward the presence of wood frogs and will not lay eggs in pools where wood frog eggs are present (Petranka et al. 1998). Interactions of this kind are unstudied in Region 2.

Competitive outcomes between wood frogs and leopard frogs can vary with environmental conditions (DeBenedictis 1974, Werner 1992, Relyea 2000.) In the absence of predators, wood frog tadpoles may outcompete leopard frog tadpoles, but with the threat

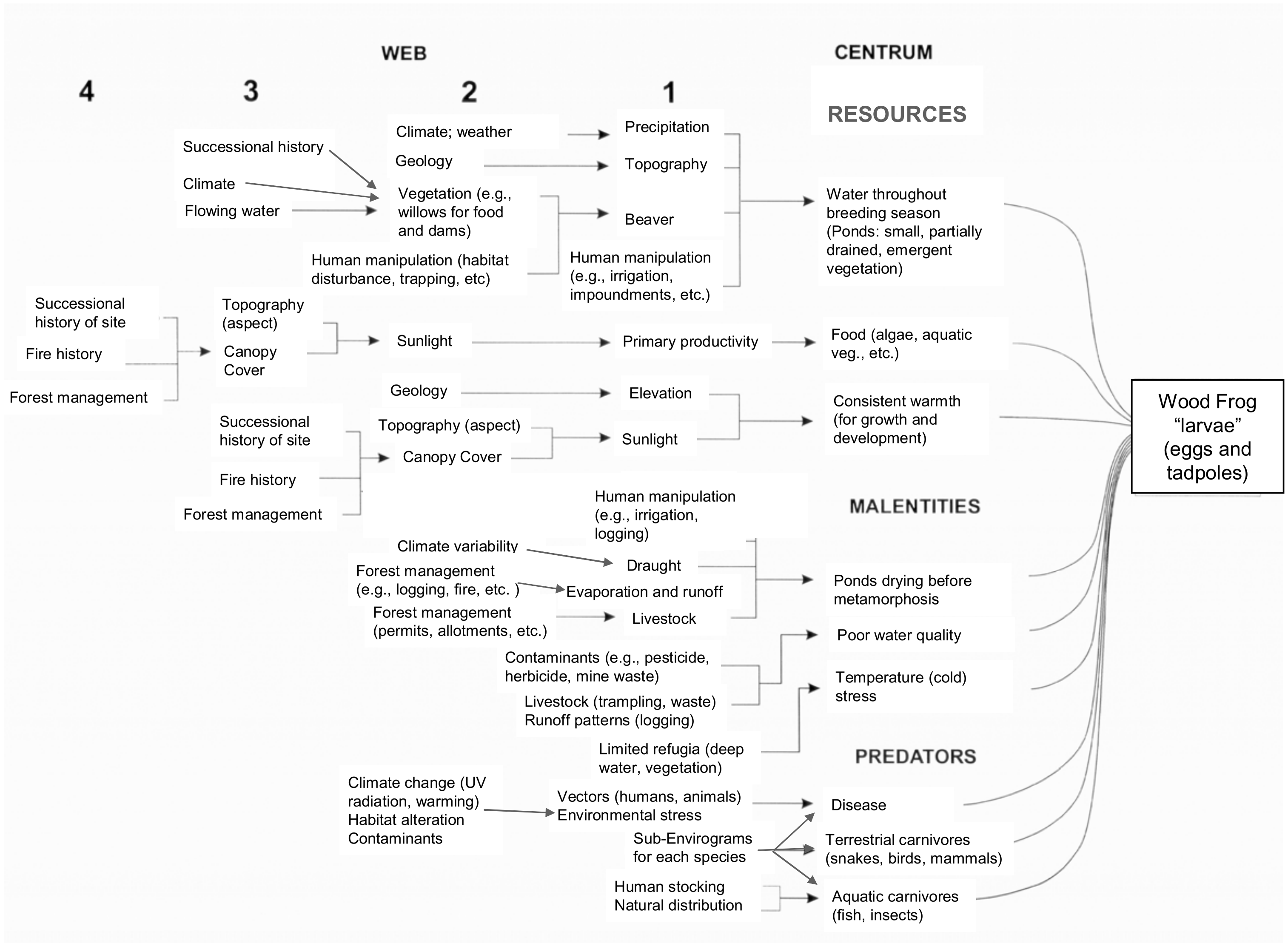

Figure 3a. Envirogram for wood frog (*Rana sylvatica*) larvae.

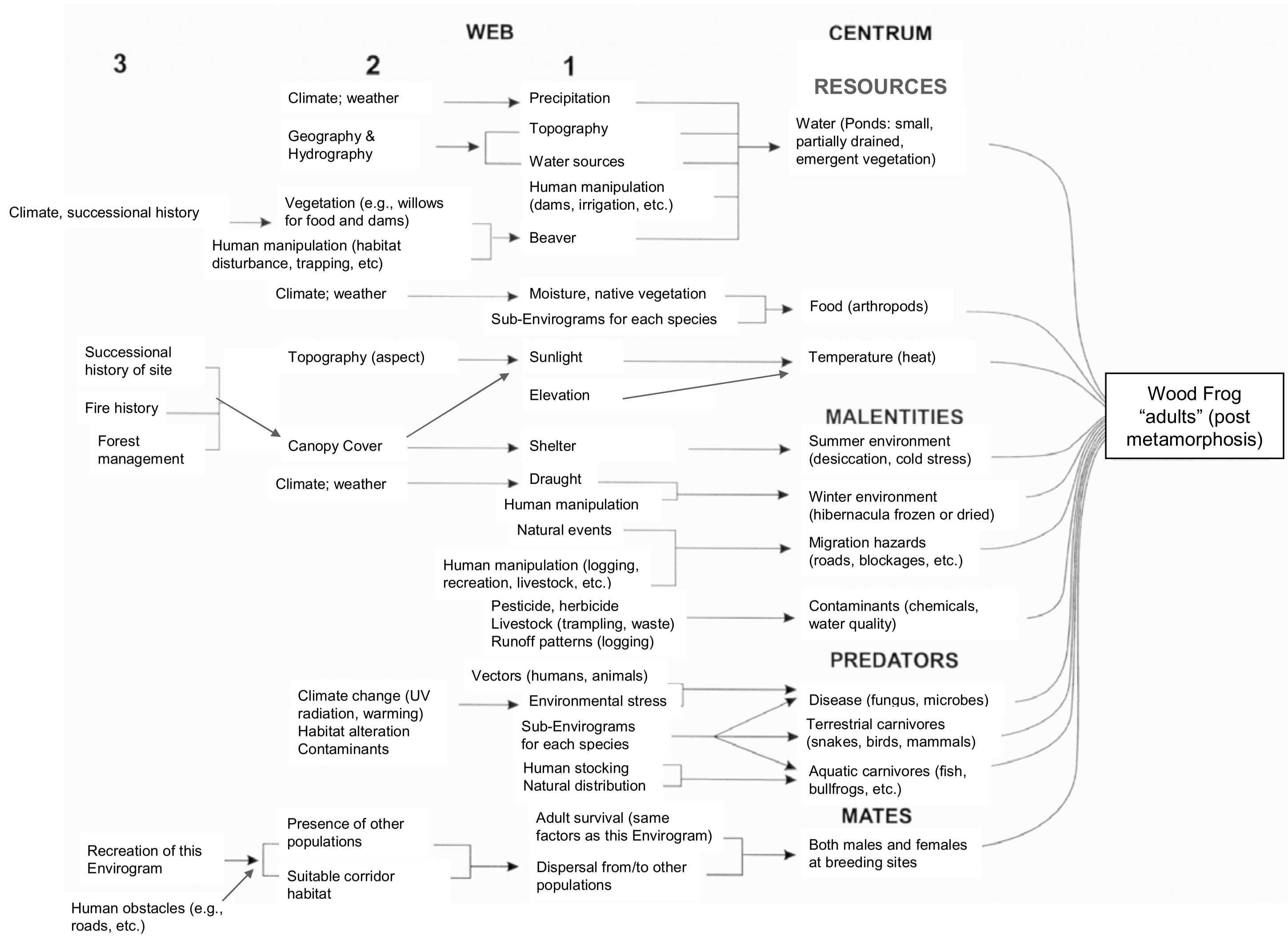

Figure 3b. Envirogram for post-metamorphosis wood frogs (*Rana sylvatica*).

of predation, wood frog larvae become less active and harvest fewer resources (Relyea 2000). Male size advantage is important in same-sex interactions, and interspecific competition between males have shown larger males are more successful breeders. However, Howard (1985) did not observe any mate choice behavior.

Parasites and disease

Two emerging infectious diseases of amphibians have been reported in wood frogs: iridovirus and amphibian chytridiomycosis, caused by *Batrachochytrium dendrobatidis*. Iridovirus-associated die-offs of wood frogs have been observed in Alaska, Massachusetts, North Carolina, Rhode Island, and Tennessee (National Wildlife Health Center 2003). The presence of *B. dendrobatidis* infection in boreal toads (*Bufo boreas boreas*) was shown to be coincident with serious declines in two populations in Rocky Mountain National Park (Muths et al. 2003) and has also been identified in chorus frogs (*Pseudacris maculata*) (Green and Muths in press). Both of these amphibians can occur sympatrically with wood frogs. Chytridiomycosis has been identified on apparently healthy wood frogs in Rocky Mountain National Park (Rittmann et al. 2003).Whether chytridiomycosis is important in wood frog survival or has an impact on population viability is unknown.

Many trematodes are known to parasitize amphibians, with little associated mortality (Crawshaw 2000), but recent studies have shown a positive correlation between the presence of the trematode *Ribeiroia ondatrae* and amphibian malformations (Johnson et al. 2002). Malformations of wood frogs have been reported in nine states, but none have been observed in Region 2 (Northern Prairie Wildlife Research Center 2002). The first intermediate hosts of *Ribeiroia* are snails (genera *Planorbella* and *Biomphalaria*), and *Planorbella* is resident in Region 2. Mobile cercariae are released from the snail after an asexual reproductive phase and exhibit a preference for limb-forming tissue in amphibian larvae (Johnson et al. 2002). This irritation of the limb buds causes deformities and has been experimentally reproduced using small beads (Sessions and Ruth 1990). A majority of malformations are not known to be lethal but may reduce fitness by inhibiting feeding or predator avoidance. Fish are also secondary intermediate hosts of Ribeiroia. Once a predator consumes the infected amphibian or fish, *Ribeiroia* becomes sexually mature and completes its life cycle. Another potential parasite, the lungworm (*Rhabdias ranae*), failed to affect the growth or survival of wood frogs in an experimental trial, though the authors reported low infection rates (Goater and Vandenbos 1997). *Rhabdias* spp. was detected in wood frogs in Rocky Mountain National Park, as were the two fungi *Saprolegnia* and *Basidiobolus* (Green and Muths in press). Further work on disease is necessary to determine the potential impacts on wood frog populations in Region 2.

Symbiotic and mutualistic interactions

We found no documentation of symbiotic or mutualistic interactions in wood frogs.

Conservation and Management

Biological Conservation Status

Current trends

No information has been published on the abundance or population trends of wood frogs in Region 2. Drought has dried many ephemeral ponds in the Rocky Mountains over the last three years (Muths and Rittmann personal observation; Zier personal observation); this has likely resulted in the extirpation of some local populations.

Similarly, no current information has been published regarding range expansions or contractions in Region 2. The current distribution of wood frogs in Colorado and Wyoming was dictated by glacial events more than 6000 years ago, so it is unlikely that range expansion will occur in the Rocky Mountain Region. The nature of the absence of wood frogs from northeastern South Dakota is uncertain. Because we have no assessment of the status of either individual populations or the structure of metapopulations of wood frogs in Region 2, it is virtually impossible to assess how the history of wood frog presence in the region or the more recent drought conditions in the region will affect the viability of extant wood frog populations.

The majority of wood frog habitat in Region 2 exists on USFS and other federal lands in Colorado and Wyoming, and so it is protected from development and urbanization but at risk from timber sales, grazing, and potentially, fire. In the Big Horn Mountains of Wyoming, continued motorcycle and all-terrain vehicle use may be degrading wetlands and moist meadows used by wood frogs outside of the breeding season (J.

Zier personal communication 2003). Drought conditions have decreased the number of hydric habitats in many areas of Region 2.

There are no point occurrence data for wood frogs in South Dakota. However, according to the South Dakota State Agricultural Service, no new farmland was created in 2002; this suggests that the amount of suitable wood frog habitat in the state did not decline due to land conversions to agriculture. State and federal agencies within the greater Prairie Pothole region are rehabilitating many wetlands, but it is unknown if target areas are former wood frog sites. The northeastern region of South Dakota has been subject to increased flooding over the last 10 years (South Dakota Department of Environmental and Natural Resources 2002), so it is possible that there has been an increase in available habitat and dispersal corridors.

Intrinsic vulnerability

In Region 2, wood frog populations occur in isolated mountain wetlands. High mountain passes and large stands of xeric coniferous forest represent barriers to dispersal. While humidity is the environmental co-variate that appears to play the most important role in regulating dispersal and home range size (Bellis 1965), the scale of the isolation of populations is perhaps a more relevant focus in the context of the region or the landscape. According to recent work by Funk et al. (2005) and others (e.g., Newman and Squire 2001), gene flow between amphibian populations separated by long distances or apparent barriers is higher than expected. Although we know the general distribution of wood frogs in Region 2, we do not know the degree of isolation (or connectivity) between populations. Questions regarding gene flow, connectivity, and degree of isolation remain unanswered but have the potential for considerable impact on long-term viability of wood frogs.

Because of our dearth of demographic data on wood frogs in Region 2, the best we can do is apply basic tenets of conservation biology to questions raised about population viability, metapopulation structure, and the ramifications of drought or habitat degradation or fragmentation. In general, extinction is area-dependent (e.g., island biogeography theory; MacArthur and Wilson 1967), and habitat fragmentation tends to lead to the loss of species and the number of populations across a landscape (Terbourgh and Winter 1980). Stochastic events, such as prolonged periods of drought, have the potential to drive local populations to extinction. If populations are isolated across a landscape, recolonization events are likely to be rare such that an extirpation at a local pond is permanent even if conditions become suitable again.

Extrinsic Threats

Direct anthropogenic and natural threats

Anthropogenic threats may be direct or indirect. Direct threats include physical, tangible alterations or perturbations to the system that affect habitat of the species of concern.

Roads are an important direct threat and a potential source of mortality when they lie between hibernacula and breeding habitats (Fahrig et al. 1995). Ashley and Robinson (1996) reported a mortality rate of 11.65 amphibians per km per day along the two-lane Long Point Causeway, in Ontario, Canada.

Frogs may be trampled by humans, off-road vehicles, pack animals, and livestock (Jennings 1996, Reaser 1996, Bartelt 1998). This may be particularly significant for wood frogs in isolated populations where immigration from other populations is unlikely. If the majority of a cohort is removed in multiple years, the recruitment rate of breeding individuals into the population and subsequently, population size, is affected.

Indirect effects are more subtle and can be difficult to detect. The effect of chemicals applied to or released into the environment by humans is a good example. Whereas a direct effect would be the death of amphibians at a site, the degradation of the food source (prey base) is an indirect effect and should be considered when examining the effects of chemicals in the environment.

Very few studies have examined the effects of pesticides and herbicides on adult amphibians; the bulk of research available on amphibian ecotoxicology is comprised of laboratory exposure of eggs and larvae to varying levels of chemical exposure. A thorough treatment of all potential chemical interactions with amphibians and amphibian habitats is beyond the scope of this paper; however, a comprehensive review of amphibian ecotoxicology is presented in Sparling et al. (2000) In addition to a review of toxicants by family (e.g., “new generation” pesticides, orthophosphates, metals), several chapters are devoted to ecological and physiological aspects of amphibians that contribute to their sensitivity to chemicals in the environment.

In general, because of permeable skin and life cycles that include a prominent aquatic component, amphibians are susceptible to the effects of pollutants. Herbicides, fire retardants, and chemical road de-icers are potential hazards to Region 2 wood frogs. Orme and Kegley (2002) provide summary data of 49 peer-reviewed studies of chemicals and their effects on wood frog embryos and larvae, and the following information about chemicals[1] was excerpted from that summary. Chemicals tested on wood frog embryos and/or tadpoles include Endosulfan, iron chloride, Fenitrothion, borax, Hexazinone, Permethrin, DDT, Triclopyr, Endirin, aluminum chloride, cupric chloride, sodium nitrate, zinc chloride, lead chloride, Thiosemicarbazide, and Toxaphene. Predominant effects included mortality, immobilization, alterations to growth rate and feeding behavior, and deformation. Thiosemicarbazide was the only chemical exposure that did not result in mortality; developmental changes and growth abnormalities were reported, however. Many of the aforementioned chemicals are employed as herbicides or pesticides and will result in mortality of wood frog prey species as well. Furthermore, chemicals such as Atrazine, Fenitrothion, and Permethrin bioaccumulate in prey species such as insects, phytoplankton, and zooplankton.

Earlier studies of the effect of Atrazine on growth rate and body size in wood frog tadpoles failed to demonstrate an effect (Gucciardo and Farrar 1996, Galbraith et al. 2000). More recently, however, Hayes et al. (2001 reported hermaphrodism and decreased laryngeal size in *Xenopus laevis* exposed to >0.1 ppb Atrazine, and a decrease in testosterone levels at higher concentrations. Hayes et al. (2002b) subsequently demonstrated similar abnormalities in native leopard frogs at breeding sites in the Western and midwestern United States. Atrazine is a widely used herbicide that is mobile after application and is detected frequently in rainfall (T. Hayes personal communication 2003, W. Sadinski personal communication 2003). It can be transported via surface water runoff, drift from sprayers, and most importantly for wilderness areas, by atmospheric transport.

Wood frogs exposed to polychlorinated biphenyls (PCBs) from a field site in New York suffered "significantly increased mortality in direct contact with PCB-contaminated sediment, and…decreased activity levels and swimming speed…" (Savage et al. 2002). PCB levels in Region 2 are unknown, but exposure of wood frogs is expected to be minimal due to the remote locations of most populations in the Rocky Mountains.

For wood frogs, some of these anthropogenic threats are theoretical rather than documented, but many have been reported for other species and should be considered as management decisions are made and research priorities determined.

Natural threats to wood frogs include aspects of weather and climate. Extremes in weather, such as prolonged drought or especially heavy precipitation, can affect the number of breeding sites available, the quality of those sites, and especially the persistence of sites. For example, wood frogs, like most amphibians in the region, require water for breeding (egg laying) and for development from egg to metamorphic frog. A minimum amount of time is necessary for development, and if the site dries before development is complete, the larvae will perish.

Weather is considered short-term, season to season, meteorological events, whereas climate has a greater scope and perhaps impact on the long-term viability of amphibian populations. Some species of frog in Great Britain are breeding earlier in the year in response to warmer temperatures in early spring (Beebee 1995, Forchhammer et al. 1998). Shifts in phenology (the timing of breeding) may have complex, and potentially negative (Donnelly and Crump 1998), effects on populations. In the Rocky Mountains, where snow dominates the landscape, the timing of breeding for some amphibians is determined by snowmelt (Corn and Muths 2002). Changes in snow accumulation or melt dates could impact early season pond breeders such as wood frogs.

Ultra-violet (UV) radiation may pose a natural threat to amphibian populations (Blaustein et al. 1997), but there are alternative theories about the role of UV-B. For example, Corn and Muths (2002) suggest that the timing of breeding may limit the amount of UV-B exposure amphibian eggs receive in the Rocky Mountains, and Palen et al. (2002) suggest that spectral characteristics of water may mediate the physiological effect of UV-B on amphibian eggs in the Pacific Northwest. The role of UV-B as a stressor to amphibian populations is likely complex (Corn 1998, Kiesecker et al. 2001, Corn 2003). Interactions between UV-B and water molds may exacerbate the effect of UV-B on amphibian embryos (Kiesecker and Blaustein 1995).

[1]Brand names are used as in cited references and imply no endorsement or condemnation of products by WYNDD, USGS, or USFS.

Anthropogenic and natural threats to habitat

Forest management practices, including logging and recreation in the form of off-road vehicle use, affect wood frog habitat. Thinning or removal of canopy adjacent to breeding ponds shortens the hydroperiod by increasing solar radiation, raising temperature beyond tolerance limits, and increasing the rate of evaporation (Bartelt 1998, DiMauro and Hunter 2002). Pond hydroperiods must be at least 85 days to ensure adequate time for complete metamorphosis to occur (Bagdonas 1968, Haynes and Aird 1981). Heavy machinery and off-road vehicles cause tire-rut pools, which frogs may use for breeding. However, pools forming in tire ruts are generally too shallow, too hot, and dry faster than natural ponds, and they likely do not hold water long enough for metamorphosis to occur (DiMauro and Hunter 2002), resulting in complete reproductive failure at these sites. Temperature and relative humidity values in coniferous plantations and clear cuts studied in Maine were outside of the preferred temperature and humidity ranges for wood frogs (5 to 25 °C, >70 percent humidity) (Waldick et al. 1999).

Gibbs (1998a) observed that species with the greatest dispersal ability were the most sensitive to forest fragmentation. Dispersal distances for wood frogs in Region 2 are unknown but are likely to be significant in terms of fragmentation, based on information from other studies. Fragmentation should be viewed as not only the mechanical act of producing fragments of habitat (habitat islands) but the loss of adjacent habitat, edge effects, and isolation. Wood frogs displayed intermediate sensitivity to fragmentation in comparison to four other species of amphibians in Connecticut (Gibbs 1998b). We expect a similar negative response to habitat fragmentation in Region 2 because the terrestrial nature and moderate dispersal tendency of wood frogs is uniform range-wide. Fragmentation may occur from the incursion of roads, logging, wetland draining, and other anthropogenic habitat alterations or from alterations occurring because of natural events (e.g., blow downs, forest fire).

Succession influences wood frog breeding site selection (Haynes and Aird 1981). Glacial potholes tend to provide ideal breeding habitat, but there are a limited number of glacial potholes in Region 2 and, therefore, a finite number of available breeding sites for wood frogs. As grasses, rushes, and sedges progressively decrease the amount of open water present, wood frogs may abandon these sites. Abandoned beaver ponds are also used, but Haynes and Aird (1981) postulated that such habitats undergo more rapid succession and in the long run are not numerous enough to offset losses of naturally formed ponds. Grazing, logging, and other human activities (e.g., off-road vehicles) alter riparian vegetation in numerous ways (Haynes and Aird 1981, Kauffman and Krueger 1984, Maxell 2002), potentially destroying appropriate breeding habitat. Grazing can have negative impacts on wood frog habitat by trampling vegetation, altering vegetation structure and vigor, and degrading water quality. Moist meadows become drier when grazed, reducing the amount of usable late season habitat and facilitating invasion by exotic grasses such as timothy (*Phleum pratense*). Meadows will return to the hydric state conducive to native plants when grazing is halted (Kauffman and Krueger 1984).

Fecal contamination of water from livestock activity can cause eutrophication and an increase in *Planorbella* snail populations, which are a reliable predictor of *Ribeiroia* fluke presence; a positive correlation exists between increased exposure of amphibians to *Ribeiroia* and incidence of malformation and mortality (Johnson et al. 2002). Johnson et al. (2002) noted that planorbid snails in western states were associated with man-made wetlands and high orthophosphate levels.

Stocking of game fish into formerly fish-free habitats has been directly correlated to declines in the federally endangered mountain yellow-legged frog (*Rana muscosa*) (Knapp and Matthews 2000, Federal Register 2003) and has been implicated in the decline of the Columbia spotted frog (*R. luteiventris*) (Pilliod and Peterson 2001, Dunham et al. 2004). These studies suggest that introduced fish likely have an adverse effect on other amphibian species, but the impacts of such introductions have not been studied for wood frogs. Hopey and Petranka (1994) reported that the selection of breeding sites by females suggests that they avoid ponds where fish are present.

Fire and fire management activities are of increasing concern in the West, a concern heightened by several years of drought. Fire, whether natural or prescribed, may benefit amphibian habitats by keeping riparian areas open (Russel et al. 1999). Boreal toads (*Bufo boreas*) in Glacier National Park have colonized areas that were burned recently (P.S. Corn and B. Hossack personal communication 2003). However, if amphibians are unable to find refuge or if fires are extreme, mortality will occur. Outside of the breeding season, wood frogs can be quite terrestrial in their habits, suggesting that forest fires could be a significant source of mortality. During the breeding season, wood frogs utilize shallow ponds that may be profoundly impacted by fire through desiccation (extreme heat, loss of forest edge) and siltation due to runoff from denuded understories. There are several fire management techniques that could harm wood frogs. For example, the use of slurry chemicals has been shown to cause mortality in aquatic invertebrates (Hamilton et al. 1996), the creation of fire breaks by hand or machine may act as inescapable pitfall traps, and the use of water from lakes may lower water levels in connected breeding ponds or adjoining wet meadows. Alternatively, given the type of habitat used by wood frogs, the species may be, to a certain extent, fire-adapted. Direct and indirect effects of fire and fire fighting are likely important considerations for managers and have not been examined specifically for wood frogs in Region 2.

Targeted areas in Region 2

Wyoming and Colorado: Due to isolation and limited dispersal ability, all wood frog populations in the Rocky Mountain Region may be at risk of extinction. Isolated populations are often defined as too far apart to be recolonized in the event of catastrophic mortality and should be targeted for protection. Whether these populations have weathered potential genetic bottlenecks is unknown, but this should also be considered.

South Dakota: Although this species has not been observed reliably for nearly a decade, wood frog populations can vary greatly from year to year and persist with occasional catastrophic losses (Berven 1990). The observations of Lehtinen and Galatowitsch (2001), Newman (personal communication 2003), and Squire and Newman (2002) suggest that it is not unreasonable to expect recolonization of historical sites by surrounding populations, as long as no major barriers to dispersal exist (e.g., roads, urbanization). Recent flooding in northeastern South Dakota may facilitate new immigrations from source populations and colonization of newly created wetlands. However, predictions regarding populations in South Dakota are mostly conjecture as no data are available.

Management and Potential Conservation Elements

Implications and conservation elements

Based on our current, limited knowledge regarding amphibian declines in general and the status of wood frogs in particular, it is difficult to identify specific elements to be addressed in the conservation of this species. The overarching theme that can be applied to efforts at preserving and protecting healthy populations of wood frogs in Region 2 is one of habitat protection. Preservation of habitat appropriate to each of the unique life stages of wood frogs (i.e., known current breeding pools, adjacent wet meadows, and associated uplands for hibernation sites) is imperative to the survival of this species in Region 2, and as such habitat is concentrated on USFS land, this government agency is responsible for much of the protection and maintenance of the majority of wood frog populations in Colorado and Wyoming. Without considering the needs of this species in all facets of forest management, it may face decline and potentially extirpation, which would result in expensive recovery plans and actions.

Although conservation concerns regarding wood frogs focus currently on habitat loss and degradation, other categories will likely become more important. Research into disease susceptibility and the concepts of connectivity via space and genetics for wood frogs is increasing, and this new information should be incorporated into management decisions whenever possible. Our concern about habitat can translate into a variety of management actions. When wood frog populations are located, appropriate measures should be taken to protect them. For example, limitations on off-road vehicle use in close proximity to breeding sites and movement corridors and restrictions on timber cutting and controlled burns may be necessary. While general prescriptions can be suggested, we are unable to provide specifics until we know more about wood frog biology and ecology. Studies continue regarding the use of habitat by anurans in the west (e.g., S. Adams unpublished data, Scherer unpublished data, Bartelt 2000, Pilliod personal communication 2003, Corn and Hossack personal communication 2003, Muths 2003), but more information is clearly needed. Examples of issues that have not been addressed thoroughly include the following: effects of fire, fire fighting, and fire suppression on wood frogs; human impact issues including habitat degradation from off-road vehicles; effects of disease; basic questions regarding the amount of area required by an individual wood frog, the extent of movements, and the degree of connectivity between populations. None of these questions has been resolved for populations in the Rocky Mountains, and any of them may have significant impact on management actions such as road building, timber sales, and fire.

Tools and practices

Inventory and monitoring

Several agencies have inventory and monitoring programs. The USFS Inventory and Monitoring Institute assists in the formulation of inventory and monitoring plans conducted by management units operating at a broad range of geographic scales. The National Park Service takes a regional approach with their Inventory and Monitoring Program. The U.S. Geological Survey (USGS) takes a national approach to amphibians with the Amphibian Research and Monitoring Initiative (ARMI), using occupancy as a common response variable. The ARMI program in the Rocky Mountains is focused primarily on Department of the Interior lands, many of which are immediately adjacent to USFS lands. There are currently amphibian monitoring projects, both broad scale and at particular sites, in Rocky Mountain, Grand Teton, Yellowstone, and Glacier national parks. Implementation of these projects follows general protocols developed at the national level under the ARMI program (http://armi.usgs.gov/ and http://www.fort.usgs.gov/research/rarmi/default.html). The ARMI program is designed to be collaborative in nature, sharing protocols and expertise with other federal and state agencies. Current funding and hiring constraints make collaboration not only attractive but necessary.

After a question has been framed, the researcher is faced with the selection of the appropriate tools to answer the question. Fortunately, methods for surveying amphibians in the western United States are well developed (Corn and Bury 1990, Fellers and Freel 1995, Heyer et al. 1994, Lepage et al. 1997, Olson 1997, Corn et al. 2000). For example, Corn et al. (2000) examined three methods of monitoring Colorado amphibian populations during the breeding season, including wood frogs. Manual call surveys, automated audio recordings, and intensive visual encounter surveys were compared for sensitivity and accuracy in detection of amphibians. Each method proved effective for different aspects of successful monitoring. Automated recorders involve an initial set-up cost (moderate), staff training, and more crew hours than other methods. However, if they are maintained properly, automated systems record calling events, including those that may be missed because they occur between manual visits. They provide the best phenological and behavior data and are able to detect the presence of rare species in an area. Given the short breeding season, and often times the sparse number of wood frogs at a breeding site, an automated system may be the best method to track breeding phenology and document presence at particular sites of interest.

Visual encounter surveys (VES; Heyer et al. 1994) are the only method that will detect non-vocal species such as tiger salamanders (*Ambystoma tigrinum*) and boreal toads, both of which are known to be sympatric with wood frogs. Since intensive surveys involve several hours at the study site, habitat inventory, climate, and behavioral data can be collected at the same time. Data collected during a VES can be used to estimate occupancy, given that various assumptions are met (McKenzie et al. 2002). Wood frogs, their eggs, and tadpoles are relatively simple to identify in Region 2 using appropriate field guides (e.g., Hammerson 1999), making the VES method particularly useful.

Population and habitat management

Habitat has been assessed for some amphibians using habitat suitability index (HSI) models. These are available for the bullfrog (*Rana catesbeiana*) (Graves and Anderson 1987) and the red-spotted newt (*Notophthalmus viridescens*) (Sousa 1985), but not for wood frogs. Methodology for assessing habitat using this tool is available (U.S. Fish and Wildlife Service 1981, http://www.nwrc.usgs.gov/wdb/pub/hsi/hsiintro.htm) and may be useful for the wood frog at specific locations.

Given the limited amount of suitable habitat in the Region 2 and the moderate dispersal capability of the species, minimizing forest corridor fragmentation is particularly important. Connectivity between populations and potential breeding sites is critical to overall population health to allow recolonization in the event of local extirpations. Information necessary to minimize the effects of fragmentation includes a quantitative assessment of what “fragmentation” means to wood frogs. While we suspect only limited dispersal capability, we do not know what constitutes a barrier to dispersal for this species (but see Funk et al. 2005, relative to Columbia spotted frogs).

Scale is also important. “Limited” dispersal ability from a human perspective may be equivalent to “moderate” ability from an amphibian perspective. This disparity in viewpoint can be critical when examining potential barriers or designating movement corridors. These questions can be answered through a variety of techniques. For example, we can focus on the physiology of the species and assess their tolerance for overland travel (*sensu* Bartelt 2000) or use radio-telemetry to assess movements of individual animals (Muths 2003). To estimate the effective population size (i.e., the number of reproducing adults in a population) or other demographic parameters (e.g., survival, emigration, immigration, or recruitment) monitoring efforts should be concentrated at breeding sites during the breeding season. This information can be helpful in determining the viability of the population or its susceptibility to perturbation. Capture-recapture studies using a unique marking technique (e.g., PIT [passive integrated transponder] tagging) that allows individuals to be identified year to year and analysis using one of several available software programs (e.g., program MARK http://www.cnr.colostate.edu/~gwhite/mark/mark.htm) can provide information on a variety of population parameters such as survival, temporary emigration, and population size (see Williams et al. 2002 for more detail).

Increasing our knowledge about landscape-scale demographics of wood frog populations will improve our ability to predict the effects of timber harvest, fire, recreation, habitat fragmentation, and disease. For example, these parameters can provide core data for in-depth modeling work (e.g., using appropriate models in program MARK) necessary to address specific *a priori* questions, such as how much temporary emigration occurs in a wood frog population, what environmental variables affect the extent of temporary emigration and, importantly, how these characteristics relate to forest management.

Captive propagation and reintroduction

Captive propagation has not been practiced for this species. Translocation and reintroduction were implemented in Missouri (egg masses; Guttman et al. 1991) and Illinois (larvae and adults; Thurow 1994) with reported success. However, results reported in Thurow (1994) were controversial regarding historical records of wood frogs at the study site and interpretation of data (lack of control populations, continual releases obscured actual success rate) (Szafoni et al. 1999). There have been few successful translocations of amphibians (Dodd and Seigel 1991) with some notable exceptions (e.g., Denton et al. 1998). Considering the lack of experience with captive propagation and the associated costs, we suggest that other management actions be implemented to secure and maintain existing populations, with captive propagation and reintroduction remaining a low priority.

Information Needs

We have no quantitative data on the status of individual wood frog populations or on the number of wood frog populations across the region. Gathering data to address these two categories of issues requires two methods. First, to examine individual populations and be able to frame questions about habitat use, dispersal distances, and estimations of specific demographic parameters, an approach including rigorous capture-recapture techniques and analysis is required (e.g., Williams et al. 2002). Second, to gain an understanding of where wood frog populations exist in Region 2, examine metapopulation dynamics, connectivity between populations, and identify potential dispersal corridors, a different approach is required. The basis of this approach is the implementation of a monitoring program using established protocols based on the random selection of sites across the region such that inferential population statistics (MacKenzie et al. 2002) can be used to track changes in the number of wood frog populations on a regional scale (e.g., Muths et al. in press). Cooperation with the USGS ARMI program and an integration of its protocols as described above would be useful in the implementation of this monitoring effort.

Implementing either or both of these processes will greatly assist managers and policymakers in preserving key habitats and the wood frog in Region 2. Importantly, gathering appropriate baseline data will facilitate the formulation of research questions that can focus on data gaps identified in this document and current management needs. Information regarding demography, genetics, number of extant breeding sites, breeding habitat, and home range requirements of wood frogs is necessary before questions about how management practices such as timber harvesting, recreation, or fire or intrinsic factors may affect Region 2 populations. Studies addressing specific questions within these topics have the potential to provide valuable management guidelines to the USFS. Example questions are presented in previous sections (Implications and potential conservations elements).

Some questions can be framed using available information on wood frogs from outside of Region 2. For example, fine scale responses to habitat alterations have been studied in eastern Canada and Maine (Lehtinen et al. 1999, Waldick et al.1999, Mazerolle 2001). While we anticipate that the response of western populations of wood frogs may be similar, the overall effect on abundance will be more severe due to the scarcity of, and distances between, suitable habitat in the Rocky Mountain Region. The basics of movement patterns are documented for the breeding season, but specific information on post-breeding season behavior is lacking (e.g., movement, habitat use, dispersal). In other cases, we may anticipate large differences. For example, the isolated nature of Rocky Mountain populations suggests that population trends may differ significantly from other regions.

There are numerous studies about many aspects of the wood frog, but relatively few are from the West. The challenge is to use available information to craft probing questions that will swiftly address some of the data gaps identified in this document. As the data gaps are minimized, forest managers will be able protect the wood frog and its habitat before the status of the species is compromised from either catastrophic natural disasters or human-caused perturbations.

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