SPECIES ASSESSMENT FOR THE NORTHERN LEOPARD FROG (*RANA PIPIENS*) IN WYOMING

prepared by

BRIAN E. SMITH[1] AND DOUG KEINATH[2]

[1]Department of Biology Black Hills State University1200 University Street Unit 9044, Spearfish, SD 5779

[2] Zoology Program Manager, Wyoming Natural Diversity Database, University of Wyoming, 1000 E. University Ave, Dept. 3381, Laramie, Wyoming 82071; 307-766-3013; dkeinath@uwyo.edu

prepared for

United States Department of the Interior
Bureau of Land Management
Wyoming State Office
Cheyenne, Wyoming

January 2004

Table of Contents

Summary

The northern leopard frog (*Rana pipiens*) is a formerly abundant frog that has experienced significant declines across its range and is considered endangered in some parts of the range but still abundant in other parts of the range. Various factors have been invoked to explain population declines in the northern leopard frog, including habitat destruction, diseases, chemical contamination, acidification, increased ultraviolet light due to loss of the ozone layer, introduced predators, overcollecting, climatic changes, and general environmental degradation. However, no one cause has emerged as the primary factor behind population declines in any area. Probably, multiple causes contribute to population declines of the species, and these causes most likely vary from site to site. Of course, northern leopard frogs are still abundant in some areas, implying that factors leading to population declines in other areas are absent or less important where the species is still common.

Conservation of this species depends on minimizing habitat alteration, removing introduced species, especially introduced predaceous fish, from breeding ponds, reducing the spread of diseases such as chytridiomycosis, ranavirus, and bacterial diseases from pond to pond, reducing chemical contamination and acidification, and eliminating overcollection where it occurs.

Introduction

Goal

This assessment of the northern leopard frog (*Rana pipiens*) addresses the biology, ecology, and conservation status of the northern leopard frog throughout its current range in Wyoming. Our goal is to provide a current summary of published information and expert interpretation of this information that can be used to develop management plans.

The northern leopard frog was selected for this assessment because it is classified as a sensitive species by the Bureau of Land Management (BLM) in Wyoming due to recently observed declines in abundance and distribution across its range in the Rocky Mountains. The northern leopard frog is, or was, one of the most visible and abundant amphibians of the northern United States and southern Canada. In some places, it is now almost completely eliminated. Restoration of the northern leopard frog in critical habitat would be an indication of a healthy ecosystem, especially a healthy aquatic ecosystem. Literally dozens of other species also frequent the small ponds in which northern leopard frogs breed, and conservation of these small ponds will have consequences that will reverberate throughout the animal and plant kingdoms. Small ponds in which northern leopard frogs breed are typically ignored by management plans and legislation, and it is critical that loss of these wetlands be minimized.

Scope, Uncertainty, and Limitations

The northern leopard frog is one of the best known frogs in North America, and we have attempted to compile the most relevant primary literature on the species that is available. However, the literature is voluminous. Even with more than 260 citations used in this report, there are still hundreds of other citations in the literature. Where reviews are available for specific topics, we have relied primarily on these reviews for sources, occasionally referring back to the original citations. In most cases, this was not possible and we extensively cite primary articles. We concentrated on literature from the Rocky Mountains but made liberal use of studies from throughout the range of the northern leopard frog, on the assumption that the biology of the frog should be similar in much of its range. Even though the species is well known, there are still extensive gaps in our knowledge. These gaps are mentioned throughout the document, but are discussed in detail in "Information Needs."

In this assessment, the strength of evidence from research is noted and alternative explanations of observational data and expert inference are described when appropriate. Peer-reviewed literature represents the strongest set of data and is therefore used preferentially to draw conclusions regarding the northern leopard frog. Hypotheses and inferences are noted with appropriate qualifications. When there was little or no research to back up specific ideas, we obtained expert opinions. This assessment should be used as a thorough, but not comprehensive, account of northern leopard frog biology in the Rocky Mountains. Information presented here does not replace the utility of sound, site-specific research when making land-use decisions affecting a particular area.

Publication

This species assessment will be published on the homepage of the Wyoming Natural Diversity Database in order to facilitate the use of this species assessment by interested parties. This will make information on the northern leopard frog accessible more rapidly than publication as a book or report, and will make revisions more efficient.

Natural History

Morphological Description

The northern leopard frog, *Rana pipiens*, is a ranid frog of moderate size (5.1 – 9.0 cm SVL), with brown or green background color, and two or three irregular rows of dark spots on the dorsum (Conant and Collins 1991; Figure 2). It is also characterized by conspicuous dorsolateral ridges bordering the spots at the edge of the dorsum. Males have swollen thumbs on their forefeet, paired vocal pouches at the sides behind the head which are visible when vocalizing, and are usually smaller than females in body size. Two mutant phenotypes occur in Minnesota and adjacent states (Conant and Collins 1991), but these phenotypes should not be encountered within the region characterized by this conservation assessment.

Eggs are deposited as single large round masses, 5-13 cm in diameter, and are black in color (Figure 3). The tadpole of the northern leopard frog is also figured by Conant and Collins (1991; see figure 119, p. 353). Tadpoles of most frogs are difficult to identify without a dissecting microscope and expert advice. Tadpoles are brown, olive, or gray above and white below. The vent is located on the lower right side of the midline of the body near the tail fin. Leopard frog tadpoles can reach total snout to vent lengths of 3.4 inches (87 mm).

Taxonomy and Distribution

Taxonomy

Pace (1974) includes a synonymy of names applied to the leopard frog complex, including *Rana pipiens*. The name *R. pipiens* was first applied by Schreber in 1782, based on a leopard frog sent to him from New York (Schreber 1782, cited in Pace 1974). Using biochemical techniques, Hillis et al. (1983) resolved the phylogeny of the Alpha and Beta groups of the *R. pipiens* complex. *Rana pipiens*, along with *R. blairi*, *R. sphenocephala*, and *R. berlandieri*, falls within the Beta division. The Alpha division contains *R. palustris*, *R. capito*, and *R. areolata*. Hillis (1988) further reviewed the literature and provided range maps of all the North American leopard frogs referred to the *R. pipiens* complex, including the northern leopard frog. Dunlap and Platz (1981) discussed areas of hybridization deduced through calling variation in the upper midwest.

Lynch (1978) discussed the distribution of the northern leopard frog and the Plains leopard frog (*R. blairi*) and zones of sympatry of the two species in Nebraska. Dunlap and Kruse (1976) discussed the distribution of the "northern" (*R. pipiens*) and "western" (*R. blairi*) "morphotypes" (now known as two distinct species) in the northern and central Plains states. From the discussion of Dunlap and Kruse (1976) it is clear that a zone of hybridization between *R. pipiens* and *R. blairi* may exist from south-central South Dakota to northeastern Nebraska. It is possible that frogs from central South Dakota and central Nebraska (Fort Pierre National Grasslands, Samuel R. McKelvie National Forest, and the eastern portion of the Nebraska National Forest) could be hybrids of the two species.

Distribution and Abundance

The northern leopard frog is basically a species of cooler climates, with a range that encompasses most of the northern states of the United States and far north into Canada. The species ranges southwards only in the western United States, in the higher elevations of the Rocky Mountains. Figure 4 shows the extent of their historical range, as reported by Stebbins (1985), Hillis (1988), and Conant and Collins (1991). Table 1 lists the states and provinces in which the northern leopard frog is found, historical abundance (if known), present abundance (if known), and the population trend (where known).

A few facts are worth noting. Localized extinctions have occurred across the range. The distribution in Washington was historically spotty (Leonard et al. 1999), and this probably has made it difficult to determine population trends. In Alberta the range of the northern leopard frog north of 55^{o}N latitude is poorly known (Russell and Bauer 1993). The northern extent of the range in Canada and Alaska is poorly known in general (Russell and Bauer 1993). Northern leopard frogs have been found up to 3355 m in southern Colorado (Hammerson 1999) and up to 2700 m in the mountains of Wyoming (Baxter and Stone 1985).

Rana pipiens has been introduced to a variety of areas. For instance, populations in Newfoundland and on Vancouver Island, British Columbia were introduced (Buckle 1971; Green and Campbell 1984) and California populations may also be introduced (Bury and Luckenbach 1976 Jennings 1984).

Population Trends

The northern leopard frog was formerly abundant across its range, but has suffered population declines throughout North America, as documented by numerous local studies, which are summarized below and in the subsequent section on Abundance and Abundance Trends.

In the western United States the species has undergone major declines or has become locally extinct. Northern leopard frogs have apparently gone extinct in the Targhee National Forest of western Wyoming and adjacent Idaho (Koch and Peterson 1995). They are severely reduced in the Laramie Basin of Wyoming but may still be common in other parts of the state (Baxter and Stone 1985; Stebbins and Cohen 1995). It is locally extinct west of the Continental Divide in Montana except for two population centers, one near Kalispell and one near Eureka (Maxell 2000). It is largely absent from central Montana where northern leopard frogs were found at only nine of 47 historical sites in the mid-1990s (Maxell 2000). It is declining in some parts of eastern Montana (Reichel 1996). Northern leopard frogs have become scarce at many sites in Colorado (Hammerson 1999). Corn and Fogleman (1984) documented extinctions at nine high elevation sites in Colorado. Northern leopard frogs have also gone extinct or become severely reduced at low elevation sites in Colorado (Hammerson 1982; Cousineau and Rogers 1991). Clarkson and Rorabaugh (1989) surveyed 13 of the 28 historical localities known in Arizona. They found that the northern leopard frog was absent from all of these localities and present at only one previously unreported locality in the White Mountains. It is now absent from its historic range in California, except for a few small populations in northeastern California (Stebbins and Cohen 1995). Leonard et al. (1999) visited 27 historical collecting localities in eastern Washington and found populations at only three of them. The species was formerly common throughout the central plains states but has declined there as well (Stebbins and Cohen 1995).

In the upper Midwest, northern leopard frogs are generally thought to be less abundant than in the past. Moriarty (1998) found them to be widespread across Minnesota but much less common than historical records indicated. Hine et al. (1975, 1981) documented a decline of northern leopard frogs in Wisconsin in the 1970s. Mossman et al. (1998) reported that northern leopard frogs underwent a further decline in Wisconsin from 1984 – 1995, although they were still common in the state. Casper (1998) reported that some investigators believed that they saw a partial rebound after 1985. Dhuey and Hay (2000) reported that they were rare in Wisconsin. Moreover, in Wisconsin they are probably far below historical population levels (Casper 1998; Mossman et al. 1998). Collins and Wilbur (1979) noted that northern leopard frogs had become rare on their study site near Ann Arbor, Michigan, during the previous 20 years.

Recent estimates of the abundance of northern leopard frogs in the lower midwestern United States are found in Lannoo (1998a). Orr et al. (1998) found them still abundant in northeastern Ohio. However, Davis et al. (1998) found northern leopard frogs to be rare or extinct (most populations) in Hamilton County, Ohio, the county in which Cincinnati is located. Mierzwa (1998) also found them to be common in northeastern Illinois. Brodman and Kilmurry (1998) reported that they were rare or uncommon at their study sites in northwestern Indiana. Minton (1998), writing from a perspective of 45 years of collecting in Indiana, stated that northern leopard frog populations have declined markedly since 1948. Lannoo et al. (1994) wrote that northern leopard frog populations had probably declined across Iowa by two to three orders of magnitude over historical levels. Hemesath (1998) was unable to determine whether there had been further declines in Indiana based on calling survey data.

Canadian populations are discussed in Green (1997) and Bishop and Pettit (1992). The distribution and abundance of the northern leopard frog is poorly known for many parts of Canada (Russell and Bauer 1993; Maunder 1997; Fournier 1997). They are rare in the Northwest Territories (Fournier 1997). Northern leopard frogs are found in Saskatchewan but are insufficiently known there to assess abundance or population trends (Didiuk 1997). The northern leopard frog has declined in abundance in British Columbia (Orchard 1992). It is now extinct or rare throughout much of Alberta (Roberts 1992; Russell and Bauer 1993; Stebbins and Cohen 1995). They are common in New Brunswick and probably have suffered no decline there (McAlpine 1997).

Despite overwhelming evidence of widespread population declines, it is important to realize that declines may not have occurred everywhere. Data showing that declines are not occurring may not be as “interesting” as data showing that declines are occurring, so such information may not be published. Generally, it is thought that eastern populations of northern leopard frogs are probably in better condition than western populations. For instance, Orr et al. (1998) concluded that population declines were not occurring at study sites in northeastern Ohio. Also, northern leopard frogs were found to be “common” in 1995 in Illinois, although probably less abundant than surveys conducted in 1855 (Mierzwa 1998). McAlpine (1997) reported no evidence of population declines in New Brunswick, Canada. McAlpine (1997), Mierzwa (1998), and Orr et al. (1998) were the only three reports we were able to find in the peer-reviewed literature that did not claim declines in northern leopard frog populations.

Habitat Requirements

Northern leopard frogs require a broad range of habitats in close proximity due to their complicated life histories. Merrell and Rodell (1968) categorized three major habitat types:

winter habitat (overwintering in lakes, streams, and ponds), summer habitat (feeding by adults in upland areas), and tadpole habitat (up to three months spent as tadpoles in shallow breeding ponds). To completely understand the types of habitats used by northern leopard frogs the habitat they use during various stages of their life history must be categorized, including habitat used by tadpoles, subadults, and adults, and any sexual differences in habitat use. Their complicated movement patterns during the year must also be considered and include habitat used for reproduction, natal dispersal, summer feeding ranges, fall migrations, and overwintering.

Another consideration when summarizing general habitat use by northern leopard frogs is that much of the relevant literature regards populations scattered all over North America. There are likely to be differences in habitat usage by northern leopard frogs between Wyoming and other North American populations.

Breeding habitat and tadpole habitat

Tadpoles obviously start as eggs, and eggs are laid in breeding ponds. Therefore, discussion of tadpole habitat requires consideration of egg laying and breeding of the northern leopard frog. In an extensive study of the life history of the northern leopard frog in Minnesota, Merrell (1977) found that they bred in mid-sized ponds; i.e., ponds that were 30 – 60 m in diameter, were from 1.5 – 2.0 m in depth, and dried "periodically every few years". Merrell (1968) also characterized breeding ponds and noted that they did not support fish populations, were not connected with other bodies of water, and dried up during droughts. Werner and Glennemeier (1999) found that northern leopard frogs required breeding ponds with an open canopy. Collins and Wilbur (1979) found that northern leopard frogs bred only in ponds that were permanent, dried completely in exceptionally dry years, or dried only by the very end of the summer. In this study, the presence of fish did not affect breeding, but subadults were only found at sites that were fishless, which coincidentally were either semi-permanent ponds or dried by the end of the summer. Semlitsch (2000a) discussed the importance of mid-sized ponds to reproductive success (i.e., egg laying, egg hatching, and successful metamorphosis) in many species of amphibians. According to Semlitsch (2000a), the most important ponds for amphibians were semi-permanent to seasonal palustrine habitats that tended to last from 30 days to one year.

Various studies of northern leopard frog breeding habitat have been made in the Rocky Mountain region. In northern Colorado and Wyoming, Corn and Livo (1989) found that northern leopard frogs bred and successfully hatched in a gravel pit, stock ponds, and beaver ponds. Hammerson (1999) noted that the northern leopard frog bred in shallow, quiet areas of permanent bodies of water, in beaver ponds, and in seasonally flooded areas adjacent to or contiguous with permanent pools or streams in Colorado. While we have not carefully measured the characteristics of breeding habitat of the northern leopard frog in the Black Hills region, our observations are in general concordance to those of Merrell (1968, 1977), Collins and Wilbur (1979), Corn and Livo (1989), and Hammerson (1999). We have found northern leopard frogs breeding in stock ponds, semi-permanent ponds, in the margin of larger lakes, and beaver ponds. When streams are used for reproduction, eggs are deposited in backwaters out of the main flow of the stream. While we have found northern leopard frogs breeding in habitat with introduced predaceous fish, we have seldom found tadpoles or metamorphosing juveniles in such habitats. Neither have we found breeding adults, tadpoles, or metamorphs in springs in the Black Hills, which we hypothesize stay too cold throughout the summer for normal development of the tadpoles. Applying the classification system of Cowardin et al. (1979) to what we would consider the "most typical" type of breeding site used by northern leopard frogs in the Rocky Mountain region, they are palustrine sites with an unconsolidated bottom and usually have a pond margin with extensive growth of cattails (*Typha* species). Cowardin et al. (1979) consider the following four features to be characteristic of palustrine systems: 1) Size <8 ha; 2) No wave-formed or bedrock shoreline; 3) Water depth typically <2 m at the deepest part of the pond; and 4) Very low salinity. Palustrine systems with an unconsolidated bottom generally have a mud bottom (often composed of bentonite in parts of the Black Hills and Wyoming) and vegetative cover <30%. The cattail margin is typical of these ponds in the Rocky Mountain region, and probably indicates some degree of permanency to the pond, although some of these sites may dry completely by late fall.

The lead author's experience in the Black Hills indicates that breeding ponds there are of roughly the size determined by Semlitsch (2000b) to be highly productive for amphibian abundance and diversity in the southeastern United States; slightly smaller than 5.0 ha. These ponds should not be connected to larger bodies of water to preclude accidental introduction of predaceous fish. These types of ponds may be the most common ponds in the landscape but they may also be the most in danger of elimination and the least protected by law and management guidelines (Semlitsch and Bodie 1998; Semlitsch 2000b). The current Black Hills National Forest Land and Resource Management Plan (USDA Forest Service 1997) makes no mention of the protection of these sorts of wetlands, and most conservation and management plans also decline to mention such habitats.

Tadpoles need bodies of water with no overhead canopy that are free of introduced predaceous fish (Kruse and Francis 1977; Hecnar and M'Closkey 1997a; Werner and Glennemeier 1999). These bodies of water should be reasonably shallow so as to be heated by the sun to temperatures suitable for rapid development, especially at higher elevations, where the growing season may be short. However, they should not be too shallow, because they would dry too rapidly for tadpoles to complete their 58-105 day larval period (Hammerson 1999).

In various locations across their range, subadult frogs, after completing their larval period, migrate across land to suitable feeding sites at larger lakes (See “Movement and Activity Patterns” above).

Adult upland habitat

Following reproduction adult northern leopard frogs move into upland habitat in which they may feed for the summer. In a study by Merrell (1970), during the summer northern leopard frogs tended to frequent grassy meadows where the grass was from “several inches to a foot” (i.e., up to 30 cm) in height. Conant and Collins (1991) point out that the northern leopard frog is one of the more terrestrial of the ranid frogs and it can be assumed that the northern leopard frog may use a considerable amount of upland habitat around breeding ponds. However, this portion of the life histories of many amphibians has been frequently neglected (Semlitsch 1998) and such is also the case for the northern leopard frog. Many citations mention movements of from 0.5 – 3.0 km from water in this species, and Dole (1971) notes that subadults move up to 5.2 km away from natal ponds. There is no reason to think that populations of the northern leopard frog in the Rocky Mountain region are different and some USDA Forest Service biologists working in the Black Hills have commented that they have found northern leopard frogs a considerable distance from water in wet meadows or grasslands (Oscar Martinez 1998, personal communication).

Adult overwintering habitat

In the fall, subadult and adult frogs migrate to overwintering sites. In general, overwinter mortality is likely an important cause of mortality for northern leopard frogs, as is known for other ranid frogs (Bradford 1983). They may hibernate under water in ponds (Emery et al. 1972; Hammerson 1999), streams (Cunjak 1986; Hammerson 1999), and rivers (Ultsch et al. 2000), many of which now contain introduced predaceous fish.

Especially important as a source of overwintering mortality may be oxygen depletion at overwintering sites (Merrell and Rodell 1968; Bradford 1983), which could account for the habit of overwintering at inflow areas being where oxygen saturation of water is relatively high (Oldfield and Moriarty 1994). This further underscores the potential importance of permanently flowing streams, springs, and wet meadows as overwintering sites in the Rocky Mountain region.

Bradford (1983) noted that anoxia was one source of mortality for overwintering frogs in California and Nevada for the mountain yellow-legged frog, *Rana muscosa*. Bradford (1983) observed that anoxia was more severe in shallow lakes or ponds (i.e., <4 m deep) and nearly all adult frogs died in these bodies of water in some winters. Repeated winterkill has been observed in ponds in northern Indiana (Manion and Cory 1952). Ultsch et al. (2000) also observed winterkill in a river in Vermont. Avoidance of wintertime anoxia is one reason why northern leopard frogs have been reported in high numbers in areas of high oxygen saturation such as stream inflow areas in ponds (Oldfield and Moriarty 1994). It may also be why they overwinter in streams, where oxygen saturation should be higher than in lakes or ponds. Northern leopard frogs remain capable of movement throughout the winter but are usually very sluggish, moving away from observers very slowly (Emery et al. 1972; Cunjak 1986). At low temperatures, frogs move more slowly than at warm temperatures (Rome et al. 1992).

Within the Rocky Mountain region, habitat use by the northern leopard frog should be similar to that throughout the range. However, there could be local adaptations of importance. For example, the Black Hills historically had no large bodies of water such as lakes (Froiland 1990), and northern leopard frogs may have used streams and possibly other types of habitats in which to overwinter in the Black Hills. Interestingly, Oscar Martinez of the USDA Forest Service found a leopard frog under snow in winter in a wet meadow that had flowing, unfrozen water (personal communication 1997). However, little else is known of potential overwintering sites for northern leopard frogs in the Black Hills or other parts of Wyoming. We would suspect that they would use the bottoms of flowing streams, the bottoms of ponds that are large enough that they don't freeze solid in winter, and possibly springs that do not freeze solid in winter. It seems unlikely that they would use the bottoms of recently created lakes for overwintering, both because these lakes may not have been used historically for overwintering and because these lakes have introduced predaceous fish such as brown trout (*Salmo trutta*) and pike (*Esox lucius*).

Landscape Pattern

As noted above, northern leopard frogs require a broad range of habitats in close proximity due to their complicated life histories. Like many species, pond-breeding amphibian populations are connected across the landscape, with each pond serving as a population and all the populations of all the ponds existing as one, or several, metapopulations. The pattern of spacing of suitable breeding sites across the landscape and upland movements made by northern leopard frogs are probably particularly important in colonization of new ponds or recolonization of ponds in which breeding populations have gone extinct, thus maintaining a healthy metapopulation of the species in any area.

Frog movements and pond spacing are two of the most important factors to consider in management of northern leopard frogs. Both factors are likely to greatly affect population density in this species as Semlitsch (2000a) has noted for other amphibians. Each pond may be more or less isolated, depending on how far it is from other ponds, the predilection of northern leopard frogs to migrate from pond to pond, the tendency of young to disperse from natal ponds, the risks associated with inter-pond migration, and the philopatry of subadult and adult frogs.

Movement has not been studied in the Rocky Mountain region, but they probably favor meadows, wetlands, or riparian areas due to their relatively humid microclimates compared to surrounding habitats (see Seburn et al. 1997, for data from other parts of their range). Without detailed studies of the genetics and movement patterns of the frogs on a given site it is difficult to know whether there is a high degree of within-population genetic variability (i.e., most genetic variability is found within a population or pond), or a high degree of among-population genetic variability (i.e., most genetic variability is found among ponds). In the former case, conservation of one or a few breeding ponds and surrounding upland habitat conserves most of the genetic variability within the metapopulation. In the latter case, more ponds must be conserved to maintain a high degree of genetic diversity within the metapopulation. In either case, the safest way to conserve high genetic diversity is to maintain as many ponds and their surrounding upland core area as possible, with numerous inter-pond migration corridors. This reduces the chance of the whole population become extinct due to an unforeseen stochastic event and facilitates recolonization of local extirpations by dispersers from neighboring ponds.

The structure of the habitat through which movement occurs is also very important. For example, Bartelt (1998) documented the deaths of thousands of western toad metamorphs (*Bufo boreas*) in Idaho following the trampling by sheep of tall grasses in which the metamorphs were living. He attributed many of the deaths to trampling, but deaths of survivors of the trampling event were caused by dessication from the loss of the relatively humid microclimate that was lost when the grasses were trampled underfoot by the sheep. In addition, Seburn et al. (1997) have shown that juvenile northern leopard frogs disperse farther and more rapidly along streams than they do over land.

Movement and Activity Patterns

Dole (1965b) and Merrell (1977) both studied movements of northern leopard frogs and found that they used a home range in the summer. Dole (1965b) found that home range sizes varied from 68 – 503 m^2 and varied in size due to habitat type, sex, and life stage (i.e., subadult or adult). Dole (1965b) found that northern leopard frogs tended to make several short distance movements within the home range and used resting sites (called "forms") that the individuals returned to on a regular basis. In this study, 33 frogs trailed for five days or longer moved straight-line distances of 7 – 53 m. However, frogs made longer distance night-time movements during rainy periods. Merrell (1977) was in general agreement with these comments.

In contrast, Fitch (1958) believed that *R. pipiens* did not use a home range in Kansas, since he marked many frogs with no recaptures. Dole (1965b) measured long distance movements (>100 m in one night) in the species in response to nocturnal summer rains but the reasons for these movements remained unknown. As temperatures rose and vegetation dried out, frogs tended to move closer to water (Merrell 1970).

Moreover, although the issue of faithfulness to natal areas and breeding sites has not been specifically studied in northern leopard frogs, it seems that they are probably not territorial (Wells 1977), but they may exhibit breeding site fidelity (Livo 1981). Merrell (1970) noted that genetic drift seemed low in northern leopard frog populations, possibly suggesting that this species might not show a high degree of philopatry to natal sites (genetic drift is greater in small and highly philopatric populations). Although many researchers assume that amphibians return to their natal ponds to breed (Semlitsch and Bodie 1998), these types of movements have not been studied in *Rana pipiens*. Eighteen percent of over 5000 wood frogs (*Rana sylvatica*) dispersed to new ponds to breed in one study (Berven and Grudzien 1990), while 27% of Fowler's toads (*Bufo fowleri*) dispersed to new ponds to breed in another study (Breden 1987). At a study site in Germany where several ponds were spaced very closely, from 80 – 98% of three species of ranids and one bufonid returned to their natal ponds to breed (Kneitz 1998; cited in Pough et al. 2001). In a study of the natterjack toad (*Bufo calamita*) in Germany, all adult males returned to their natal ponds to call, but the sample (nine toads) was small (Sinsch 1997).

Northern leopard frog movement patterns have been studied by Bovbjerg and Bovbjerg (1964), Bovbjerg (1965), Dole (1965a, b, 1967, 1968), Merrell (1970, 1977), and Seburn et al. (1997). Movement patterns consist of spring movement from overwintering sites to breeding ponds (Dole 1967; Merrell 1970 1977), adult dispersal into upland foraging habitat during the summer (Dole 1965a, b; Dole 1968), natal dispersal from breeding ponds (Bovbjerg and Bovbjerg 1964; Bovbjerg 1965; Seburn et al. 1997), and fall migration to overwintering sites (Merrell 1970, 1977).

In the spring, frogs in Minnesota moved from overwintering sites in deep water of larger lakes to the shore but would not leave the lakeshore until temperatures were above 10^{o}C (Merrell 1970). Sexually mature frogs migrated from overwintering sites to breeding ponds and did so sometimes under extremely dry conditions and during daylight, even becoming dusty while doing so (Merrell 1970). In contrast, subadult frogs stayed near the larger lakes (Merrell 1970). This seems unusual given the fact that many larger ponds have longer seasonal hydroperiods and may therefore have predaceous fish that prey on subadult frogs (Semlitsch 2000a).

In Minnesota tadpoles metamorphosed into subadult frogs in July (Merrell 1970, 1977). Following metamorphosis, young northern leopard frogs stayed close to the breeding ponds until their tails had been fully resorbed (Merrell 1977). Dole (1965a) agreed that small frogs were closely tied to water. Following this period of breeding pond fidelity, mass migrations to larger lakes occurred and sometimes would result in mass mortality events along roadways (Bovbjerg and Bovbjerg 1964; Bovbjerg 1965; Merrell 1977).

Dispersal of young frogs was also studied by Seburn et al. (1997), who marked 938 metamorphs at a source pond in southern Alberta. Of these, 104 were recaptured. They dispersed up and down streams and across land, since they were found at ponds up to 4.0 km from the source pond that were not connected to the source pond by waterways. On average they dispersed twice as far up and down streams as across land. They reached dispersal ponds within 1 km of the source pond within three weeks, while the more distant ponds were reached within six weeks.

In fall, frogs migrated to overwintering sites in lakes, streams, and rivers (Merrell 1970; Emery et al. 1972; Cunjak 1986; Ultsch et al. 2000). Fall migration of northern leopard frogs In Minnesota usually occurred at night from mid-September through October, but seemed to end by late October (Merrell 1970). At the overwintering area in the fall, disturbance of frogs caused them to swim directly into deep water, in contrast to their summer behavior in which they tended to return to shore (Merrell 1970). They hibernated on lake bottoms, often under debris, and tended to congregate near areas of high oxygen concentration such as the bottom of spillways (Merrell 1970). They may also excavate shallow pits on the bottom of sandy ponds as overwintering sites (Emery et al. 1972).

Anecdotal information is available on how far northern leopard frogs can move. Merrell (1970) marked 107 frogs (their age was not noted) and released them in “favorable” habitat, only to return a day later to find no frogs except one 0.40 km from the release point. Seburn et al. (1997) recorded subadult movements up to 2.1 km while Dole (1971) recorded maximum subadult movements of 5.2 km. These are estimated straight-line movements and undoubtedly the reported distances underestimate the full extent of distance traveled by these individuals.

Semlitsch (2000a) has pointed out that it is critical to understand the movement patterns of any species of amphibian if a successful management strategy is to be developed. Any such strategy will depend on the movement pattern of the species and on the spatial distribution and size of ponds and migration corridors (Semlitsch 2000a). Semlitsch and Bodie (1998) and Semlitsch (2000b) convincingly showed that elimination of wetlands <5 ha in size could prevent some species from reaching and colonizing new ponds, depending on the movement patterns of species and the spatial distribution of wetlands suitable for reproduction by these species. Semlitsch (1998) measured the dispersal distances of several southeastern salamanders and determined that core habitat for salamanders consisted of the wetlands habitat in which they bred and a surrounding upland area to which they dispersed following breeding. The upland habitat was described by Semlitsch (1998) as "buffer" habitat but is more appropriately considered "core" habitat, as it is necessary for the survival of local populations (Semlitsch, personal communication, March 2001). Semlitsch (1998) found that an upland area that included up to 164 m of upland habitat around a pond would contain roughly 95% of salamanders of six species studied. Based on what is known of *Rana pipiens* movements, an area containing 95% of a population of these frogs would probably be much greater.

Northern leopard frogs are similar to the salamanders that were reviewed by Semlitsch (1998) in that the frogs also use wetland habitat for breeding and spend considerable amounts of time away from the pond after the breeding season feeding in upland habitat (personal observations). It is not known, however, how large an upland area should surround each breeding site to manage a population of northern leopard frogs nor what types of routes frogs use to migrate between breeding ponds or disperse from the natal area as subadults. Given the importance of identifying movement corridors to management strategies, the general lack of knowledge of movement patterns and home range use among northern leopard frogs is a serious impediment to managing the species.

Reproduction and Survivorship

Breeding Biology

The reproductive biology of northern leopard frogs has been studied in Michigan (Collins and Wilbur 1979), Minnesota (Merrell 1965, 1968, 1970, 1977), Colorado and Wyoming (Corn and Livo 1989), and in the laboratory (Noble and Aronson 1942; Aronson and Noble 1945; McClelland and Wilczynski 1989). Ponds suitable for breeding are described earlier in this work (see the Habitat section above).

General: As soon as males leave overwintering sites, they travel to breeding ponds and call in shallow water around suitable pond sites (Merrell 1965, 1968, 1970, 1977; Oldfield and Moriarty 1994; Hammerson 1999). Like many pond-breeding frogs, male northern leopard frogs attract females by giving breeding calls from specific locations within a breeding pond, with several males typically calling together to form a breeding chorus. Females come to males and breed at the calling sites. After breeding, females immediately leave the ponds, while males stay in the chorus continuing to call (Merrell 1977). This results in a preponderance of males at breeding ponds (Merrell 1977).

Egg masses were attached to emergent vegetation such as sedges (*Carex* spp.) or rushes (*Scirpus* spp.) in Colorado and Wyoming (Corn and Livo 1989). Wright and Wright (1949) reported that egg masses were flattened spheres that were 75 – 150 mm by 5 – 75 mm in dimension. Like all ranid frogs, there is no parental care in this species. Mean water depth of 39 oviposition sites was 12.9 cm (standard deviation = 3.3 cm). In Minnesota, egg masses were left in the area in which males had been calling and were placed in water less than 40 cm in depth that was exposed to the sun (Merrell 1977). Hammerson (1999) stated that egg masses were attached to vegetation just below the surface in warm shallow water from 7 – 25 cm deep, while Merrell (1977) noted that egg masses were attached to vegetation "a few cm" below the water surface. The temperature of egg masses was typically 2 – 3°C higher than the water temperature adjacent to the egg masses (Merrell 1970). Merrell (1977) suggested that the dark pigmentation of the embryos caused them to act like black bodies, implying that it was adaptive for females to lay their eggs in locations in ponds that would receive a substantial amount of solar radiation. It may also help embryos to avoid freezing during short periods of cold springtime weather (Merrell 1977). Warm temperatures also speed development in amphibian eggs and larvae (Duellman and Trueb 1986).

Breeding Calls

Noble and Aronson (1942) described the mating call as a quavering sound pronounced phonetically as "ir-a-a-a---a-a-h", lasting about three seconds. Wright and Wright (1949) described the call as a long, low guttural note lasting three or more seconds followed by three to six short notes each a second or less in length. The call starts softly and grows louder as the vocal sacs inflate (Noble and Aronson 1942). Pace (1974) pointed out that male northern leopard frogs do not have external vocal sacs, but have well-developed internal vocal sacs. Davidson (1996) provided a recording of northern leopard frogs calling in the Rocky Mountains. As described by Wright and Wright (1949), choruses in the eastern United States (near Ithaca, New York) were conspicuous, although an individual call was very quiet. However, various workers have found choruses to vary in volume. Bishop et al. (1997) described breeding choruses of northern leopard frogs as "low volume". Peterson (1974) came across a "faintly vocalizing" chorus at Stockade Lake in the Black Hills. We have found it very difficult to hear breeding choruses in the Black Hills. Calling can be nearly indiscernible over other night-time sounds and calls may be sporadically given. However, Dunlap and Platz (1981) found little variation in calls across a transect from Wisconsin to Idaho. Merrell (1977) stated that northern leopard frogs tended to call while floating in water, but Noble and Aronson (1942) noted that northern leopard frogs also called from land if particularly excited.

Pace (1974) gave the most extensive description of the call of the northern leopard frog and provided sonograms of the various components of the call. She divided the call into three components, including a long many-pulsed trill, a series of short trills, and a series of pulses that usually terminated calls. Typically, male frogs gave calls that consisted of several of these sounds, usually commencing with the longer trills, unless they were in the middle of a larger chorus. They usually followed these longer trills with the shorter trills, ending the typical call with a series of a few pulses. To the typical observer, this call sounds like a kind of lower frequency trill that may descend in frequency and end with what seems to be a few short grunts (personal observations). Pace (1974) found that male frogs were stimulated to call by playbacks of the longer trills, and isolated males gave calls that consisted of a longer series of the longer trills. She concluded that the long, slow, trilled call functioned as a long-range call that attracted females, and the shorter, rapid trills were short-range calls that helped females to find the calling male at close distances. Finally, the calls typically were terminated by some short terminal sounds that were used to maintain separation amongst males in choruses (the third part of a typical call).

Northern leopard frogs give one other type of call; a release call. Male northern leopard frogs will clasp virtually anything with the general size and shape of a female frog and have been found clasping floating beer cans, females of other *Rana* species, a *Bufo americanus* (American toad) female, a dead female northern leopard frog, and a bowfin (*Amia calva*) fish (Merrell 1977). It is therefore not surprising that the other vocalization males will give a release call when clasped by other males (Merrell 1977; McClelland and Wilczynski 1989). Females also give the release call if not in mating readiness (McClelland and Wilczynski 1989). McClelland and Wilczynski (1989) gave a sonogram of the release call.

Male calling has been recorded following the onset of daytime air temperatures of 15 – 20°C (Merrell 1977; Corn and Livo 1989). Specific sites used for calling and breeding within ponds were described by Merrell (1977) as being the warmest part of the pond, typically in water of 40 cm depth or less in an unshaded location with maximal exposure to sunlight. The water temperature during calling was usually 20°C or more (Merrell 1977). Merrell (1977) believed that differences in temperature within ponds typically resulted in the use of one spot, one to two meters in diameter, to lay eggs even when most breeding ponds in his study area were 30 – 60 m in diameter.

Breeding Phenology

Hammerson (1999) gave an excellent summary of breeding phenology for populations at various elevations in Colorado. Northern leopard frogs show geographic variation in the timing of reproduction and egg-laying that is probably determined by various environmental cues. Corn and Livo (1989) noted that two to three days of air temperatures of 15 – 20°C were needed to initiate calling activity at their study sites in northern Colorado and southern Wyoming. Elevation at these sites was 1555 – 2520 m. Corn and Livo (1989) also recorded precipitation but noted that calling and breeding at their sites seemed to correspond more with temperature than with precipitation. Corn and Livo (1989) found that calling started anywhere from mid-March to early to late May, depending on elevation. At these sites, eggs were laid within two to three days following the onset of chorusing (Corn and Livo 1989). In the San Luis Valley of Colorado at elevations of 2285 m, Hammerson (1999) reported calling extending into late June. In the Black Hills and vicinity, calling has been recorded in May and June (Smith et al. 1998).

In Minnesota northern leopard frogs bred from mid-March to mid-May depending on the weather, but usually bred in April (Merrell 1977). At lower elevations in Colorado northern leopard frogs began breeding in March, but at higher elevations they often did not start breeding until April or May (Hammerson 1999). High elevation populations studied in northern Colorado began breeding in May (Corn and Livo 1989). In the Black Hills the timing of reproduction is uncertain, but calling has been heard in April at mid-elevation (ca. 1500 m) ponds (personal observations). The timing of courtship and breeding doubtless is sooner in southern populations and at lower elevations.

Hatching time and time to metamorphosis also varies geographically, probably dependent on environmental variables, especially temperature. Hine et al. (1981) reported that hatching occurred in 5 – 9 days when temperatures were at or above 10^{o}C. Wright (1914) reported that eggs hatched in 13 – 20 days in the vicinity of Ithaca, New York. Wright and Wright (1949) reported that tadpoles usually transformed in 60 – 80 days. Corn (1981) reported that the larval period ranged from 58 – 105 days, but his study ended before individuals were fully transformed. The 105-day larval period was reported at the highest elevation sites (Corn 1981), suggesting a relationship with elevation. Ryan (1953) noted that northern leopard frogs metamorphosed in the Ithaca area from June 30 to August 15, with most individuals metamorphosing in the first half of July. Wright and Wright (1949) also reported that most individuals metamorphosed in July in the Ithaca area. Corn (1981) observed egg laying in late May and early June at elevations of 2035 – 2365 m in Larimer County, Colorado (northern Colorado) with metamorphosis from mid-July through mid-September. In various high elevation sites in Colorado, Hammerson (1999) reported metamorphosis throughout August. Mosimann and Rabb (1952) collected newly metamorphosed tadpoles July 26, 1950, in Liberty Co., north-central Montana. The lead author has observed large numbers of tadpoles in some ponds in the Black Hills in July, but has not taken detailed notes on their development.

Population Demographics

Data on age to maturity, age at first reproduction, and age at death are incomplete. In a population Ryan (1953) studied in the vicinity of Ithaca, New York, female northern leopard frogs did not become sexually mature until at least their first year following metamorphosis, and he felt that most frogs were not sexually mature until their second year following metamorphosis. Force (1933) estimated that northern leopard frogs attained reproductive maturity at three years of age in northern Michigan. Baxter (1952) reported that sexual maturity in females was not achieved until late in the second year in frogs from the vicinity of Laramie, Wyoming (2200 m), and these females laid eggs in the third year following metamorphosis. At elevations of 2600 m female frogs did not attain sexual maturity until late in the third year with these eggs being laid in the fourth year following metamorphosis (Baxter 1952). Leclair and Castanet (1987) reported that males in Quebec populations reached sexual maturity at an age of two years. In Quebec populations, few male frogs lived to be older than four or five years (Castenet 1987). A leopard frog in captivity lived for five years and 11 months (Flower 1936). It is probably reasonable to assume that most northern leopard frogs living in the wild seldom reach their sixth year. It also seems reasonable to conclude that female northern leopard frogs may breed two or three during their lives, and certainly no more than four times. This agrees in general with the conclusions of Corn and Livo (1989) in southern Wyoming and northern Colorado, who wrote that the three classes of clutch sizes occurring at their study site corresponded to three age classes of frogs.

There seems to be no other information on growth rates, age at sexual maturity, or age at death in any natural populations of the northern leopard frog. Corn and Livo (1989) recorded an average of 3045 eggs per clutch (range 645 – 6272 eggs), which may mean that females produce some 9000 eggs during their lifetime, assuming three reproductive bouts during three consecutive years.

The number of eggs laid in a clutch appears to vary widely, even within a population. Livezey and Wright (1947) estimated a clutch size of 3500 – 6500 eggs for northern leopard frogs, Merrell (1965) reported from 2000 to more than 5000 eggs in some Minnesota clutches, and Hupf (1977) counted from 1000 – 7000 eggs in an unreported number of preserved females from Nebraska. Corn and Livo (1989) counted from 645 – 6272 eggs in clutches at their study ponds, with a mean of 3045 eggs per clutch. Corn and Livo (1989) also reported three distinct size classes of clutches. They suggested that this roughly corresponded to three different size classes of females at their study sites. Hatching success at six ponds was 70 – 99% (Corn and Livo 1989).

There are no studies of survival rates of northern leopard frogs for reaching sexual maturity, but it is likely that mortality is significant after hatching, since hatching success seems high, from 70 – 99% at the sites studied by Corn and Livo (1989) to around 95% at sites studied by Hine et al. (1981). There are also no studies of survivorship at any other life stage in northern leopard frogs, however, Merrell (1977) has provided some interesting insights from work done near Minneapolis/St. Paul, Minnesota. Merrell (1977) counted a total of 173 egg masses at eight adjacent breeding ponds. At 2000 – 5000 eggs per mass (determined from studies of Merrell 1965), Merrell (1977) calculated that the number of eggs at his study sites ranged from 346,000 – 865,000. Capture/mark/release data obtained in July prior to dispersal of the young metamorphs indicated that approximately 20,000 metamorphs existed in the area. It should be noted that Merrell (1977) used a Lincoln – Peterson index to derive this estimate, probably an inappropriate estimator for an open population such as the one under study (Krebs 1999). The study of Merrell (1977) would then indicate a mortality rate of at least 94% and possibly as high as 97% in the tadpole stage. Another study found a ratio of newly metamorphosed frogs to sexually mature adult frogs somewhere between 15:1 and 20:1 (Merrell 1969). This would further indicate a 93 – 95% mortality rate between metamorphs and sexually mature frogs. These numbers should all be considered approximate due to the techniques used, but they would still indicate a mortality rate that is very high, probably over 90%, for the young age classes (i.e., from tadpole to metamorph and from metamorph to the adult stage).

Estimates of mortality rates derived from the data of Merrell (1977) show rather clearly that northern leopard frogs are probably rather typical r-selected species with a type III survivorship curve and probably show large fluctuations in population dynamics from year to year (Begon et al. 1996). This is typical of many amphibians, and it can be difficult to determine whether population density is trending upward or downward due to these large natural fluctuations in population density (Pechmann et al. 1991; Pechmann and Wilbur 1994). Species that are r-selected can recover from low population densities due to high potential growth rates, but they can also go locally extinct if affected by severe mortality pressures at times when population densities are low (Begon et al. 1996).

Various estimates of the population density of northern leopard frogs exist. Merrell (1968) found populations of 124 – 1568 individuals at six breeding ponds in Minnesota. Exact sizes of these ponds were not given, although Merrell (1968) stated that they were “about 50 to 100 feet in diameter” (15.4 – 30.8 m). Hine et al. (1981) found 2 – 76 frogs at six ponds in Wisconsin that were from 0.02 – 32 ha in size. Hine et al. (1981) compared these data to those of Merrell (1968) to argue that there had been serious declines in northern leopard frog populations in the upper

Midwest. Merrell (1977) provided an estimate of about 20,000 newly metamorphosed frogs in an area of about 15 ha in Minnesota and he sampled about 25,000 frogs of all ages in this area.

Food Habits

Most of what is known about the food habits of tadpoles, subadults, and adult northern leopard frogs is anecdotal. Merrell (1977) considered northern leopard frog tadpoles to be generalist herbivores but he also noted that they sometimes scavenged on dead animals including conspecifics. Hendricks (1973) examined gut contents in tadpoles of the Rio Grande leopard frog (*Rana berlandieri*), formerly known as *R. pipiens* and closely related to the northern leopard frog. He described this species as a filter feeder that primarily ate free-floating algae. Franz (1971) found that *R. pipiens* tadpoles mostly ate various species of free-floating green algae and blue-green algae. Alford (1999) pointed out that high densities of tadpoles of various species may be the primary consumers in some ecosystems and are known to reduce the standing crop and change the species composition of algae. For example, Lamberti et al. (1992) found that tailed frog (*Ascaphus truei*) tadpoles at a density of 5 tadpoles per square meter could reduce periphyton biomass by 98% and chlorophyll a by 82% in streams in Washington. Some ponds in parts of the Rocky Mountain region can have northern leopard frog tadpoles in this density range and higher (personal observations).

Subadult and adult northern leopard frogs are carnivorous and are usually described as generalist insectivores. Merrell (1977) noted that northern leopard frogs became carnivorous at metamorphosis and fed primarily on insects. However, they tended to feed on anything that moved and that was small enough to fit into their mouths, including smaller northern leopard frogs. Breckenridge (1944) reported such unusual items as a small garter snake, ruby-throated hummingbirds, and a yellow warbler in the stomachs of northern leopard frogs. Drake (1914) also noted the propensity of northern leopard frogs to snap at anything that moved and that was small enough to be swallowed. In dissecting 209 adult northern leopard frogs, Drake (1914) found that they primarily ate "insects" (this category was not further broken down), spiders, mollusks, crustaceans, and various other arthropods. Whitaker (1961) found that they primarily ate insects as well, mostly coleopterans (beetles) and orthopterans (grasshoppers), but also dipterans (flies and associated groups), hemipterans (the true bugs), and hymenopterans (wasps and their allies). Linzey (1967), in a study of 463 specimens, also concluded that subadult and adult northern leopard frogs ate primarily insects. Nearly one quarter of the food items were beetles. Linzey (1967) also split his data up by life stage (adults and subadults), identified all food items to family, and identified seasonal variation. He found that all life stages seemed to be opportunistic carnivores; they ate the largest things that fit into their mouths and the most common prey items available at the time. Miller (1978) noted that northern leopard frogs were opportunistic predators, feeding on insects that were most abundant. He also noted that northern leopard frogs only preyed on moving prey. Merrell (1977) reared northern leopard frogs in the laboratory on mealworms and crickets.

Community Ecology

There are a variety of studies of the community ecology of the northern leopard frog. Various studies of the predators of the northern leopard frog are anecdotal and consist mainly of lists of potential predators, but several are experimental. There are several studies on competition and predation of northern leopard frog tadpoles in company with other tadpoles or in combination with a variety of predators. A few studies on the competitors of adult northern leopard frogs exist. There is a growing body of literature on the parasites and diseases of ranid frogs in general, and there are a variety of studies on other aspects of ecology.

Basic Community Ecology

Several studies have been done on *Rana pipiens* and their role in amphibian communities (DeBenedictis 1974; Smith-Gill and Gill 1978; Woodward 1982, 1983; McAlpine and Dilworth 1989; Hecnar and M'Closkey 1998; Relyea and Werner 2000; Relyea 2001a, 2001b). These studies can be divided into studies of *R. pipiens* tadpoles (DeBenedictis 1974; Smith-Gill and Gill 1978; Woodward 1982, 1983; Relyea and Werner 2000; Relyea 2001a, 2001b) and adults (McAlpine and Dilworth 1989; Hecnar and M'Closkey 1998). They can be further divided into studies on competition (DeBenedictis 1974; Smith-Gill and Gill 1978; Woodward 1982; McAlpine and Dilworth 1989), predation (Woodward 1983; Relyea and Werner 2000; Relyea 2001a, 2001b), and general ecology (McAlpine and Dilworth 1989; Hecnar and M'Closkey 1998).

Although no studies examining tadpole densities or their role in structuring the community have been completed in Wyoming or the nearby Rocky Mountains, *Rana pipiens* tadpoles can clearly be dominant species in some semi-permanent Rocky Mountain ponds during the spring and early summer (personal observations). Woodward (1982, 1983) found that temporary pond breeders were often superior competitors to permanent pond breeders, and that some temporary pond breeders ate tadpoles of permanent pond breeders (Woodward 1982). For example, *Spea multiplicata* ate the tadpoles of *R. pipiens* (Woodward 1982). Although they are at a competitive disadvantage to temporary pond breeders, Woodward (1983) found that *R. pipiens* tadpoles are better able to avoid predation because they tend not to move very much, as compared to tadpoles of temporary pond breeders. He also found that there are more tadpole predators in permanent ponds, thus explaining why *R. pipiens* might have evolved this important behavioral trait.

Two papers examine various biotic and abiotic parameters and how they affected the distribution of adult frogs in Canada. McAlpine and Dilworth (1989) investigated competition and microhabitat of various anurans in New Brunswick and Hecnar and M'Closkey (1998) examined species richness patterns of various frogs in Ontario. McAlpine and Dilworth (1989) found that green frogs (*Rana clamitans*) and *R. pipiens* overlapped significantly in diet (the two frogs are similar in size), and seemed to divide the niche by microhabitat. In terrestrial habitats, *R. pipiens* tended to be found in areas of denser vegetation. They were found farther from shore than *R. clamitans* when in ponds. Both tended to be found in the diet of bullfrogs (*R. catesbeiana)*. Whether these patterns of microhabitat use by *R. pipiens* are similar in Wyoming is unknown. Hecnar and M'Closkey (1998) underscore the effect of predatory fish on amphibian presence; it was one of the most significant factors structuring the amphibian community across much of southwestern Ontario. They also found that various vegetation factors accounted for the patterns of species richness that they observed, with increased amphibian richness in areas richer in woodlands. The species accounting for this result were various species of amphibians associated with woodlands, but did not include *R. pipiens*.

Natural Predators

Northern leopard frogs are eaten by a variety of predators at all life stages. Merrell (1977) reported that most mortality occurred in the tadpole stage, and most of this appeared to be from predators, although overwintering mortality seemed to be important in subadults as well and predation can be a substantial source of overwinter mortality. Merrell (1977) noted that various early authors recorded the following as predators of tadpoles: Mallards (*Anas platyrhynchos*), blue-winged teal (*Anas discors*), newts (unknown species), waterfowl, fishes, aquatic insects, leeches, diving beetle larvae (Dytiscidae) and adult diving beetles (*Dytiscus* species), dragonfly larvae (Libellulidae and probably other families), caddisfly larvae (Phryganeidae), backswimmers (genus *Notonecta*), and giant water bugs (*Belostoma* species). Spiders (Lycosidae and Pisauridae) may also eat tadpoles (Merrell 1977). Various species of garter snakes (*Thamnophis* species) have been recorded to feed on tadpoles, as have water snakes (genus *Nerodia*). Tiger salamander

(*Ambystoma tigrinum*) adults and tadpoles are known to feed on frog tadpoles (Petranka 1998). In fact, populations of tiger salamander tadpoles have completely eliminated frog tadpoles in experimental interactions (Morin 1983). In the Black Hills the breeding period of the tiger salamander overlaps with that of the northern leopard frog and they may breed in similar ponds (unpublished observations). Paedomorphic tiger salamanders (Petranka 1998) also occur in the Rocky Mountains (Smith unpublished observations) and we suspect that they would readily eat northern leopard frog eggs and tadpoles. Hammerson (1999) noted that pied-billed grebes (*Podilymbus podiceps*) and tiger salamanders (*Ambystoma tigrinum*) preyed on northern leopard frog tadpoles in Colorado. Important tadpole predators that Woodward (1983) identified in his predation experiments were Belostomatids (diving beetles), Notonectids (backswimmers), Aeshnid (dragonfly) larvae, *Ambystoma tigrinum* (tiger salamander) larvae, *Gambusia affinis* (mosquitofish), Corydalid (dobsonfly) larvae, and garter snakes (*Thamnophis marcianus*).

In a series of studies, Relyea and Werner (2000) and Relyea (2001a, b) examined morphological and behavioral plasticity in response to predation threats in tadpoles of a number of amphibian species, including the tadpoles of *Rana pipiens*. Increases in tail depth should result in better swimming speed of tadpoles (Wassersug and Hoff 1985; McCollum and Leimberger 1997). Relyea and Werner (2000) found that *R. pipiens* tadpoles were marginally smaller with deeper tailfins and more robust tail musculature when reared in the presence of the larvae of *Anax* species (dragonflies), a known predator on frog larvae, but the difference was not significant. Relyea (2001a, b) found that responses to predators were complex and varied according to predator and anuran species. In the presence of *Anax* larvae and mudminnows (*Umbra* species), *R. pipiens* larvae became less active, while their activity levels did not change in the presence of *Notophthalmus viridiscens* (eastern newts) or *Dytiscus* species (giant water beetles) (Relyea 2001a). Relyea (2001b) explained why these behavioral differences probably occurred;

Notophthalmus viridiscens and *Dytiscus* were relatively inefficient predators on *R. pipiens* tadpoles, while *Umbra* and *Anax* had high capture efficiencies. Relyea (2001a) also found that *R. pipiens* tadpoles changed morphoslogy in the presence of *Umbra* species, developing smaller bodies with deeper tail fins, a result that was not found to be significant when they were reared with *Anax* larvae (Relyea and Werner 2000). This result was not obtained when *R. pipiens* tadpoles were reared with any of the other predators. When taken together, Relyea and Werner (2000) and Relyea (2001a, b) showed that the responses of various species of anurans to various species of predators were complex, with changes in morphology and behavior depending on the predators to which they were exposed. Probably most importantly as regards the natural history of *R. pipiens*, these studies showed that predation is probably a significant factor structuring various aspects of the natural history of anuran tadpoles, including *R. pipiens*.

Most authors have combined discussions of predation on subadults with that on adults. Dole (1965b, 1968) asserted (without evidence) that snakes were major predators of subadult and adult northern leopard frogs. Hammerson (1999) reported that recently metamorphosed frogs were preyed upon by great blue herons (*Ardea herodias*), burrowing owls (*Athene cunicularia*), northern water snakes (*Nerodia sipedon*), and western terrestrial garter snakes (*Thamnophis elegans*). According to Merrell (1977), the most common predators on adult and subadult northern leopard frogs were garter snakes (genus *Thamnophis*). He claimed that northern leopard frogs supported large populations of garter snakes. Leeches also fed on northern leopard frogs, leaving them debilitated and presumably more likely to die (Merrell 1977). Merrell (1977) also reported that various predators such as fishes, snakes, turtles, amphibians, birds, and mammals all fed on adult northern leopard frogs. The lead author has observed garter snakes feeding on northern leopard frogs in the Black Hills (unpublished observations).

Introduced predators

Introduced predators have the capacity to overwhelm northern leopard frog populations since the frogs have not evolved along with such predators, and these predators deserve special mention. Bullfrogs (*Rana catesbeiana*) are well known to cause the elimination of populations of ranid frogs, especially in the western United States, where bullfrogs have been widely introduced (Stebbins and Cohen 1995). Although northern leopard frogs and bullfrogs co-occur in parts of the range of the northern leopard frog, in areas where bullfrogs have been introduced northern leopard frogs have declined (Hammerson 1982, 1999). Since it is well known that bullfrogs can cause serious declines when introduced to areas where they are not native (Stebbins and Cohen 1995), introductions of bullfrogs should be treated as a major management concern. Such introductions need to be identified and eliminated.

Introduced predaceous fish are another serious issue that probably has caused declines of northern leopard frogs, because they are not natural predators of tadpoles, and *R. pipiens* therefore probably have no natural defense against them. Introduced predaceous fish known to occur in Wyoming are the rainbow trout (*Oncorhynchus gairdneri*), brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), northern pike (*Esox lucius*), largemouth bass (*Micropterus salmoides*), green sunfish (*Lepomis cyanellus*), and rock bass (*Ambloplites rupestris*). The various trout species will all eat tadpoles (Smith et al. 1998) and probably also eat frog eggs, the northern pike eats hibernating adult frogs (unpublished data), and the bass and sunfish will probably eat eggs and tadpoles. Kruse and Francis (1977) found that largemouth bass, green sunfish, and black bullhead (*Ictalurus melas*) all ate northern leopard frogs. Bluegill sunfish (*Lepomis macrochirus*) will also eat northern leopard frogs (Relyea 2001b). Brönmark and Edenhamn (1994) showed that introduced predaceous fish reduced the abundance of tree frogs (*Hyla arborea*) and Hecnar and M'Closkey (1997b) showed that introduced predaceous fish reduced the abundance and diversity of frog communities in Canada, including those in ponds that contained northern leopard frogs. Bovbjerg (1965) reported that the introduction of truckloads of young fish by the Iowa Conservation Commission completely exterminated a population of northern leopard frog tadpoles at his study site following stocking of the slough under study. Introduced fish also eat overwintering northern leopard frogs, which are extremely vulnerable to predation (Emery et al. 1972). In the Black Hills the lead author observed that ponds with breeding colonies of chorus frogs (*Pseudacris triseriata*) and northern leopard frogs that also contained predaceous fish had no successful metamorphs later in the active season. However, no systematic study of this phenomenon has been conducted.

It is probable that overwinter mortality associated with predation by introduced predaceous fish in streams and larger ponds is another modern source of mortality for the northern leopard frog. Within the Rocky Mountain region, introduced fish include brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), and rainbow trout (*Salmo gairdneri*). Northern pike (*Esox lucius*) are intentionally introduced by sport fishermen to some areas. Brook trout are smaller, insectivorous trout that probably do not eat frogs the size of northern leopard frogs. Cunjak (1986) reported no leopard frogs in stomach contents of >100 brook trout he examined from his study site. However, splake (a non-fertile hybrid of lake trout, *Salvelinus namaycush*, and brook trout), have been reported to eat northern leopard frogs in the winter (Emery et al. 1972). Brown trout are more piscivorous and may well eat adult northern leopard frogs. Ice fishermen in North Dakota have reported northern leopard frogs in the stomachs of northern pike caught during mid-winter (unpublished data). It is probable that all of these predators, except mosquitofish, can be found in or near Wyoming.

Competitors

Larval amphibians have provided an excellent system in which to study competition amongst a closely related group of competitors (Wilbur 1997), and is thus the life stage that has been emphasized in studies of amphibian competition. It is not known whether adult northern leopard frogs could have competitors other than those listed below in the Rocky Mountains, but generalist insectivores of similar sizes to adult northern leopard frogs have the potential to be competitors.

DeBenedictis (1974) and Smith-Gill and Gill (1978) studied competition between *Rana pipiens* and the wood frog (*R.. sylvatica*) a frog that breeds slightly earlier in the spring than northern leopard frogs but frequently in the same types of ponds. DeBenedictis (1974) conducted a field study, while the study of Smith-Gill and Gill (1978) was a laboratory study designed to examine some of the predictions of competition as determined by the Lotka-Volterra competition equations. The tadpoles of these two species have a high degree of temporal overlap in most parts of the range of the northern leopard frog. The wood frog and northern leopard frog co-occur in the Rocky Mountains in parts of Colorado and Wyoming (Conant and Collins 1991). DeBenedictis (1974) found that the intensity of competition depended on the amount of food, predation, and density of the two species and in some situations did not occur at all. Smith-Gill and Gill (1978) also found complex density effects and discussed these with relation to the Lotka-Volterra competition equations.

In much of their range, northern leopard frogs co-occur with the tiger salamander (*Ambystoma tigrinum*) and may breed in the same ponds. These two species may compete as larvae, and the tiger salamander may prey on northern leopard frog larvae, but no studies of the interactions of the two have been published.

Parasites and Disease

Three basic types of diseases have been identified in amphibians: Viruses, fungal infections, and bacterial infections (Carey et al. 1999). Of these three Carey et al. (1999) and Daszak et al. (1999) wrote that only viruses and fungal infections have been implicated in mass mortality events. However, the bacterial diseases collectively called "red leg" have been reported to cause mass mortality events by Faeh et al. (1998). The term "red leg" may refer to the symptomology of a variety of different bacteria (Faeh et al. 1998) but is frequently associated with *Aeromonas hydrophila*, a bacterium blamed for the disappearance of boreal toads (*Bufo boreas*) at several sites in Colorado (Carey 1993). However, Carey et al. (1999) stated that they believed that bacterial infections were largely secondary to fungal and viral infections.

Specific types of iridoviruses known as ranaviruses are known to infect ranid frogs (Cunningham et al. 1996; Daszak et al. 1999) and some amphibian declines are blamed on this virus (Jancovich et al. 1997; Daszak et al. 1999). Daszak et al. (1999) reported that ranaviruses were extremely lethal, with 100% mortality in exposed tadpoles. Tadpoles are most susceptible to these viruses but all life stages can acquire the disease (Daszak et al. 1999). Infected metamorphs die without apparent signs of infection, and infected adults show no overt signs or may display a general weakness (Daszak et al. 1999). Secondary bacterial infections are common in cases of ranavirus. Movements of amphibians like bullfrogs, which are commonly introduced, have probably spread ranaviruses around the country (Daszak et al. 1999). In South Dakota, tiger salamanders are often introduced as fish bait and this species has an iridovirus of its own (Daszak et al. 1999). Although a link between ranaviral infections and amphibian declines is suspected, it is less clear than the link between chytridiomycosis and amphibian declines (Daszak et al. 1999).

Chytridiomycosis, a disease of anurans caused by a chytrid fungus (*Batrachochytrium dendrobatidis*), has recently been blamed for frog declines around the world (Berger et al. 1998;

Morell 1999; Daszak et al. 1999, 2000), and has been found in northern leopard frogs (Carey et al. 1999). The disease was first blamed for amphibian declines in Australia in 1998, but it probably emerged separately on two continents at around the same time (Berger et al. 1998) and has been found in frogs collected as far back as 1978 (Milius 2000). Of concern to persons involved with field surveys, chytrids may also be spread by introduced amphibians or by humans that visit wetland areas (e.g., by boots or survey gear that become contaminated by the fungus). The signs of chytridiomycosis are loss of the righting reflex, lethargy, and abnormal posture (Daszak et al. 1999).

Carey et al. (1999) discussed hypotheses that could explain the apparent recent increases in the susceptibility of amphibians to infectious disease. Among several hypotheses they suggested that these pathogens can be introduced to frog habitats by fish stocking, introduction of non-native amphibians such as bullfrogs or extralimital populations of tiger salamanders, wind-blown insects, the activity of birds or other animals, by workers monitoring amphibian ponds, or by anglers or other tourists. As a standard protocol for amphibian survey and monitoring, investigators should sterilize boots and other gear with a solution of 10% standard household bleach (1:10 by volume) by completely soaking the gear in this solution for at least 10 seconds and then rinsing it with fresh water. This methodology is commonly used in veterinary clinics to prevent the transmission of virulent disease.

Like many amphibians, northern leopard frogs collected in the wild probably have a high parasite load. There have been various field investigations of the parasites of *Rana pipiens*, including Prudhoe and Bray (1982), Baker (1987), and McAlpine and Burt (1998), but it is not known whether such parasites cause population-level declines. Goldberg et al. (2001) have discussed the helminths of northern leopard frogs from North and South Dakota. In addition, Dyer

(1991) has reviewed records of parasites found in northern leopard frogs. Fried et al. (1997) found that some parasites are particularly lethal to northern leopard frog tadpoles. Of particular interest are trematode parasites in the genus *Ribeiroia*, which have emerged as a potential cause of limb abnormalities in Pacific treefrogs (*Pseudacris regilla*) (Sessions and Ruth 1990; Johnson et al. 1999) and western toads (*Bufo boreas*) (Johnson et al. 2001).

Symbiotic and Mutualistic Interactions

Nothing is known of mutualistic or symbiotic interactions in *Rana pipiens*.

Conservation

Conservation Status

Federal Endangered Species Act

Rana pipiens is not listed as threatened or endangered under the Endangered Species Act.

Bureau of Land Management

The northern leopard frog is currently on the BLM sensitive species list in Wyoming (BLM Wyoming 2001) and Colorado. There are no BLM offices in South Dakota, Nebraska, or Kansas so this species is not ranked by the BLM in these states.

Forest Service

Rana pipiens is listed as a sensitive species within the USDA Forest Service Region 1 (USDA Forest Service 1999) and Region 2 (USDA Forest Service 1994).

State Wildlife Agencies

The northern leopard frog has no special status in most states, except for several states near the periphery of the range. The species is considered of special concern in Idaho, Colorado, Indiana, and Connecticut. Montana considers the species endangered on the western side of the continental divide and of special concern to the east. Northern leopard frogs are protected in Oregon and endangered in Washington. Across Canada, the species is of special concern, which is a status that affords them minimal protection.

The Wyoming Game and Fish Department (WGFD) assigns the northern leopard frog a state special concern rank of NSS4 (Native Species Status 4). The NSS4 rank is based on WGFD estimates that *R. pipiens* in Wyoming is widely distributed throughout its native range, the populations are relatively stable, and the critical habitat is stable (Oakleaf et al. 2002). WGFD ranks native species on a scale of NSS1 to NSS7, with NSS1 representing critically imperiled species and NSS7 representing stable or increasing species. These ranks are assigned by WGFD biologists as a way to roughly prioritize wildlife concerns in the state, but they carry no legal, regulatory, or management weight per se.

Natural Heritage Ranks

The northern leopard frog is considered G5 (globally secure) by the Natural Heritage Network. However, it is ranked from S3 (vulnerable) to S1 (critically imperiled) by virtually all western states and provinces (Figure 1). This illustrates a common conception of the species; it is often thought to be relatively secure within its range in the plains and eastern states (or the Plains region within mountainous states, such as Montana), but is relatively rare in its range within the Rocky Mountains. The northern leopard frog does not occur in Kansas, where plains leopard frogs predominate.

Biological Conservation Issues

Extrinsic Threats

Prioritizing risk factors to northern leopard frogs in Wyoming difficult because risk factors will vary from site to site and are incompletely known in any case. The following should be taken as a tentative prioritization. In some ways these risks are presented as much in order of ease of avoidance of risk as they are in order of clear and present danger to northern leopard frog populations. Beyond items 1 and 2 (of nearly equal importance), the order of the list is speculative. What is not speculative, however, is the fact that all these factors have affected northern leopard frogs at certain study sites throughout North America.

1. Protection of Known and potential breeding sites

Semlitsch and Bodie (1998) and Semlitsch (2000b) noted that breeding ponds that produced the highest density and biodiversity of amphibians are not protected by current federal law. Such is also the case in the Black Hills; in addition, the current Forest Plan for the Black Hills National Forest does not provide for the protection of waters appropriate for the reproduction of large numbers of northern leopard frogs (USDA Forest Service 1997). Streams, springs, and large lakes are protected; what is needed by northern leopard frogs are the smaller seasonal and semi-permanent ponds of <5 ha often left unprotected by law and ignored by management plans (Semlitsch and Bodie 1998; Semlitsch 2000b).

Upland areas surrounding these ponds are used throughout the summer as foraging habitat and should also be protected (Semlitsch 1998, 2000a). For use of upland habitat by northern leopard frogs see publications by Dole and Merrell cited in this report. Although Semlitsch (1998) refers to upland habitat as a "buffer zone", it is more appropriately referred to as "core habitat area" (Semlitsch, personal communication, March 2001) and should be protected as such. Dole (1965 a and b) showed that northern leopard frogs typically used a home range of about 68 – 503 m^2. However, this doesn't indicate how much upland core area should be protected to conserve an entire population because some of the population will have home ranges farther from the breeding pond than other members of the population.

Studies of Semlitsch (1998) on pond-breeding salamanders could be used as a start to protect upland core area for northern leopard frogs. Semlitsch (1998) reported that a "buffer zone" (i.e., core upland habitat) extending 164 m in all directions from each breeding pond is needed to conserve 95% of the adult breeding population of various pond-breeding salamanders foraging in the upland habitat following the breeding season. This core area is highly species specific, however. The larger salamanders Semlitsch (1998) studied are similar in mass to northern leopard frogs and use upland core areas of 150 – 200 m surrounding breeding ponds. This might be taken as a general indication of the amount of upland core area needed by northern leopard frogs. Thorough studies are needed specific to northern leopard frogs for more definitive management recommendations.

2. Control of Introduced predaceous fish

These have been clearly implicated in the decline of some frogs (Bovbjerg 1965; Brönmark and Edenhamn 1994; Hecnar and M'Closkey 1997b) and are found in much of Wyoming. Ongoing management by various agencies to maintain introduced predaceous fish makes it difficult to resolve the conflict between this priority and the need to protect populations of northern leopard frogs. Some of the ponds discussed in this report are found in drainages that are not connected to waterways suitable for introduced predaceous fish and are therefore excellent sites in which to promote the growth of vigorous populations of northern leopard frogs. However, many ponds are connected to waterways with introduced predaceous fish and many ponds that are not connected to such waterways have introduced predaceous fish. Only with communication and cooperation amongst agencies involved in management of introduced predaceous fish might it be possible to resolve conflicts between management for the production of introduced predaceous fish and northern leopard frogs.

Because introduced predaceous fish often do well in habitats not extensively used by northern leopard frogs, such as streams and lakes (but see Protection of Overwintering Sites below), it might be possible to separate areas for fish propagation from habitats used by northern leopard frogs. However, a major impediment to management of ponds for northern leopard frogs is the predilection of the public to introduce predaceous fish to any body of water that may be suitable for their propagation (and also to ponds that are not suitable). We have found predaceous fish in all sorts of ponds on USDA Forest Service lands in the Black Hills. It must be made clear to the public that this is not permitted, and the USDA Forest Service will probably have to monitor ponds managed for northern leopard frogs for the presence of introduced predatory fish. If fish are found, they might be safely removed using electroshock or rotenone, but only when northern leopard frogs are not in the pond at the same time. However, if ponds are used by frogs for breeding and overwintering, it would be difficult or impossible to use either of these techniques without damaging the frog population. In addition, ponds without frogs but with fish may become good frog habitat if fish were to be removed. Therefore, timing for removal of predatory fish is critical. In any regard, all involved agencies must realize that management for the maintenance of introduced predaceous fish for sport fishermen and management for the conservation of the northern leopard frog are mutually exclusive management objectives at the scale of individual ponds. Collaborative and innovative solutions must be found and researched.

3. Protection of Overwintering sites.

Since overwintering mortality can be high at times in ranid frogs (Bradford 1983) it is important that overwintering sites be identified and protected. Northern leopard frogs use lakes, larger ponds, and streams in which to overwinter (Merrell 1977; Cunjak 1986). Introduced predaceous fish are likely to exert predation pressure on frogs in all these habitat types during the winter. Other, somewhat atypical, overwintering sites may be used, but the importance of these relative to those noted above is unclear and probably very site specific. For instance, a frog observed by Oscar Martinez (USDA Forest Service personal communication) apparently overwintering in a wet meadow under snow cover is interesting, but it is hard to know what to make of this observation with regard to management action.

4. Protection of Water quality.

The complex life cycle of amphibians and the permeability of their skin make them especially susceptible to ecotoxicological agents (Cooke 1981; Bishop 1992; Hall and Henry 1992), so there has generally been great interest in their response to such agents. Harfenist et al. (1989), Pauli et al. (2000), and Sparling et al. (2000a) have all summarized the voluminous literature on the ecotoxicology of amphibians. The database of Pauli et al. (2000) is particularly useful, since it is searchable using a variety of parameters including species, contaminant, author, and study type (i.e., field study, lab study, and other types). There has been extensive work on the effect of water quality on *Rana pipiens* as well. A literature search of Pauli et al. (2000) for studies on Rana pipiens returned 412 citations, and a comprehensive summary of this literature is beyond the scope of my work. However, review articles by Harfenist et al. (1989), Diana and Beasley (1998), and Sparling et al. (2000a) provide a useful summary of existing ecotoxicological data on amphibians.

Diana and Beasley (1998) offered a concise review of toxicant studies in amphibians, including brief summaries of studies on polychlorinated biphenyls, benzene, phenol, crankcase oil, mercury, cadmium, lead, hydrogen ions (acidification), aluminum, nitrate fertilizers, trichlopyr, triazine herbicides, phenoxy herbicides, dipyridyl herbicides, glyphosate (found and tested in Roundup®), pyrethroids, cholinesterase-inhibiting insecticides, carbamate insecticides, organophosphorus insecticides, organochlorine insecticides, and rotenone. Diana and Beasley (1998) pointed out that, collectively, the amount of toxicants dumped into the environment constituted an enormous amount of chemical pollution and likely contributed to amphibian declines across the world. Breeding ponds used by northern leopard frogs tend to collect all manner of toxicants from runoff water, and *R. pipiens* doubtless are exposed to these agents at all points in their life cycle range-wide. Also, the skin of amphibians is highly permeable (Duellman and Trueb 1986), so the toxicants undoubtedly enter the body of northern leopard frogs.

It is impossible to meaningfully discuss water quality issues and *Rana pipiens* without relevant background data on water quality throughout Wyoming. Unfortunately, Wyoming is large and diverse, while reports on water quality generally address a smaller scale. Such reports are compiled by local, state, and federal agencies, especially the United States Geological Survey, who have published studies for the Black Hills (e.g., Williamson and Hayes 2000; Williamson and Carter 2001). These reports are available to appropriate officials but are typically not published; much data has also been collected that is never published in reports. It is not possible to effectively summarize the types of toxicants to which *R. pipiens* may be exposed without writing an extensive review of water quality throughout the region, which would involve tracking down this scattered literature and data. This is far beyond the scope of this assessment. However, we can generally summarize types of ecotoxicological hazards to which *R. pipiens* may be exposed. The interested reader is referred to a case study of the ecotoxicology of northern leopard frogs in the Black Hills of Wyoming and South Dakota for an example of the type of work that is needed to effectively summarize water quality issues in particular drainages (Smith, in preparation). Moreover, we expect water quality vary across Wyoming due to natural causes and because toxic inputs vary from place to place. The toxic inputs discussed in below are those that seem to be of most concern in the Rocky Mountain west, but not all are a concern in every locality. There are 11 main factors that contribute to poor water quality in wetland habitats frequented by *R. pipiens*:

1) **Pesticides**: As noted by Sparling et al. (2000b), this was one of the most studied classes of ecotoxicological agents. Throughout the United States numerous pesticides are used, the

most common being 2, 4-D Amine, Escort®, Plateau®, and Roundup®. Unfortunately, pesticide use is one of the more difficult inputs to study, and typically it is necessary to contact county extension agents throughout a region to get a sense of the types of pesticides that are most commonly used. Atrazine has been used, but its use is being phased out by the U. S. Environmental Protection Agency. However, its effects can be alarming, even at low and ecologically relevant doses (Hayes et al. 2002), and it has a long half-life, approximately five to six years. Hayes et al. (2002) found that it created hermaphroditic Xenopus laevis (African clawed frogs, a common experimental frog) and emasculated male frogs. It was commonly used in the northern Great Plains and was found in 80 – 90% of the row-crop acreage in the region in the 1980s (Grue et al. 1986). The effects of most of the pesticides are probably highest at lower elevations, since few crops are grown at higher elevations. Pesticides may be little used in much of Wyoming, since much of the area is rangeland. However, no region-wide statistics exist on the extent of the use of pesticides. Many of the commonly used pesticides have short half-lives; usually from one week to 30 days.

Studies conducted in other areas may have some general relevance to northern leopard frog populations in Wyoming. Berrill and co-workers (Berrill et al. 1993, 1994, 1997) studied various pesticides that are commonly used in agriculture and silviculture in Canada. Berrill et al. (1993) found that the pyrethroid insecticides permethrin and fenvalerate did not kill eggs or tadpoles when exposed to low levels of these insecticides. However, they caused delayed growth of tadpoles and abnormal behavior, such as twisting rather than darting away after being prodded by investigators. Both of these results indicated that higher mortality could occur in the wild to tadpoles exposed to these chemicals or hatched from eggs exposed to these chemicals than in non-exposed eggs and tadpoles. The effects of the insecticides were different at different temperatures and were lessened at lower dosages. However, Berrill et al. (1993) pointed out that the concentrations used in their study were considered to be low concentrations. Both of these insecticides are commonly used in the United States as well as Canada.

Berrill et al. (1994) studied herbicides used to manage coniferous forests in Canada. They exposed northern leopard frog embryos and tadpoles to low levels of the insecticide fenitrothion and the herbicides triclopyr and hexazinone. None of these pesticides affected hatching success or subsequent behavior in tadpoles exposed to them as eggs in the levels used in these experiments. However, newly hatched tadpoles were very sensitive to the concentrations used in this study, 2.4 – 4.8 ppm triclopyr and to 4.0 – 8.0 ppm fenitrothion, becoming paralyzed or dying. Berrill et al. (1997) exposed northern leopard frogs to low levels of the insecticides permethrin, fenvalerate, and fenitrothion and the herbicides hexazinone, triclopyr, glyphosate, bromoxynil, triallate, and trifluralin, which are used in the management of coniferous forests and croplands in Canada. Embryos were again unaffected by the exposures but newly hatched tadpoles were paralyzed or killed. Most importantly, the authors concluded that amphibian tadpoles are generally similar to freshwater fish in their vulnerability to various pesticides.

Other studies have looked at the exposure of northern leopard frogs to pesticides in the field Ouellet et al. (1997) sampled northern leopard frogs in farm ponds and non-farm ponds in the St. Lawrence River Valley of Québec, Canada, and found substantial amounts of a variety of hindlimb deformities in frogs from farmland habitats. They blamed pesticides for the hindlimb deformities but established no causal link. Leonard et al. (1999) blamed the loss of leopard frog populations in Washington partially on water quality issues stemming from the use of DDT. They noted that a large amount of pesticides had been found in waters throughout their Columbia River Plateau study area and pointed out the recent results of Berrill et al. (1997) on the effects of low levels of pesticides on larval stages of amphibians. However, the conclusions of Leonard et al. (1999) were largely conjectural.

2) **Fertilizers**: Only one study has looked at the effects of fertilizers on northern leopard frogs (Hecnar 1995). In this study northern leopard frog tadpoles were exposed to chronic and acute doses of ammonium nitrate fertilizer. In acute tests northern leopard frog tadpoles suffered severe weight loss and an LC50 of 22.6 mg/l was calculated. In chronic tests, northern leopard frog tadpoles lost weight and also died, even at fairly low dosages of 10 mg/l. The northern leopard frog was the most severely affected of three species tested. Hecnar (1995) pointed out that the differential mortality of the species tested would likely cause shifts in species composition in free-living communities of amphibians. The chorus frog, Pseudacris triseriata, was much less affected than the northern leopard frog. The chorus frog is a common resident in Wyoming, so shifts in community composition

might occur in the area. Fertilizer effects may not be important in much of Wyoming, again because few crops are grown, but fertilizer runoff from various sources besides cropland (lawns and golf courses, for example) can be substantial.

3) **Mining and metal contamination**: Mining has been practiced in Wyoming for much of the last century. Although mining has become less important and less destructive in recent years, residue from mining still remains and many parts of the region have not been carefully studied. Mining causes acidification and also precipitates metals from mining residue and surrounding soils. Some authors have found devastating effects of mining on local herpetofauna, even decades after mines have closed (Porter and Hakanson 1976). Porter and Hakanson (1976) found that an entire drainage in Colorado was devoid of amphibian life decades after mining had ceased because of runoff from mining residue. Linder and Grillitsch (2000) reviewed the effects of metals on amphibians. Acidification is another potential effect of mining on amphibians, which is discussed below.
4) **pH/acidification**: Acidification has been studied intensively in frogs due to the potential for acid rain to cause amphibian declines (see symposium in the Journal of Herpetology, volume 26, number 4, December 1992). Mining also causes acidification (Diana and Beasley 1998). Schlichter (1981), Freda and Dunson (1985), Corn and Vertucci (1992), Freda and Taylor (1992), and Long et al. (1995) have all studied the effects of low pH or acid rain in northern leopard frogs. Northern leopard frog eggs cannot develop normally at pH 5.8 or lower (Schlichter 1981). Northern leopard frog tadpoles were amongst the most sensitive to low pH of all species tested so far, with an LC50 pH of 4.06 (Freda and Taylor 1992). Northern leopard frog sperm also shows decreased motility at lower pH, with 50% of normal motility at pH 5.5 and maximum motility at pH above 6.5 (Schlichter 1981). Northern leopard frogs also show chronic effects of decreased pH, with increasing mortality over time when exposed to low pH (Freda and Dunson 1985). Low pH also acts synergistically with higher levels of UV-B that might result from loss of the ozone layer (Long et al. 1995).

Although development in Wyoming is often more diffuse than elsewhere in the range of Rana pipiens, acidification of Wyoming's water can result from acid rain or mining. As Porter and Hakanson (1976) have shown, acidification can be extreme in localized cases due to point sources, such as old mine tailings. However, Corn and Vertucci (1992) found that declines of Rana pipiens in the Colorado and Wyoming Rocky Mountains were, in general, probably not due to acidification of ponds, since the ponds were simply not acidic enough to affect northern leopard frogs. Nevertheless, acidification should not be completely discounted as a source of mortality for R. pipiens, since mining residue could cause acidification as well as acid rain from upwind power plants, which was primarily the concern of Corn and Vertucci (1992).

5) **Roadways**: Roads create a number of problems for amphibians besides deaths on roads by automobiles, as has been reported by Bovbjerg and Bovbjerg (1964), Bovbjerg (1965), Merrell (1977), and Ashley and Robinson (1996). Motor oil washes off of roads during rain and snowmelt, and when suspended in water can kill some amphibians (Sparling 2000). Sedimentation and toxic runoff from roads can also affect amphibians in ponds (Welsh and Ollivier 1998; Trombulak and Frissell 2000). New road construction should be minimized and old logging, mining, and ranch roads closed when they serve no useful purpose.

6) **Lumberyards**: The production of treated lumber uses various chemicals and lumberyards are common throughout the Rocky Mountains. Coal tar creosote, used in treating lumber, is a well-known carcinogen, for example (Holme et al. 1999). Some of these agents are polycyclic aromatic hydrocarbons (PAHs), and Sparling (2000) reviewed their effects in amphibians, but there are few studies of this class of pollutants on amphibians in the field or laboratory.

7) **Cattle grazing**: Cattle produce considerable amounts of waste products that run into waterways. This is especially true of cattle feedlots, which produce inordinate amounts of waste that may run off into amphibian breeding ponds. Grazing by cattle has also been reported to effect water quality (Buckhouse and Gifford 1976), water chemistry (Jefferies and Klopatek 1987), and water temperature (Van Velson 1979). The changes are subtle over time (Elmore and Beschta 1987), but profoundly alter aquatic ecosystems (Kauffman and Krueger 1984). High levels of cattle grazing and cattle drinking out of or standing in frog breeding ponds should increase the levels of nitrates and fecal coliform bacteria in these ponds. Two tadpoles collected in a heavily polluted pond used by cattle in Lawrence County, South Dakota, had deformed mouthparts and irritated skin (Smith unpublished data). Reaser (2000) found that cattle grazing influenced the decline of the Columbia

spotted frog (Rana luteiventris) at a study site in Nevada. Ross et al. (1999) recommended that cattle be fenced out of sensitive wetlands in this area to conserve R. luteiventris. We recommend studies of the effects of cattle on northern leopard frog tadpoles in breeding ponds in Wyoming. Impacts could be mitigated by excluding cattle from key breeding ponds used by R. pipiens and the surrounding upland habitat. Water for cattle could be routed to metal stock tanks downstream from such ponds.

8) **Sedimentation**: Sedimentation can also run into waterways due to erosion caused by a variety of sources. Sedimentation can cover eggs in water and probably inhibits gas exchange by eggs. Road cuts are sources of sedimentation, cattle are known to cause erosion by trampling streamside vegetation and slopes, and logging can increase erosion. Large fires could also increase the sediment load in nearby waterways.

9) **Rotenone**: This chemical is commonly used in fisheries management and can have negative effects on northern leopard frogs (Hamilton 1941). Northern leopard frog tadpoles could not survive levels of rotenone typically used to sample fish (Hamilton 1941). Metamorphs survived for 24 hours, but Hamilton (1941) gave no further details about morbidity or mortality in metamorphs following the initial 24 hours of exposure. However, he concluded that rotenone had substantially the same effect on tadpoles (or other organisms that use gills to breathe) as on fish; the chemical was lethal to most of these organisms. Rotenone should not be used in waterways used by northern leopard frogs during the breeding season.

10) **Polychlorinated biphenyls (PCBs)**: There is a large literature on PCBs which has been summarized by Sparling (2000). Phaneuf et al. (1995) studied PCB contamination in northern leopard frogs in Canada. If there are large manufacturing processes that utilize PCBs near northern leopard frog habitat, they would be of serious concern.

11) **Arsenic**: Birge and Just (1973, cited in Linder and Grillitsch 2000) found that high levels of sodium arsenite were lethal to R. pipiens tadpoles. Williamson and Carter (2001) reported that arsenic levels could occasionally be very high from natural causes in some streams in the Black Hills. It is not possible to manage such naturally occurring arsenic, but it should be monitored since it can act synergistically with other noxious agents.

In summary, the various agents discussed in this section have the potential to seriously affect amphibians. More notably, *R. pipiens* seem to be somewhat more sensitive to many of these agents than most amphibians that have been tested. As Sparling et al. (2000b) noted, overall input of these agents into aquatic systems is considerable and is probably partially responsible for the decline of amphibians worldwide. There is no way to assess the potential impact of any of these agents on northern leopard frogs statewide without extensive study. The most important local considerations would be pollution from cattle, input of pesticides into streams and breeding ponds, mining, acid rain, and runoff from roadways (including sedimentation). Almost none of these have been extensively investigated in Wyoming, nor have they been investigated in small ponds of standing water where *R. pipiens* breeds. Typically, local, state, and federal studies are conducted on running water, large lakes, or aquifers, where human health concerns are more immediate. Further studies on water quality in Wyoming would be useful, but these studies should concentrate on breeding ponds rather than on streams and other waterways, as has been the case in the past. Finally, we would recommend consulting the database of Pauli et al. (2000) on specific pesticides that are being used by applicators or when new treatments are planned. Similarly, this database can be consulted for the effects of specific chemicals. Pauli et al. (2000) provided literature for all chemicals that had been investigated in amphibians as of the publication date of this database.

This section would not be complete without a discussion of limb malformations, known from forty states and four provinces (Northern Prairie Wildlife Research Center 1997). The most famous recent reports were those in Minnesota, which were virtually all from metamorphic northern leopard frogs (Helgen et al. 1998). These frogs usually do not survive long because locomotion and basic behavior is seriously compromised by these gross malformations (Merrell 1969). Helgen et al. (1998) featured several photographs of the affected frogs, most of which had multiple hind limbs or missing hind limbs, although some front limbs were also affected. Helgen et al. (1998) assumed that the cause must be a teratogen or possibly a chemical that disrupts normal endocrine function. The Minnesota Pollution Control Agency sampled the water in which these frogs were found to search for possible causes including pesticides, heavy metals, or polychlorinated biphenyls, but Helgen et al. (1998) did not report these results. Encysted parasites have also been implicated as a possible cause of some limb malformations (incidents of multiple legs) in amphibians (Sessions and Ruth 1990; Johnson et al. 1999; Sessions et al. 1999). However, a study by Meteyer et al. (2000) showed that limb malformations in frogs probably have several causes. Limb malformations are not a new phenomenon, and Merrell (1969) reported a high frequency of malformations in metamorphic northern leopard frogs collected at a site in Minnesota in 1965. Hoppe (2000) also discussed various historical reports of limb malformations. Northern leopard frogs with limb malformations should be reported to the Northern Prairie Wildlife Research Center, which collects such reports from around North America (http://www.npwrc.usgs.gov/narcam).

5. Protection of migratory pathways

Northern leopard frogs frequently migrate across the landscape for several reasons including dispersal of metamorphs (Dole 1971; Merrell 1977), summer movements associated with feeding (Dole 1965b, 1967; Merrell 1977), and migrations to and from overwintering sites (Dole 1967; Merrell 1977). The routes they take on these migrations probably include wet meadows, tall grass, and riparian corridors. It is likely that grazing and timber removal can jeopardize such habitat, especially areas of tall grass that may exist between suitable reproduction sites or between overwintering sites and breeding ponds. However, deMaynadier and Hunter (1998) found that aquatic ranids were less affected by clearcutting than were the more terrestrial ranids, such as wood frogs (*Rana sylvatica*), and some salamanders. Without detailed studies it is hard to know what areas to protect beyond those afforded some protection in the Forest Service Plan, such as wet meadows and riparian corridors (USDA Forest Service 1997). It is necessary to know the placement of suitable breeding ponds and overwintering sites before it will be possible to infer potential migration routes and protect these routes.

6. Control of introduced infectious diseases

As discussed above in the section on Parasites and Diseases, this potential cause of amphibian declines is fairly well documented, but the transmission vectors are poorly known (Carey et al. 1999). Carey et al. (1999) noted that introduction of exotics (e.g., bullfrogs) might spread disease. Since introductions of bullfrogs are common across the United States, it is possible that an introduction could cause additional damage by introducing chytridiomycosis, ranavirus, or a bacterial infection. More commonly introduced in the Rocky Mountain region are tiger salamanders, which are sometimes used as bait by fishermen. Tiger salamanders are known to harbor iridoviruses (Daszak et al. 1999). Diseases could be introduced to ponds through several other means as well, as noted in the Parasites and Diseases section, such as by fishermen or other tourists and investigators surveying and monitoring northern leopard frogs.

7. Control of road-related mortality

It has been known for some time that roads cause extensive mortality of juvenile *Rana pipiens* (Bovbjerg and Bovbjerg 1964; Bovbjerg 1965; Merrell 1977). Recently, Ashley and Robinson (1996) showed that young-of-the-year *R. pipiens* were disproportionately represented amongst dead herpetofauna at their study site in Ontario. Carr and Fahrig (2001) found that traffic density within a 1.5 km radius of frog breeding ponds was negatively associated with the abundance of northern leopard frogs, suggesting that the viability of populations can also be affected by road mortality. Road associated factors such as sedimentation and runoff of toxic compounds can also affect aquatic communities nearby roads (Welsh and Ollivier 1998; Trombulak and Frissell 2000). If roads affect populations of frogs, it is likely that other types of habitat disturbance, especially logging, would negatively affect populations of northern leopard frogs. The placement of new roads should be considered in relation to their effects on frog populations. In addition, frogs and their habitat should be considered when decisions are made to close or manage old roads.

8. Control of other habitat disturbances

Other activities can have unexpected effects on northern leopard frogs as shown by Nash et al. (1970) in their study of the immobility reaction in leopard frogs in response to generalized noise. This reaction would be of importance in any area of human activity, particularly in areas nearby construction or timbering operations. This reaction increases road mortality and probably interrupts feeding behavior. In addition, the loss of beaver in the Black Hills and concomitant reduction in wetlands habitat across the area (Parrish et al. 1996) has reduced the habitat available for breeding by the northern leopard frog. Beaver, which create much suitable *R. pipiens* breeding habitat, have likely decreased from historic levels in many parts of the west. Redoubled efforts to reintroduce beaver and protect beaver habitat would no doubt also benefit the northern leopard frog.

9. Control of over collection

Human collectors capture northern leopard frogs and their tadpoles, typically for use in biology teaching laboratories or as fish bait. Overcollecting of northern leopard frogs by humans has accounted for the removal of large numbers of frogs from the wild (Gibbs et al. 1971; Moriarty 1998). From 1995 – 1999, 174,772 northern leopard frogs were collected in Nebraska for export to two biological supply houses; approximately 120,000 were collected in 1996 alone. Of these, 161,296 were exported by a single individual (Dan Fogell, personal communication). The extent of collection of northern leopard frogs or their tadpoles is unknown in Wyoming.

10 Stratospheric ozone levels and ultraviolet penetration

Recent concern over the loss of the ozone layer has prompted investigations of the effects of increasing levels of ultraviolet light on limb deformities in northern leopard frogs (Ankley et al. 1998, 2000). Elevated levels of ultraviolet light can cause hind limb malformations in the laboratory (Ankley et al. 1998) and in the field (Ankley et al. 2000), but it is unclear what the significance of these results is for populations of northern leopard frogs in natural situations. Crump et al. (1999) found that incident light levels had no significant effect on *Rana pipiens* in the field.

Abundance and Abundance Trends

The northern leopard frog was formerly abundant across its range but has suffered wide-ranging population declines. In the western United States the species has undergone major declines or has become locally extinct. It is locally extinct west of the Continental Divide in Montana except for two population centers, one near Kalispell and one near Eureka (Maxell 2000). It is largely absent from central Montana where northern leopard frogs were found at only nine of 47 historical sites in the mid-1990s (Maxell 2000). It is declining in some parts of eastern Montana (Reichel 1996). Northern leopard frogs have apparently gone extinct in the Targhee National Forest of western Wyoming and adjacent Idaho (Koch and Peterson 1995). They are severely reduced in the Laramie Basin of Wyoming but may still be common in other parts of the state (Baxter and Stone 1985; Stebbins and Cohen 1995). Northern leopard frogs have become scarce at many sites in Colorado (Hammerson 1999). Corn and Fogleman (1984) documented extinctions at nine high elevation sites in Colorado. Northern leopard frogs have also gone extinct or become severely reduced at low elevation sites in Colorado (Hammerson 1982; Cousineau and Rogers 1991). Clarkson and Rorabaugh (1989) surveyed 13 of the 28 historical localities known in Arizona. They found that the northern leopard frog was absent from all of these localities and present at only one previously unreported locality in the White Mountains. It is now absent from its historic range in California, except for a few small populations in northeastern California (Stebbins and Cohen 1995). Leonard et al. (1999) visited 27 historical collecting localities in eastern Washington and found populations at only three of them. The species was formerly common throughout the central Plains states but has declined there as well (Stebbins and Cohen 1995).

In the upper Midwest, northern leopard frogs are generally thought to be less abundant than in the past. Moriarty (1998) found them to be widespread across Minnesota but much less common than historical records have indicated. Mossman et al. (1998) reported that northern leopard frogs underwent a significant (but largely undocumented, however see Hines et al. 1981) decline in Wisconsin in the 1970's, though they were still common in the state. Casper (1998) reported that some investigators believed that they saw a partial rebound after 1985. Dhuey and Hay (2000) reported them to be rare in Wisconsin. Nevertheless, in Wisconsin they are probably far below historical population levels (Casper 1998; Mossman et al. 1998). Collins and Wilbur (1979) noted that northern leopard frogs had become rare on their study site near Ann Arbor, Michigan, during the previous 20 years.

Recent estimates of the abundance of northern leopard frogs in the Midwestern United States are found in Lannoo (1998). Orr et al. (1998) found them still abundant in northeastern Ohio. However, Davis et al. (1998) found northern leopard frogs to be rare or extinct (most populations) in Hamilton County, Ohio, the county in which Cincinnati is located. Mierzwa (1998) also found them to be common in northeastern Illinois. Brodman and Kilmurry (1998) stated that they were common in Indiana, although they are listed by the state as a species of special concern and were rare or uncommon at study sites in northwestern Indiana. However, Minton (1998), writing from a perspective of 45 years of collecting in Indiana, stated that northern leopard frog populations have declined markedly since 1948. Hemesath (1998) wrote that northern leopard frog populations had probably declined across Iowa by two to three orders of magnitude over historical levels, but lack of baseline data prevented her from reaching a definitive conclusion.

Canadian populations are discussed in Green (1997) and Bishop and Pettit (1992). The distribution and abundance of the northern leopard frog is poorly known for many parts of Canada (Russell and Bauer 1993; Maunder 1997; Fournier 1997). They are rare in the Northwest Territories (Fournier 1997). Northern leopard frogs are found in Saskatchewan but are insufficiently known there to assess abundance or population trends (Didiuk 1997). The northern leopard frog has declined in abundance in British Columbia (Orchard 1992). It is now extinct or rare throughout much of Alberta (Roberts 1992; Russell and Bauer 1993; Stebbins and Cohen 1995). They are common in New Brunswick and probably have suffered no decline there (McAlpine 1997).

It is important to realize that population declines may not have occurred everywhere. Data showing that declines are not occurring may not be as "interesting" as data showing that declines are occurring and these data may therefore not be published. McAlpine (1997), Mierzwa (1998), and Orr et al. (1998) were the only three reports we were able to find in the peer-reviewed literature that did not claim declines in northern leopard frog populations. Orr et al. (1998) concluded that population declines were not occurring at study sites in northeastern Ohio. Also, northern leopard frogs were found to be "common", but probably less abundant than surveys conducted in 1855, in 1995 in Illinois (Mierzwa 1998). McAlpine (1997) reported no evidence of population declines in New Brunswick, Canada. Generally, it is thought that eastern populations of northern leopard frogs are probably in better condition than western populations. All things considered, the prevalence of literature documenting declines from across North America offers some evidence that populations of northern leopard frogs throughout may be at risk throughout their range.

Distribution Trends

Not only has abundance declined, but the range of the northern leopard frog has contracted in recent time, particularly in the western United States. It is absent in several parts of Montana where it was formerly present (Maxell 2000). Clarkson and Rorabaugh (1989) found that they had disappeared from several historical localities in Arizona. They are now absent from their historic range in California (Stebbins and Cohen 1995). They are also missing from various historical sites in eastern Washington (Leonard et al. 1999).

It is probably significant that the Natural Heritage status of northern leopard frogs is "vulnerable" in Wyoming and its southern neighbor, Colorado (Figure 1), two states dominated by the Rocky Mountains. Koch and Peterson (1995) reported that the northern leopard frog may be extinct in the Targhee National Forest of western Wyoming and adjacent Idaho. They are also reduced in the Laramie Basin of Wyoming (Baxter and Stone 1985; Stebbins and Cohen 1995) and have become scarce at sites throughout Colorado (Hammerson 1999). Corn and Fogleman (1984) documented extinctions at nine high elevation sites in Colorado. Hammerson (1982) and Cousineau and Rogers (1991) also reported extinctions at various low elevation sites in Colorado. Range reductions and extinctions reported throughout the range of the northern leopard frog are probably preceded by population fragmentation, which makes further reductions and extinctions more likely.

Intrinsic Vulnerability

The northern leopard frog may be intrinsically vulnerable to disturbance factors for a number of reasons, including:

1) Their use of small ponds for reproduction: Northern leopard frogs use small ponds (ca. <8 ha) in which to breed (Merrell 1968, 1977; Collins and Wilbur, 1978; Corn and Livo, 1989; Hammerson, 1999). Ponds of this size are typically not protected by law (Semlitsch 2000b) and often not discussed by management plans. It is imperative that management plans take into consideration the presence of small ponds across the landscape and protection of these ponds to foster healthy populations of northern leopard frogs.
2) Their use of upland habitats for summertime foraging: Closely tied to the use of small ponds for reproduction is the use of upland habitats for summertime foraging by northern leopard frogs. Although Semlitsch (1998) has determined the size of upland habitat around ponds that is used by salamander populations, such work has not been done on northern leopard frogs. This is a critical information need. Semlitsch (1998) found that an upland area of up to 164 m surrounding each breeding pond might be sufficient to protect 95% of the adult population of salamanders of various species that use a pond for reproduction in the spring.
3) The permeable skin of most amphibians: The skin of freshwater amphibians is highly permeable (Duellman and Trueb, 1986). It is possible that many toxins could be incorporated into the body of amphibians, including northern leopard frogs. Since northern leopard frogs serve as prey items for several species (see pp. 34-36), the presence of toxins in the body of northern leopard frogs would have repercussions throughout the food web of a habitat in which northern leopard frogs occurred. In this sense, northern leopard frogs might serve as a key indicator species in ecosystems in which they occur. It is possible that population sizes of northern leopard frogs might indicate overall ecosystem health in these ecosystems. However, there seems to be little work on the presence of toxins in northern leopard frogs in the wild.
4) Their susceptibility to fatal diseases which seem to be prevalent: Chytridiomycosis and ranavirus have emerged as critical threats to northern leopard frogs in many parts of their range (Cunningham et al., 1996; Jancovich et al., 1997; Carey et al., 1999; Daszak et al.,

1999). Currently, these diseases are not monitored throughout the range of the frog, and there are many potential vectors that could introduce these diseases into northern leopard frog breeding ponds. Predatory fish are frequently introduced into watersheds in which frogs breed, accidental or intentional introductions of predatory fish and fish bait (salamanders, which can also be infected by iridoviruses, Jancovich et al., 1997), and human travel amongst breeding ponds are all common throughout the range of northern leopard frogs and are potential vectors for disease. An irruption of chytridiomycosis or ranavirus in localized areas could threaten populations of northern leopard frogs throughout an area, since these diseases can be 100% fatal (Daszak et al., 1999; Jancovich et al., 1997). Steps should be taken to minimize this threat.

5) Their vulnerability to introduced predaceous fish: Introduced predatory fish remain a serious and well known threat to northern leopard frogs. Federal and state agencies introduce such fish throughout the range of the northern leopard frog. Because the USDA Forest Service allows multiple use of national forests as part of its mission, it seems unlikely that fish introductions can be halted. Also, accidental or intentional introductions of predatory fish by the public will probably be difficult to guard against. However, it may be possible to reduce the overall effects of such introductions by limiting them in time and space, for example, by managing some watersheds for native wildlife such as amphibians, while others are managed for recreation. In addition, a public information campaign to inform the public of the harm of accidental or intentional introduction of predatory fish into fishless ponds might help to reduce the frequency of these introductions.

6) The necessity of overland migration routes to reach and colonize new ponds: Northern leopard frogs may use various mesic habitats, such as streamsides, riparian areas, and wet meadows for overland migration. It is probably also important that these habitats be left relatively undisturbed if northern leopard frogs are to colonize new ponds, so that populations either grow or remain stable in any given locality. Skelly et al. (1999) showed that there was high turnover of northern leopard frog populations in a metapopulation in Michigan, and it seems likely that this would be the case in other areas. Migration routes need to be maintained to ensure that frogs are able to colonize new breeding ponds or to recolonize ponds at which they have gone extinct. This should help to maintain stability of metapopulations. Mesic habitats are probably also needed for summertime foraging.

Conservation Action

Existing or Future Conservation Plans

There is one management plan in existence for the northern leopard frog (Seburn 1992; cited in Fisher 1999), but we have not been able to locate a copy of this plan. Maxell (2000) covers some aspects of the management of the northern leopard frog as part of a more general publication on the management of the 14 species of amphibians found on the national forests of Montana. We are not aware of any other regulatory mechanisms, management plans, or conservation strategies for the northern leopard frog.

Conservation Elements

Inventory and Monitoring

As usually done by biologists, a survey is a study in which investigators attempt to delineate the boundaries of a species' range or its occurrence within a specified portion of a range. An attempt to determine the abundance of the species within the area of interest is also usually made. An inventory, on the other hand, is usually a study in which biologists attempt to ascertain the current status of a species within its range or within a portion of its range. This implies that the investigators will attempt to determine the abundance of the species within the study area. Especially important would be determinations of the specific localities where northern leopard frogs are found and effective population sizes of populations of frogs at these sites. An overall survey of the northern leopard frog within the Wyoming has never been undertaken and an inventory of the species cannot start without such a survey. Any monitoring of the status of northern leopard frogs (i.e., an ongoing inventory) would necessarily start with a comprehensive survey of the species, preferably with concomitant determination of effective population sizes at sites where frogs are found. These data should be entered into a GIS database and this data should be maintained and updated on a regular basis so managers always have access to the latest available information.

Heyer et al. (1994) compiled existing techniques for surveying and monitoring amphibians. They and their contributors also discussed associated issues such as standardization and quantification, research design including data management and planning of studies, estimation of population size, and data analysis. Of the survey and monitoring techniques discussed in Heyer et al. (1994), the following techniques could be useful in surveying and monitoring northern leopard frogs in Wyoming:

1) Acoustic monitoring, i.e., call surveys (Berrill et al. 1992, Peterson and Dorcas 1994, Zimmerman 1994, Bishop et al. 1997, Bonin et al. 1997, Lepage et al. 1997, Johnson 1998, Mossman et al 1998);
2) Drift fences and pitfall traps (Corn 1994, Dodd and Scott 1994, Smith et al. 1996a, b);
3) Various quadrat sampling techniques (Jaeger 1994a, b, Jaeger and Inger 1994);
4) Cover boards (Fellers and Drost 1994; Bonin and Bachand 1997, Davis 1997); and
5) Visual encounter surveys (Crump and Scott 1994, Smith et al. 1996a, b, 1998).

Various marking techniques can be used in conjunction with these survey methods to mark and track amphibians in the field (Dole 1972; Green 1992; Ashton 1994; Heyer 1994; Richards et al. 1994; Madison 1997; Madison and Farrand 1997; Semlitsch 1998).

Acoustic monitoring

Probably the simplest, least expensive and most commonly used practice to survey amphibian populations is the call survey (Berrill et al. 1992; Peterson and Dorcas 1994; Zimmerman 1994; Bishop et al. 1997; Bonin et al. 1997; Lepage et al. 1997; Johnson 1998; Mossman et al. 1998). Call surveys may be set up a number of ways, including traveling along transects randomized by habitat, at locations specified along a roadway (itself a kind of transect), and other methods. In the

Black Hills, we have typically carried out call surveys by first surveying during daytime hours for ponds in which northern leopard frogs may occur, then traveling among potential breeding ponds to listen for breeding choruses of frogs and recording whether we heard choruses and sometimes estimating the size of the chorus. Usually, ponds are visited at least three times during the breeding season to verify whether the pond is being used as a chorus site. The longest lasting and most successful set of yearly call surveys has been the volunteer call survey ongoing in Wisconsin since 1981 (Mossman et al. 1998).

Depending on the species, call surveys can be an excellent way to survey and monitor frogs, but not all anurans are easily surveyed and the calls of some frog species vary in volume geographically. For example, Bishop et al. (1997) noted that northern leopard frogs have low volume calls that may be hard to hear. Smith et al. (1996b) have pointed out that northern leopard frogs call sporadically and at very low volume in the Black Hills region. They have cautioned against the use of call surveys to survey or inventory the species in the Black Hills. Bonin et al. (1997) have also advised against the use of the technique to quantitatively assess the extent of frog declines over several years. Before auditory techniques, such as audio strip transects (Zimmerman 1994), breeding site surveys (Scott and Woodward 1994), automated data loggers (Peterson and Dorcas 1994) or basic acoustic monitoring (Rand and Drewry 1994) are used for ongoing monitoring, these techniques should be evaluated for their efficacy in Wyoming.

Drift fences and pitfall traps

Drift fences and pitfall traps can be installed and periodically monitored to assess the abundance of amphibians at a study site (Corn 1994). Drift fences can also be installed at breeding sites, completely encircling the site and trapping every individual entering or leaving the site (Dodd and Scott 1994). Drift fences are long fences made of sheet metal and placed flush to the ground such that amphibians cannot climb over or burrow under the fence. Pitfall or funnel traps are placed along the fence to trap amphibians moving along the fence. In our experience it can be difficult to train non-herpetologists to properly install drift fences and we recommend that a herpetologist be consulted and survey teams be properly trained if drift fences are to be used at any ponds to survey northern leopard frogs. We believe that the primary use of drift fences would be for studies of northern leopard frog breeding ponds or studies of movement in the species, not as a routine method of survey. Drift fences can be costly, both in terms of materials and construction effort, although once installed they can be cheaply and easily operated.

Quadrat and patch sampling

Upland habitats can be quantitatively sampled using quadrat sampling (Jaeger and Inger 1994), transect sampling (Jaeger 1994a), and patch sampling (Jaeger 1994b). Each of these techniques relies on sampling various sizes and shapes of plots to determine how many amphibians occur per unit area of sampled habitat. Of all the techniques discussed, these are the only techniques that can provide information on the number of animals per unit of habitat.

Patch sampling (Jaeger 1994b) refers to the sampling of patches where frogs are more likely to occur, which in the case of northern leopard frogs should be habitat near breeding ponds, along streams, or in riparian corridors. One general drawback to patch sampling is that the habitat is not randomly sampled, because habitats that investigators think lack frogs are not sampled. However, as long as the data are not presented as being a random sample of all possible habitats, patch sampling is an appropriate tool that can be used to survey amphibians.

Patch sampling can be combined with quadrat or transect sampling. During the breeding season, northern leopard frogs are concentrated at ponds, but following breeding they are dispersed in upland habitat and may be more difficult to locate (although it may still be expected that frogs will be found near ponds, streams, or riparian areas). Therefore, the areas nearby ponds, streams, and in riparian strips can be selected as patches in which to search for northern leopard frogs following the breeding season. To systematically sample these areas, researchers might restrict searches to areas immediately adjacent to ponds (for example, the 200 m area discussed on p. 55), along streams, and in riparian corridors. They can then conduct quadrat or transect samples (quadrats are square plots while transects are basically long strip-like plots; some researchers make little distinction between the two) in these patches to assess the numbers of adult frogs using these habitats. These combined techniques could result in an assessment of frog density around breeding ponds, along streams, and in riparian corridors following the breeding season.

Cover boards

Cover boards are objects such as plywood boards that are placed in the environment to take advantage of the fact that many amphibians take refuge under such objects (Fellers and Drost 1994). They can be placed in various arrays as a method of quantitatively surveying amphibians. The technique has proven useful to monitor salamander populations (Bonin and Bachand 1997; Davis 1997), but there are differences in how species use cover boards and the types of cover boards favored by different species (Bonin and Bachand 1997; Davis 1997). They are probably best used for salamanders and snakes and have not been validated for use with northern leopard frogs. Construction techniques and suggested arrays can be found in Bonin and Bachand (1997) and Davis (1997). Cost would be minimal following initial testing and construction of cover boards. Unlike drift fences, cover boards could be left in place unmonitored for long periods of time since specimens can leave or use cover boards at will and are not trapped in pitfalls or funnel traps that cause rapid desiccation and must be checked frequently.

Marking techniques

Any technique that allows the hand capture of specimens can be used in conjunction with marking techniques as part of a larger study on breeding or movement patterns. Amphibians can be marked and tracked using a variety of devices including thread bobbins (Heyer 1994), radiotransmitters (Richards et al. 1994), radioactive tags (Ashton 1994), toe clipping (Green 1992), and passive integrated transponder (PIT) tags. Thread bobbins have been used to track northern leopard frogs (Dole 1972). The device is a spool of thread attached to a harness that is tied around the body of the frog just ahead of the hind legs. It can be used to track frogs over distances of up to 50 m (Heyer 1994). The technique is somewhat time-consuming but is inexpensive and can provide basic information on the movements of northern leopard frogs in the field (Dole 1972). There are occasional harmful effects of the harness as the frogs can become entangled in the string or the harness can irritate the frog (Dole 1972).

Radiotracking has been used on larger animals for a number of years but with miniaturization of transmitters it has recently (within the last ten years) been successfully used on amphibians in the field, including ranid frogs (Rathbun and Murphey 1996; Lamoureux and Madison 1999; Mathews and Pope 1999; Bull 2000; Bull and Hayes 2001) and *Rana pipiens* in particular (Waye 2001). The technique is time-consuming, expensive, requires detailed training of investigators, and also may require invasive surgery to install transmitters. However, it is the best way available to obtain detailed information on the movement of animals in the field.

Radioactive tags have also been used to monitor amphibian movements in the field (Ashton 1994) and have been used in salamanders for several years (Semlitsch 1998). Radioactive tags are particularly useful for small organisms that cannot be tracked using radiotransmitters. The tags can be detected from up to 5 m by scintillation counters (Semlitsch 1998), so they can be used to find specific locations of frogs where a restricted movement area is expected. However, although this technique is available, there are concerns over handling of the tags, health effects on frogs with implanted tags, and environmental effects that may argue against studies using radioactive tags.

Toe clipping has long been used to mark various animals in the field and is best used in conjunction with recapture surveys to roughly track northern leopard frogs over time. A basic pattern for numbering frogs using toe clipping is outlined by Green (1992). When effectively used in conjunction with other sampling techniques, toe clipping can be used to monitor the movements of individuals and can be used to derive a mark-recapture estimate of population density using a number of open population estimators given in Krebs (1999). Deriving a mark-recapture estimate of population size at most ponds would probably require marking and recapturing large numbers of northern leopard frogs. Since toe clipping is invasive it should not be used unless it is part of a determined effort to monitor frog movements or derive population estimates. Toe clipping, when done in conjunction with basic sampling, is simple and inexpensive to implement.

Individual northern leopard frogs may be identifiable through unique markings. Robert Newman, of the University of North Dakota, has identified a number of wood frogs through computer analysis of photographs of unique patterns on their back (personal communication 1997). The spotted pattern across the back of northern leopard frogs might serve to uniquely identify individuals should an intensive study of population sizes or movements be undertaken at certain sites. The technique is time consuming and management of the individual records could be difficult. Attempting to discern one frog from another using specific markings could be difficult or impossible. We are not aware of anyone that has attempted such a study in northern leopard frogs.

Finally, passive integrated transponder (PIT) tags can be used to mark individuals as well. These are small glass rods, usually no more than 10 mm in length, that are inserted under the skin of individuals. A reading device reads uniquely coded numbers from the tags when waved over the marked individuals. Such tags have been used for several years to mark Jemez Mountain salamanders (*Plethodon neomexicanus*) a slim and small salamander with a snout-vent length of only 4.7 – 6.5 cm (Charles Painter, New Mexico Department of Game and Fish, personal communication 2000). They would probably work to mark northern leopard frogs as well, again as part of a detailed movement or population study. They and the reader are somewhat expensive to purchase, but are much less expensive than radiotransmitters and do not have the safety issues associated with radioactive tags. However, PIT tags are invasive to install since they must be inserted into the abdomen of animals.

Visual encounter surveys (adults and eggs)

Herpetologists for many years have simply walked around and looked in suitable habitat for amphibians. This is frequently the most productive way to search for amphibians, and if properly quantified, is a suitable technique to survey and monitor many species (Crump and Scott 1994). Proper quantification of search effort should involve recording the amount of time spent actively searching, not including time spent traveling, stopping to take photos, etc. Crump and Scott (1994) called the technique a visual encounter search. Investigators simply approach a survey area and walk around the area searching for the species of interest, possibly flipping suitable cover objects all the while. After a pre-determined period of time, the search is halted and results (number of specimens encountered) are recorded. We have used this technique in all of the survey work we have conducted and it has worked well to find all species (Smith et al. 1996a, b; 1998). Typically we have used a three or four person crew and have conducted a two person-hour search at each survey site. The time was derived by using a three person crew for 40 minutes (3 persons by 40 minutes = 2 person-hours) or a four person crew for 30 minutes (4 persons by 30 minutes = 2 person-hours).

For northern leopard frogs the lead author has also used visual encounter searches for subadults, adults, and metamorphs after the breeding season. We have also used this method to search for developing tadpoles using a dipnet that is swept through shoreline vegetation. Sometimes tadpoles are obvious using this technique but sometimes I have not found tadpoles at sites at which I have found metamorphs later in the season. During the breeding season I have found that northern leopard frogs are cryptic and hard to locate either by sight or by sound. The tadpoles are sometimes hard to find as well perhaps because they are hiding in dense cover. We have also found it difficult to provide accurate counts of northern leopard frogs because they can be present in large numbers (e.g., hundreds of tadpoles or metamorphs) or are otherwise hard to count (e.g., several individuals jump and escape simultaneously). Unless precise numbers are required, we usually record northern leopard frogs as "present" or "absent" at study sites and provide only a rough indication of abundance. Given that failure to see frogs during a single survey is not proof of absence, we recommend surveying a site at least three times, preferably including at least one visit during breeding and after suspected metamorphosis of tadpoles, before recording northern leopard frog absence. Crump and Scott (1994) covered the assumptions and limitations of the visual encounter technique and provided a sample data sheet.

Another survey method useful in monitoring northern leopard frogs is egg mass survey (Corn and Livo 1989; Werner et al. 1999; Crouch and Paton 2000). In this type of survey, investigators visit ponds that are suspected to have breeding populations of northern leopard frogs to search for their egg masses. These, as described on page 29, are laid in clumps on submerged vegetation slightly below the water surface and may be found by trained investigators. Since each clump is laid by a single female, simply counting all egg masses found in a pond gives an estimate of the number of females using the pond for reproduction. If a 1:1 sex ratio is assumed, the total breeding population size could be determined, but it is important to recognize that not all females may breed during a given year, the sex ratio may not be 1:1, and there would be an undetermined number of sexually immature individuals in the population. Also, egg mass surveys require additional training, since it is often difficult for non-specialists to identify northern leopard frog eggs.

Funnel trapping

Aquatic funnel trapping is a technique that can be used to detect the presence of northern leopard frog tadpoles in breeding ponds. Various types of funnel traps are described in Adams et al. (1997). These traps are placed in ponds, where tadpoles swim into them and are captured. The traps are checked on a frequent basis and tadpoles are identified and released. The materials used are not expensive (minnow traps and even used two-liter plastic soda bottles can be used for the purpose), but they need to be checked daily or every few days during the tadpole growing season. Additional training is necessary for this technique, because non-specialists often find it difficult to differentiate the various tadpoles found in Wyoming.

Population and Habitat Management

Few papers have addressed management concerns for amphibians, fewer still have looked at ranid frog management, and none have done so specifically for northern leopard frogs. Semlitsch (2000a) is the most extensive review of the amphibian management literature available and deMaynadier and Hunter (1995) have reviewed forest management practices and their affect on amphibians in North America. However, Lannoo (1998b) has provided perhaps the most succinct summation of a potentially successful strategy for conservation of frog populations in North America. Modified for northern leopard frogs in the Rocky Mountain west, this advice might be to provide a series of seasonal or semi-permanent ponds that are connected by upland migration corridors plus habitat for terrestrial life history stages (the upland core areas advocated by Semlitsch 1998 and 2000a).

To briefly summarize the findings of deMaynadier and Hunter (1995), we can conclude that several standard forestry practices can adversely affect populations of amphibians in general, and probably have some effect on northern leopard frogs. First, most amphibians do not use habitat in recently clear-cut areas, and there is a general association of stand age and abundance. However, microhabitat variables such as herbaceous cover, downed wood, and litter depth appear to be more important than broad-scale stand features. Amphibians better tolerate habitats that provide a variety of near-ground cover because these habitats provide a broad range of microclimates that allow effective behavioral thermoregulation and avoidance of desiccation. Therefore, timbering operations that strive to minimize understory disturbance are probably better for conserving amphibian populations than other types of forestry practices. Also, scattering this type of disturbance around the landscape is probably beneficial; i.e., smaller clear-cut areas interspersed amongst areas that have not been cut or have been cut using less intrusive treatments is better than large areas of clear-cutting. Secondly, riparian corridors are used as migration pathways by several amphibians, and we can expect that the wider they are and the more connected northern leopard frog breeding ponds are to these riparian zones, the better off populations of northern leopard frogs will be. Third, roadways can isolate populations or reduce their size, sometimes even if these roadways are low or no-use roadways. This might be less of a problem for the northern leopard frog because they are known to migrate long distances under less than ideal conditions. However, heavily used roads may result in substantial mortality of migrating frogs. Finally, the little data that we currently have on prescribed burning has shown that amphibians sometimes tolerate prescribed burning rather well. However, all these conclusions are largely based on types of amphibians other than ranid frogs and remain to be tested in this group.

Semlitsch (2000a) has provided a wider-ranging review of various management practices that is less focused on specific types of forestry practices. He identifies several threats to local and regional amphibian populations including habitat destruction and alteration, global climate change, chemical contamination, diseases, invasive species, and commercial exploitation. Among this group we have already discussed the threats, namely habitat destruction, chemical contamination, diseases, and invasive species (see the Extrinsic Threats section) and conservation issues such as local population dynamics and metapopulation dynamics (see, for example, the Landscape Pattern, Activity and Movement Patters, Habitat, and Population Demography sections) as emphasized by Semlitsch (2000a). It short, it is imperative that all the habitat needs of *R. pipiens* are met within a landscape that allows ready access to all necessary components in a configuration that maximizes connectivity and minimizes mortality associated with movement between components.

Captive Propagation and Reintroduction

Captive propagation and reintroduction in herpetological conservation has a mixed history. A recent success is documented by Sexton et al. (1998), who reported that reintroduced wood frogs began expanding into formerly occupied habitat at sites in Missouri. However, a recent reintroduction of boreal toads (*Bufo boreas*) into Rocky Mountain National Park was a failure (Muths et al. 2001). Dodd and Seigel (1991) document many such failures from the herpetological literature.

Since 1999, a project has been underway to reintroduce northern leopard frogs into some areas of Alberta (Fisher 1999; Kendell 2001, 2002). Young frogs were raised from egg masses collected at various localities (Kendell 2001) and were released into the wild in spring of the following year. Of 6692 tadpoles successfully hatched from four egg masses, 1477 young frogs were released at three release sites in the spring of next year. None of these frogs were observed during later surveys at the release sites. Kendell (2002) reported that approximately 4500 young frogs had been released during the three years of the project. Of these, 13 were recaptured at the release sites, and calling activity was recorded for the first time in the third year of the project. Kendell (2002) predicted eventual success of the project, based on the fact that calling activity was recorded during 2001 and many of the released frogs were not yet sexually mature.

Although work in Alberta has shown that a reintroduction program can potentially be successful, a tremendous amount of effort has obviously been expended in this research. About 21,000 tadpoles were reared in 2001 in a predator-free exclosure, for example, which resulted in only 13 subadult or adult frogs being collected in 2001 (Kendell 2002). Each of the thousands of small frogs that are released have to be marked to determine survival (Kendell 2001, 2002) and a field laboratory was maintained to raise the frogs (Kendell 2001, 2002). While none of the authors of these various reports have reported the cost of this project, one could imagine that it is considerable. While the effort is worthwhile if it works to restore northern leopard frogs to areas in which they are now extinct, the expense is obviously considerable compared with protecting known populations of frogs. Also, while eventual success may look likely to Kendell (2002), it is by no means assured.

Information Needs

Survey and monitoring: It is not clear how many surveys of northern leopard frogs have been undertaken in Wyoming. It is critical that baseline data are obtained to assess the abundance of northern leopard frogs in the state and then to begin tracking population trends. Many of the information needs identified in this report cannot be completed before basic surveys have been conducted. Heyer et al. (1994), Olson et al. (1997), and suggestions in this report can be used to institute a survey program.

Mapping of suitable habitat: Northern leopard frog habitat has not been mapped in Wyoming although the Wyoming Natural Diversity Database is currently attempting to generate a predictive habitat model that will help focus mapping efforts (Keinath in preparation). Available, suitable habitat needs to be clearly identified, mapped, and tracked through time in order to effectively conserve the species.

At a small scale, northern leopard frogs likely need seasonal and semi-permanent ponds that are probably <5 ha in size (e.g., Semlitsch and Bodie 1998, Semlitsch 1998, 2000a, b). The lead author has used National Wetlands Inventory maps on parts of the Black Hills National Forest to locate potential northern leopard frog breeding habitat but have found them to be frequently inaccurate, perhaps because of the dense forests found throughout the Black Hills. There appears to be no substitute for ground surveys of appropriate northern leopard frog breeding habitat. When found, these ponds need to be located using GPS and then downloaded into an appropriate GIS system to find these ponds in the future and track presence and absence of northern leopard frogs at these sites over time. Mapping of northern leopard frog sites should be relatively quick and inexpensive with the appropriate equipment and software. As Oscar Martinez has demonstrated on parts of the Spearfish-Nemo District in the Black Hills National Forest, when these ponds are located and protected, the result is large and growing populations of the northern leopard frog over time (personal observations).

Characterization of suitable habitat: Unfortunately, although we have good studies of the natural history of the northern leopard frog to guide mapping efforts (Merrell 1977), the habitat of the species has not been carefully characterized in a quantitative sense (but see Beauregard and Leclair 1988) and has not been studied in most of Wyoming. A good herpetologist can guide a mapping team to "good" northern leopard frog habitat but the mapping team may not easily find such habitats without special training. Quantitative characterization of ponds used by northern leopard frogs should be relatively easy and some work has already been done (Smith et al. 1998).

Upland habitat and migration corridors that are used extensively by northern leopard frogs will probably be more difficult to find than breeding habitat but should also be easy to characterize once found. Unfortunately, mapping needs to be completed and habitat models need to be developed to guide conservation efforts. These types of data are needed to develop any habitat management plan (as envisioned by Semlitsch 2000a) for the northern leopard frog in Wyoming.

Studies of overwintering sites can be difficult to undertake. Cunjak (1986) relied on SCUBA techniques to study frogs overwintering in streams in Ontario while Merrell (1977) relied on simple but careful visual observations early in spring and late in the fall to report on frogs entering and leaving overwintering sites. Currently we know very little about where northern leopard frogs may overwinter in Wyoming.

Radio tracking in late fall could show where frogs go to overwinter and the migratory pathways taken to reach these sites. Such a study would be expensive but the data obtained would be invaluable and difficult to obtain in any other manner. Otherwise I would recommend observation of frogs at appropriate times of the year or checking potential overwintering sites, such as springs, wet meadows, lakes, and streams, in the winter. Investigating potential overwintering sites in winter would obviously present numerous logistical difficulties. Northern leopard frogs are also difficult to observe in mid-winter as they become covered in debris on the bottom of lakes and streams (Cunjak 1986; J. Grier, North Dakota State University, personal communication 1998). This aspect of northern leopard frog natural history may well be the most challenging to investigate.

Studies of movements: Movement studies are probably the most time-intensive and difficult field studies to conduct on amphibians. They would, however, give us detailed information on how the habitat is used by subadult and adult northern leopard frogs that may be difficult to obtain any other way. They would also address two critical questions: How much upland habitat is needed to conserve 95% of the northern leopard frog population at a particular breeding pond (i.e., how much core upland habitat needs to be protected around each pond), and what habitat features are used for migration by subadult and adult northern leopard frogs (i.e., how do we protect migration corridors used by frogs)? As a side benefit, movement studies conducted over numerous years would give information on the basic demography of populations. Another benefit to movement studies is that they could be combined with studies of other issues in northern leopard frog conservation, including timber practices, burning, the effects of roads, mining, and overwintering, and in fact are critical in studies of most of these potential conservation issues.

Disease, pollution, and limb malformations: Any potential disease outbreaks should be carefully noted and investigated. Determination of the presence of disease would have to be made by a qualified wildlife disease specialist. Investigators whose works are cited in the "Community Ecology; Parasites and Diseases" section (pp. 39-41) should be alerted and consulted. Any large kills of northern leopard frogs should be reported (these could represent death by disease or by chemicals). Pesticides used in Wyoming should be investigated, especially if large amounts will be used to combat disease or insect outbreaks. Kills of northern leopard frogs could result from overuse of pesticides or accidental (or intentional) pesticide spills. Any limb malformations observed should be reported to an appropriate biologist in charge of the affected district, to the lead author, to the various state game departments, and especially to the limb malformations website maintained by the Northern Prairie Wildlife Research Center (Northern Prairie Wildlife Research Center 1997).

Effect of introduced predaceous fish: Sport fishing is a large industry throughout the Rocky Mountains and it is unlikely to diminish in importance. It can be assumed that management agencies will continue to manage for the presence of sport fish that are predators on all life stages of the northern leopard frog. The industry depends on predaceous fish that have been introduced in many areas throughout Wyoming. Therefore, it can be assumed that northern leopard frogs have not evolved a natural defense against these predators and that some of their life history strategies put them into the same habitats occupied by these predators. All life stages are probably vulnerable, but there may be certain life stages that are more subject to predation than others. Some unanswered questions are: Are eggs and tadpoles more vulnerable than subadult and adult frogs to predation by introduced predaceous fish? What types of introduced fish are most likely to eat which life history stages? Are frogs likely to suffer predation during the overwintering period? Do frogs overwinter in habitats that are also used by introduced predaceous fish? Is predation by introduced predaceous fish ameliorated in certain types of habitats, and can introduced fish be kept out of these habitats? Given the likelihood that management objectives for northern leopard frogs will continue to clash with management objectives for sport fishing it is imperative that management agencies come up with innovative and collaborative means of managing for these two conflicting objectives.

Some of these studies could be rather simple; for example, breeding ponds can be sampled for predaceous fish and monitored to determine the likelihood of successful frog metamorphosis at these ponds. One would expect decreased or no metamorphosis at breeding ponds with predaceous fish. Another simple study would be to examine the stomach contents of predaceous fish captured in winter by ice fishermen. Anecdotal evidence from North Dakota showed that stomachs of pike caught in winter contained many northern leopard frogs (unpublished data). Other studies could be much more difficult. Determining effective means to isolate frogs from introduced fishes could be one of the biggest challenges in deriving a management plan for the northern leopard frog.

Grazing effects: Cattle grazing is prevalent throughout public and private lands in Wyoming and can easily affect all life stages of leopard frogs. Cattle can affect breeding ponds through erosion of pond margins or by direct effects. Erosion leads to siltation, which can cover eggs with silt and impede respiration through their surface. Cattle can affect tadpoles in breeding ponds through the toxicity of nitrogen buildup from manure accumulation in and around the ponds. One simple and inexpensive study that is needed is to examine series of tadpoles from fenced and unfenced ponds. Post-mortem of two diseased tadpoles collected at one pond open to cattle in 1998 showed that the tadpoles had deformed mouthparts and skin irritation consistent with exposure to an aquatic irritant (Smith et al. 1998).

The effects of cattle on upland frog habitat would be more difficult to study, but might be accomplished with a controlled study of ponds where fences were set at different circumferences from each pond. Mark-recapture techniques can be used to determine if the protection of a core upland habitat area results in a higher density of northern leopard frogs at a site. Such a study would serve several purposes as it should tell us something about the size of core upland areas needed to foster large and healthy northern leopard frog populations. These core sizes can be applied broadly across the forest to manage timber harvest and other practices that could adversely affect frog populations.

Grazing effects on migration corridors on grazing allotments would be much more difficult. It would seem that streamside vegetation and riparian corridors should be protected as northern leopard frog migration routes. However, the only controlled studies possible would be to allow cattle to invade such corridors between ponds to try to determine the result on northern leopard frog populations. The results of such a study might be difficult to interpret. A more direct study of streamsides and riparian corridors would be to simply directly mark and follow frogs in these corridors or to survey for frogs in these corridors during appropriate times of the year.

Timber removal: As has been shown by deMaynadier and Hunter (1995) in their review of forest management practices and their effect on amphibian populations, timber removal practices have significant effects on amphibian populations. As part of studies on other aspects of northern leopard frog biology in Wyoming, study sites could be picked such that some sites are located in or nearby areas under different types of forest removal practices so as to investigate the effects of these practices on northern leopard frogs. Such a study would be long-term and therefore somewhat costly but would represent value added to any ongoing studies while costing relatively little additional funding to implement.

Effect of roadways: The results of Wyman (1991) demonstrated that roadways can cause heavy mortality in some amphibian populations. However, the results of deMaynadier and Hunter (1995) showed that this is not necessarily the case depending on the road type. An objective of management should be to reduce the number and extent of these roads. It would seem logical to combine movement studies with a study of the effect of roadways by picking a few breeding ponds near different types of roads as study sites. If done in combination with a broader study on the movement of northern leopard frogs a study on road effects would simply represent value added to a current study and would not cost anything beyond funds spent on the broader movement study.

Genetic studies: It would be relatively easy to collect frogs from several sites across the forest, sample small pieces of tissue (this should not increase mortality or morbidity of the frogs as very small amounts of tissue are needed), and subject them to genetic analysis. However, the genetic data needed are very fine-grained and require considerable expertise and funding to obtain.

Such data would be invaluable and could tell us the extent of philopatry at specific ponds, the extent of genetic connectedness of each pond, and whether there is high within - or among - site genetic variation in northern leopard frogs in the Rocky Mountains. These data can be used to guide management strategies by telling us something about which ponds need conservation attention (for example, which ponds serve as sources for colonization) and the extent and direction of movement of frogs from pond to pond.

Prescribed fire and fire suppression: It would be of a great deal of interest to investigate the effects of fire on northern leopard frog populations. This could be done either opportunistically, for example by tracking frog populations within recently burned areas, or through studies that specifically address the effects of a prescribed fire regime on northern leopard frog populations. In the latter case, studies on some other aspect of northern leopard frog biology, such as the movements of northern leopard frogs, could be modified by placing study sites within areas under prescribed burn regimes and in areas in which fire is suppressed. The study sites in both study areas could then be compared. Again, such a study would represent value added to an ongoing study while costing relatively little additional funding to implement.

Tables and Figures

Table 1: States and provinces in which the northern leopard (*Rana pipiens*) frog is found, historical abundance (if known), present abundance (if known), and the population trend (where known).

State or Province	Historical Abundance	Present Abundance	Population Trend
Alberta	Unknown[1]	Uncommon[1,2,3]	Declining[1,2,3]
Arizona	Uncommon[4]	Uncommon[4]	Declining[4]
British Columbia	Unknown	Unknown	Unknown
California	Extralimital?[5,6]	Uncommon[3]	Declining[3]
Colorado	Unknown	Uncommon[7,8,9]	Declining[7,8,9,10]
Connecticut	Unknown	Unknown	Unknown
Idaho	Unknown	Uncommon[11]	Declining[11]
Illinois	Unknown	Common[12]	Stable[12]
Indiana	Common[13]	Uncommon[13,14]	Declining[13,14]
Iowa	Common[15]	Uncommon[15]	Declining[15]
Kentucky	Unknown	Unknown	Unknown
Maine	Unknown	Unknown	Unknown
Manitoba	Unknown	Unknown	Unknown
Massachusetts	Unknown	Unknown	Unknown
Michigan	Uncommon[16]	Unknown	Declining[16]
Minnesota	Common[17]	Common[17]	Declining[17]
Montana	Unknown	Uncommon[18,19]	Declining[18,19]
Nebraska	Unknown	Unknown	Unknown
Nevada	Unknown	Unknown	Unknown
New Brunswick	Unknown	Common[20]	Stable[20]
New Hampshire	Unknown	Unknown	Unknown
New Mexico	Unknown	Unknown	Unknown
New York	Unknown	Unknown	Unknown
Newfoundland	Extralimital[21,22]	Unknown	Unknown
North Dakota	Unknown	Unknown	Unknown
Northwest Territories	Unknown	Uncommon[23]	Unknown
Nova Scotia	Unknown	Unknown	Unknown
Ohio	Unknown	Common[24]	Stable[24]
Ontario	Unknown	Unknown	Unknown
Pennsylvania	Unknown	Unknown	Unknown
Quebec	Unknown	Unknown	Unknown
Saskatchewan	Unknown	Unknown[25]	Unknown[25]
South Dakota	Unknown[26]	Common[26,27,28,29,30]	Unknown[26]
Utah	Unknown	Unknown	Unknown
Vermont	Unknown	Unknown	Unknown
Washington	Uncommon[31]	Uncommon[31]	Declining[31]
West Virginia	Unknown	Unknown	Unknown
Wisconsin	Common[32]	Common[32]	Declining[32,33,34,35]
Wyoming	Unknown	Unknown	Declining[3,11,36]

Table 1 Footnotes: If no reference is given, the data are unknown for the various provinces and states that are listed. References: 1 = Russell and Bauer (1993); 2 = Roberts (1992); 3 = Stebbins and Cohen (1995); 4 = Clarkson and Rorabaugh (1989); 5 = Bury and Luckenbach (1976); 6 = Jennings (1984); 7 = Hammerson (1999); 8 = Hammerson (1982); 9 = Cousineau and Rogers (1991); 10 = Corn and Fogleman (1984); 11 = Koch and Peterson (1995); 12 = Mierzwa (1998); 13 = Minton (1998); 14 = Brodman and Kilmurry (1998); 15 = Lannoo (1994); 16 = Collins and Wilbur (1979); 17 = Moriarty (1998); 18 = Maxell (2000); 19 = Reichel (1996); 20 = McAlpine (1997); 21 = Buckle (1971); 22 = Green and Campbell (1984); 23 = Fournier (1997); 24 = Orr et al. (1998); 25 = Didiuk (1997); 26 = B. Smith, personal observation; 27 = Peterson (1974); 28, 29, 30 = Smith et al. (1996a, b; 1998); 31 = Leonard et al. (1999); 32 = Mossman (1998); 33, 34 = Hine et al. (1975, 1981); 35 = Dhuey and Hay (2000); 36 = Baxter and Stone (1985).

Figure 1: Map of Natural Heritage ranks for the northern leopard frog (*Rana pipiens*) as presented by NatureServe (http://www.natureserve.org/).

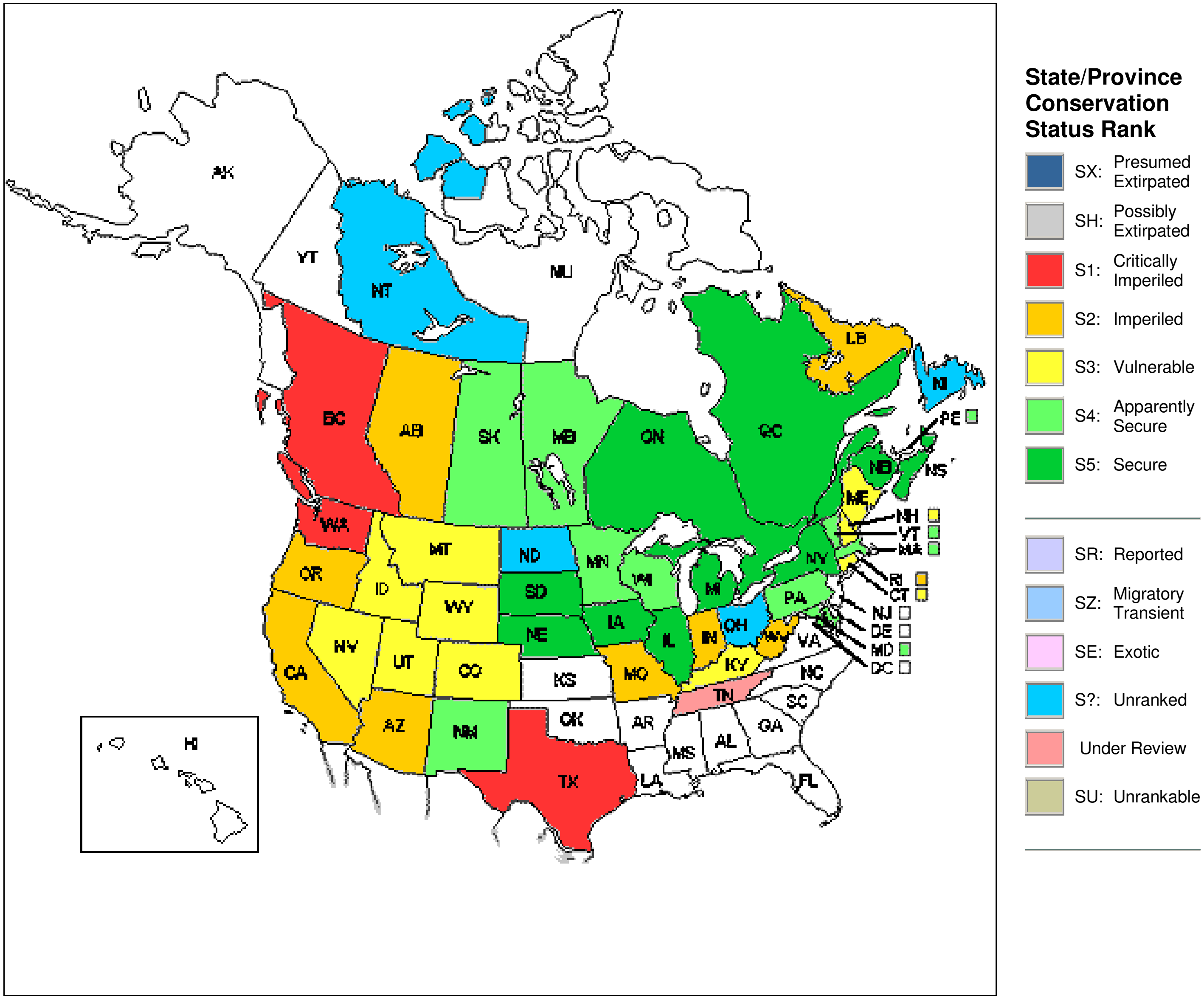


Figure 2: Photograph of adult northern leopard frogs (*Rana pipiens*), courtesy of Suzanne L. Collins, The Center for North American Herpetology.

Figure 3: Photograph of northern leopard frog egg masses from the Pyramid Lake Paiute Tribe Reservation.

Figure 4: Extent of northern leopard frog (*Rana pipiens*) current and historical range, as reported by Stebbins (1985, 2003), Hillis (1988), and Conant and Collins (1991). Historic distribution is roughly represented by the dashed line.

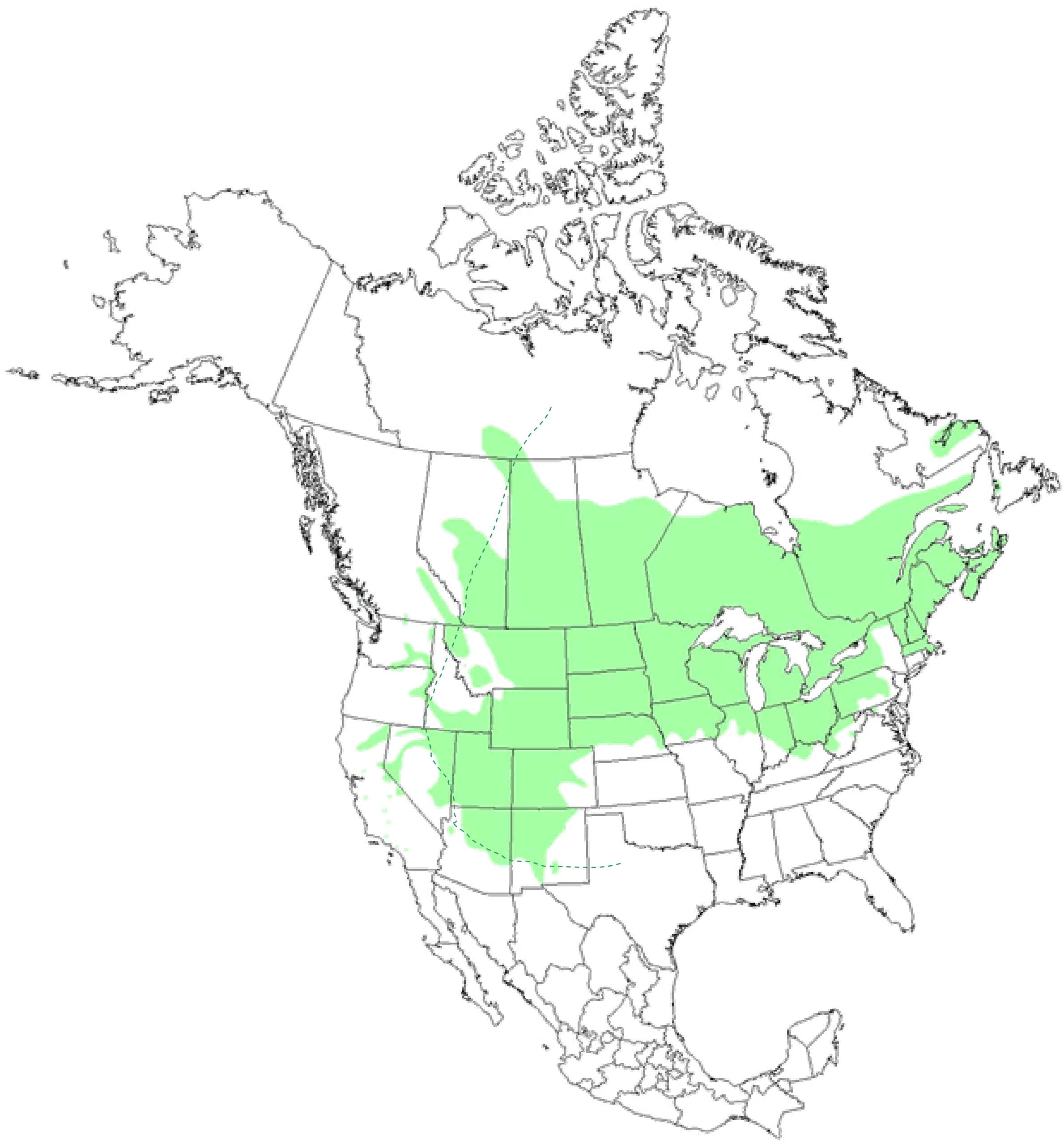
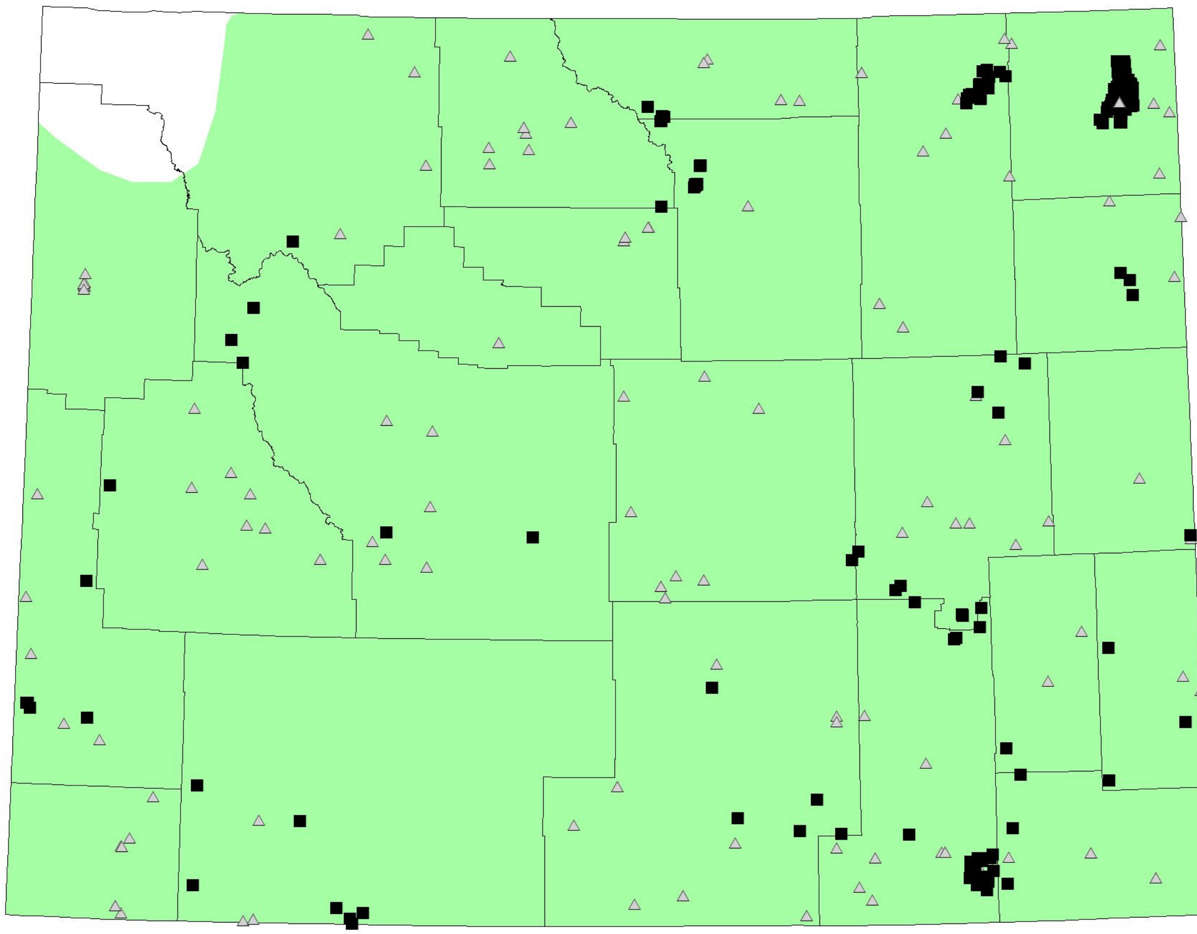


Figure 5: Range and occurrences of northern leopard frog (*Rana pipiens*) in Wyoming from the Wyoming Natural Diversity Database. Solid black squares represent occurrences documented since 1980 and gray triangles represent historic occurrences documented before 1980.



Literature Cited

Adams, M. J., K. O. Richter, and W. P. Leonard. 1997. Surveying and monitoring amphibians using aquatic funnel traps. Pp. 47-54 in Olson, D. H., W. P. Leonard, and R. B. Bury, eds. Sampling Amphibians in Lentic Habitats: Methods and Approaches for the Pacific Northwest. Northwest Fauna No. 4. 134 pp.

Alford, R. A. 1999. Resource use, competition, and predation. Pp. 240-278 in McDiarmid, R. W. and R. Altig, eds. Tadpoles: The Biology of Anuran Larvae. The University of Chicago Press, Chicago, Illinois. 444 pp.

-----, and S. J. Richards. 1999. Global amphibian declines: A problem in applied ecology. Annual Review of Ecology and Systematics 30:133-165.

Ankley, G. T., J. E. Tietge, D. L. DeFoe, K. M. Jensen, G. W. Holcombe, E. J. Durham, and S. A. Diamond. 1998. Effects of ultraviolet light and methoprene on survival and development of *Rana pipiens*. Environmental Toxicology and Chemistry 17:2530-2542.

-----, J. E. Tietge, G. W. Holcombe, D. L. DeFoe, S. A. Diamond, K. M. Jensen, and S. J. Degitz. 2000. Effects of laboratory ultraviolet radiation and natural sunlight on survival and development of *Rana pipiens*. Canadian Journal of Zoology 78:1092-1100.

Ashley, E. P., and J. T. Robinson. 1996. Road mortality of amphibians, reptiles, and other wildlife on the Long Point Causeway, Lake Erie, Ontario. Canadian Field-Naturalist 110:403-412.

Ashton, R. E., Jr. 1994. Tracking with radioactive tags. Pp. 158-166 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C. 364 pp.

Aubry, K. B., and Hall, P. A. 1991. Terrestrial amphibian communities in the southern Washington Cascade Range. Pp. 327-338 in Ruggiero, L. F., K. B. Aubry, A. B. Carey, and M. H. Huff, eds. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S.D.A. Forest Service General Technical Report. PNW-GTR-285.

-----, L. L. C. Jones, and P. A Hall. 1988. Use of woody debris by plethodontid salamanders in Douglas-fir forests in Washington. Pp. 32-37 in Szaro, R.C., K. E. Severson, and D. R. Patton, eds. Management of Amphibians, Reptiles, and Mammals in North America. U.S.D.A. Forest Service General Technical Report. RM-166. 458 pp.

Baker, M. R. 1987. Synopsis of the Nematoda parasitic in amphibians and reptiles. Memorial University of Newfoundland, Miscellaneous Publications in Biology 11:1-325.

Bartelt, P. E. 1998. *Bufo boreas* mortality. Herpetological Review 29:96.

Baxter, G. T. 1952. Notes on growth and the reproductive cycle of the leopard frog, *Rana pipiens* Schreber, in southern Wyoming. Journal of the Colorado-Wyoming Academy of Science 4:91.

-----, and M. D. Stone. 1985. Amphibians and Reptiles of Wyoming, 2nd ed. Wyoming Game and Fish Department. 137 pp.

Beauregard, N., and R. Leclair, Jr. 1988. Multivariate analysis of the summer habitat structure of *Rana pipiens* Schreber, in Lac Saint Pierre (Québec, Canada). Pp. 129-143 in Szaro, R. C., K. E. Severson, and D. R. Patton, eds. Management of Amphibians, Reptiles and Small Mammals in North America. U.S.D.A Forest Service General Technical Report RM-166. 458 pp.

Begon, M., J. L. Harper, and C. R. Townsend. 1996. Ecology: Individuals, Populations, and Communities, 3rd ed. Blackwell Science Ltd., Editorial Offices: Osney Mead, Oxford, London. 1068 pp.

Berger, L., R. Speare, P. Daszak, D. E. Green, A. A. Cunningham, C. L. Gogging, R. Slocombe, M. A. Ragan, A. D. Hyatt, K. R. McDonald, H. B. Hines, K. R. Lips, G. Marantelli, and H. Parkes. 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. Proceedings of the National Academy of Sciences 95:9031-9036.

Berrill, M., S. Bertram, D. Brigham, and V. Campbell. 1992. A comparison of three methods of monitoring frog populations. Pp. 87-93 in Bishop, C. A., and K. E. Pettit, eds. Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy. Occasional Paper Number 76, Canadian Wildlife Service, Ottawa, Ontario. 120 pp.

Berrill, M., S. Bertram, A. Wilson, S. Louis, D. Brigham, and C. Stromberg. 1993. Lethal and sublethal impacts of pyrethroid insecticides on amphibian embryos and tadpoles. Environmental Toxicology and Chemistry 12:525-539.

Berrill, M., S. Bertram, L. McGillivray, M. Kolohon, and B. Pauli. 1994. Effects of low concentrations of forest-use pesticides on frog embryos and tadpoles. Environmental Toxicology and Chemistry 13:657-664.

Berrill, M., S. Bertram, and B. Pauli. 1997. Effects of pesticides on amphibian embryos and larvae. Pp. 233-245 in Green, D. M, ed. Amphibians in Decline: Canadian Studies of a Global Problem. Herpetological Conservation, Number One. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri. 338 pp.

Bertram, S., and M. S. Berrill. 1997. Fluctuations in a northern population of gray treefrog, *Hyla versicolor*. Pp. 57-63. in Green, D. M, ed. Amphibians in Decline: Canadian Studies of a Global Problem. Herpetological Conservation, Number One. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri. 338 pp.

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

Bishop, C. A. 1992. The effects of pesticides on amphibians and the implications for determining the causes of declines in amphibian populations. In C. A. Bishop and K. E. Pettit, eds. Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy. Ottawa, Ontario, Canadian Wildlife Service. Occasional Paper Number 76.

Bishop, C. A., and K. E. Pettit. 1992. Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy. Canadian Wildlife Service, Occasional Paper No. 76.

Bishop, C. A., K. E. Pettit, M. E. Gartshore, and D. A. MacLeod. 1997. Extensive monitoring of anuran populations using call counts and road transects in Ontario (1992 to 1993). Pp. 149-160 in Green, D. M, ed. Amphibians in Decline: Canadian Studies of a Global Problem. Herpetological Conservation, Number One. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri. 338 pp.

Blaustein, A. R., and D. B. Wake. 1995. The puzzle of declining amphibian populations. Scientific American 272(4):56-61.

Bonin, J., and Y. Bachand. 1997. The use of artificial covers to survey terrestrial salamanders in Québec. Pp. 175-179 in Green, D. M, ed. Amphibians in Decline: Canadian Studies of a Global Problem. Herpetological Conservation, Number One. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri. 338 pp.

Bonin, J., M. Ouellet, J. Rodrigue, J. L. DesGranges, F. Gagné, T. F. Sharbel, and L. A. Lowcock. 1997. Measuring the health of frogs in agricultural habitats subjected to pesticides. Pp. 246-257 in Green, D. M, ed. Amphibians in Decline: Canadian Studies of a Global Problem. Herpetological Conservation, Number One. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri. 338 pp.

Bovbjerg, R. V. 1965. Experimental studies on the dispersal of the frog, *Rana pipiens*. Proceedings of the Iowa Academy of Science 72:412-418.

Bovbjerg, R. V., and A. M. Bovbjerg. 1964. Summer emigrations of the frog *Rana pipiens* in northwestern Iowa. Proceedings of the Iowa Academy of Science 71:511-518.

Bradford, D. F. 1983. Winterkill, oxygen relations, and energy metabolism of a submerged dormant amphibian, *Rana muscosa*. Ecology 64:1171-1183.

Breckenridge, W. J. 1944. Reptiles and Amphibians of Minnesota. University of Minnesota Press, Minneapolis, Minnesota. xiii + 202 p.

Breden, F. 1987. The effect of post-metamorphic dispersal on the population genetic structure of Fowler's toad, *Bufo woodhousei fowleri*. Copeia 1987:386-395.

Brodman, R., and M. Kilmurry. 1998. Status of amphibians in northwestern Indiana. Pp. 125-136 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

Brönmark, C., and P. Edenhamn. 1994. Does the presence of fish affect the distribution of tree frogs (*Hyla arborea*)? Conservation Biology 8:841-845.

Bull, E. L. 2000. Comparison of two radio transmitter attachments on Columbia spotted frogs (*Rana luteiventris*). Herpetological Review 31:26-28.

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

Bury, R. B., and P. S. Corn. 1988. Douglas-fir forests in the Oregon and Washington Cascades: Relation of the herpetofauna to stand age and moisture. Pp. 11-22 in Szaro, R. C., K. E. Severson, and D. R. Patton. Management of Amphibians, Reptiles, and Small Mammals in North America. U.S.D.A. Forest Service General Technical Report. RM-166. 458 pp.

Cameron, J. A. 1940. Effects of fluorine on hatching time and hatching stage in *Rana pipiens*. Ecology 21:288-292.

Carey, C. 1993. Hypothesis concerning the causes of the disappearance of boreal toads from the mountains of Colorado. Conservation Biology 7:355-362.

Carey, C., N. Cohen, and L. Rollins-Smith. 1999. Amphibian declines: An immunological perspective. Developmental and Comparative Immunology 23:459-472.

Carr, L. W., and L. Fahrig. 2001. Effect of road traffic on two amphibian species of differing vagility. Biological Conservation 15:1071-1078.

Casper, G. S. 1998. Review of the status of Wisconsin amphibians. Pp. 199-205 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

Clarkson, R. W., and J. C. Rorabaugh. 1989. Status of leopard frogs (*Rana pipiens* complex: Ranidae) in Arizona and southeastern California. Southwestern Naturalist 34:531-538.

Collier, A., J. B. Keiper, and L. P. Orr. 1998. The invertebrate prey of the northern leopard frog, *Rana pipiens*, in a northeastern Ohio population. Ohio Journal of Science 98:39-41.

Collins, J. P., and H. M. Wilbur. 1979. Breeding habits and habitats of the amphibians of the Edwin S. George Reserve, Michigan, with notes on the local distribution of fishes. Occasional Papers of the Museum of Zoology, University of Michigan. No. 686:1-34.

Conant, R., and J. T. Collins. 1991 A Field Guide to Reptiles and Amphibians: Eastern and Central North America, 3rd ed. Houghton Mifflin Company, Boston, Massachusetts. 450 pp.

Cooke, A. S. 1981. Tadpoles as indicators of harmful levels of pollution in the field. Environmental Pollution Series A 25:123-133.

Corn, P. S. 1981. Field evidence for a relationship between color and developmental rate in the northern leopard frog (*Rana pipiens*). Herpetologica 37:155-160.

Corn, P. S. 1994. What we know and don't know about amphibians declines in the west. Pp. 59-67 in W. W. Covington and L. F. DeBano, eds. Sustainable Ecological Systems: Implementing an Ecological Approach to Land Management. U. S. D. A. Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO. General Technical Report RM-247.

Corn, P. S., and J. C. Fogleman. 1984. Extinction of montane populations of the northern leopard frog (*Rana pipiens*) in Colorado. Journal of Herpetology 18:147-152.

Corn, P. S., and L. J. Livo. 1989. Leopard frog and wood frog reproduction in Colorado and Wyoming. Northwestern Naturalist 70:1-9.

Corn, P. S., and F. A. Vertucci. 1992. Descriptive risk assessment of the effects of acidic deposition on Rocky Mountain amphibians. Journal of Herpetology 26:361-369.

Cousineau, M., and K. Rogers. 1991. Observations on sympatric *Rana pipiens*, *R. blairi*, and their hybrids in eastern Colorado. Journal of Herpetology 25:114-116.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of Wetlands and Deepwater Habitats of the United States. U.S. Government Printing Office, Washington, D. C. 103 pp.

Crashaw, G. J. 1997. Diseases in Canadian amphibian populations. Pp. 258-270 in Green, D. M. J., ed. Amphibians in Decline: Canadian Studies of a Global Problem. Herpetological Conservation, Number One. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri. 338 pp.

Crouch, W. B., and P. W. C. Paton. 2000. Using egg-mass counts to monitor wood frog populations. Wildlife Society Bulletin 28:895-901.

Crump, D., M. Berrill, D. Coulson, D. Lean, L. McGillivray, and A. Smith. 1999. Sensitivity of amphibian embryos, tadpoles, and larvae to enhanced UV-B radiation in natural pond conditions. Canadian Journal of Zoology 77:1956-1966.

Crump, M. L., F. R. Hensley, and K. L. Clark. 1992. Apparent decline of the golden toad: Underground or extinct? Copeia 1992:413-420.

Crump, M. L., and N. J. Scott, Jr. 1994. Visual encounter surveys. Pp. 84-92 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayak, and M. Foster, eds. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C. 364 pp.

Cunjak, R. A. 1986. Winter habitat of northern leopard frogs, *Rana pipiens,* in a southern Ontario stream. Canadian Journal of Zoology 64:255-257.

Cunningham A. A., T. E. S. Langton, P. M. Bennett, J. F. Lewin, S. E. N. Drury, R. E. Gough, and S. K. MacGregor. 1996. Pathological and microbiological findings from incidents of unusual mortality of the common frog (*Rana temporaria*). Philosophical Transactions of the Royal Society of London 351:1539-57.

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

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife: Threats to biodiversity and human health. Science 287:443-449.

Davidson, C. 1996. Frog and toad calls of the Rocky Mountains: Vanishing voices. Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York.

Davis, T. M. 1997. Non-disruptive monitoring of terrestrial salamanders with artificial cover objects on southern Vancouver Island, British Columbia. Pp. 161-174 in Green, D. M., ed. Amphibians in Decline: Canadian Studies of a Global Problem. Herpetological Conservation, Number One. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri. 338 pp.

Davis, J. G., P. J. Krusling, and J. W. Ferner. 1998. Status of Amphibians in Minnesota. Status and Conservation of Midwestern Amphibians. Pp. 166-168 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

DeBenedictis, P. A. 1974. Interspecific competition between tadpoles of *Rana pipiens* and *Rana sylvatica*: An experimental field study. Ecological Monographs 44:129-151.

deMaynadier, P. G., and M. L. Hunter, Jr. 1995. The relationship between forest management and amphibian ecology: A review of the North American literature. Environmental Review 3:230:261.

deMaynadier, P. G., and M. L. Hunter, Jr. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. Conservation Biology 12:340-352.

Dhuey, B., and R. Hay. 2000. Frog and toad survey. Pp. 140-147 in 1999 Wildlife Survey Summary Report. Wisconsin Department of Natural Resources, Madison, Wisconsin.

Dial, N. A., and C. A. B. Dial. 1987. Lethal effects of diquat and paraquat on developing frog embryos and 15-day-old tadpoles, *Rana pipiens*. Bulletin of Environmental Contamination and Toxicology 38:1006-1011.

Diana, S. G., and V. R. Beasley. 1998. Amphibian toxicology. Pp. 266-277 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

Didiuk, A. 1997. Status of amphibians in Saskatchewan. Pp. 110-116 in D. M. Green, ed., Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri.

Diller, L. V., and R. L. Wallace. 1994. Distribution and habitat of *Plethodon elongatus* on managed young growth forests in north coastal California. Journal of Herpetology 28:310-318.

Dodd, C. K., Jr., and D. E. Scott. 1994. Drift fences encircling breeding sites. Pp. 125-141 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D. C. 364 pp.

Dole, J. W. 1965a. Spatial relations in natural populations of the leopard frog, *Rana pipiens* Schreber, in northern Michigan. American Midland Naturalist 74:464-478.

Dole, J. W. 1965b. Summer movement of adult leopard frogs, *Rana pipiens* Schreber, in northern Michigan. Ecology 46:236-255.

Dole, J. W. 1967. Spring movements of leopard frogs, *Rana pipiens* Schreber, in northern Michigan. American Midland Naturalist 78:167-181.

Dole, J. W. 1968. Homing in leopard frogs, *Rana pipiens*. Ecology 49:386-399.

Dole, J. W. 1971. Dispersal of recently metamorphosed leopard frogs, *Rana pipiens*. Copeia 1971:221-228.

Dole, J. W. 1972. The role of olfaction and audition in the orientation of leopard frogs, *Rana pipiens*. Herpetologica 28:258-260.

Drake, C. J. 1914. The food of *Rana pipiens*. The Ohio Naturalist 14:257-269.

Duellman, W. E., and L. Trueb. 1986. Biology of Amphibians. McGraw-Hill, Inc. New York, New York. 670 pp.

Dunlap, D. G., and K. C. Kruse. 1976. Frogs of the *Rana pipiens* complex in the northern and central plains states. Southwestern Naturalist 20:559-571.

Dunlap, D. G., and J. E. Platz. 1981. Geographic variation of protein and call in *Rana pipiens* from the northcentral United States. Copeia 1981:876-879.

Dupuis, L. A., J. N. M. Smith, and F. Bunnell. 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. Conservation Biology 9:645-653.

Dyer, W. G. 1991. Helminth parasites of amphibians from Illinois and adjacent Midwestern states. Transactions of the Illinois State Academy of Science 84:125-143.

Emery, A. R., A. H. Berst, and K. Kodaira. 1972. Under-ice observations of wintering sites of leopard frogs. Copeia 1972:123-126.

Faeh, S. A., D. K. Nichols, and V. R. Beasley. 1998. Infectious diseases of amphibians. Pp.259-265 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

Fellers, G. M., and C. A. Drost. 1994. Sampling with artificial cover. Pp. 146-150 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D. C. 364 pp.

Fisher, C. 1999. Feasibility of northern leopard frog translocations in Alberta: A review of physiological, ecological, methodological requirements for successful repatriations and results from field investigations. Alberta Environment, Fisheries, and Wildlife Management Division, Edmonton, AB. Unpublished report. 30 pp.

Fitch, H. S. 1958. Home ranges, territories, and seasonal movements of vertebrates of the Natural History Reservation. University of Kansas Publications, Museum of Natural History 11:63-326.

Flower, S. S. 1936. Further notes on the duration of life in animals II: Amphibia. Procedings of Zoological Society of London: 369-394.

Force, E. R. 1933. The age of the attainment of sexual maturity of the leopard frog *Rana pipiens* (Schreber) in northern Michigan. Copeia 1933:128-131.

Fournier, M. A. 1997. Amphibians in the Northwest Territories. Pp. 100-106 in D. M. Green, ed., Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri.

Franz, R. 1971. Notes on the distribution and ecology of the herpetofauna of northwestern Montana. Bulletin of the Maryland Herpetological Society 7:1-10.

Freda, J., and W. A. Dunson. 1985. Field and laboratory studies of ion balance and growth rates of ranid tadpoles chronically exposed to low pH. Copeia 1985:415-423.

Freda, J., and D. H. Taylor. 1992. Behavioral response of amphibian larvae to acidic water. Journal of Herpetology 26:429-433.

Fried, B., P. L. Pane, and A. Reddy. 1997. Experimental infection of *Rana pipiens* tadpoles with *Echinostoma trivolvis* cercariae. Parasitology Research 83:666-669.

Froiland, S. G. 1990. Natural History of the Black Hills and Badlands. The Center for Western Studies, Augustana College, Sioux Falls, South Dakota. 225 pp.

Gibbs, E. L., G. W. Nace, and M. B. Emmons. 1971. The live frog is almost dead. Bioscience 21:1027-1034.

Goldberg, S. R., C. R. Bursey, R. G. McKinnell, and I. S. Tan. 2001. Helminths of northern leopard frogs, *Rana pipiens* (Ranidae), from North Dakota and South Dakota. Western North American Naturalist 61:248-251.

Grant, B. W., K. L. Brown, G. W. Ferguson, and J. W. Gibbons. 1994. Changes in amphibian biodiversity associated with 25 years of pine forest regeneration: Implications for biodiversity management. Pp. 355-367 in Majumdar, S. K., F. J. Brenner, J. E. Lovich, J. F. Schalles, and E. W. Miller, eds. Biological Diversity: Problems and Challenges. Pennsylvania Academy of Science, Philadelphia, Pennsylvania.

Green, D. M. 1992. Fowler's toads (*Bufo woodhousei fowleri*) at Long Point, Ontario: Changing abundance and implications for conservation. Pp. 37-43 in Bishop, C. A., and K. E. Pettit, eds. Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy. Occasional Paper Number 76, Canadian Wildlife Service. 120 pp.

Green, D. M. 1997. Amphibians in Decline: Canadian Studies of a Global Problem. Herpetological Conservation, No. 1, Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri. 338 pp.

Hall, R. J., and P. F. P. Henry. 1992. Review. Assessing effects of pesticides on amphibians and reptiles: Status and needs. Herpetology Journal 2:65-71.

Halliday, T. R., and M. Tejedo. 1995. Intrasexual selection and alternative mating behaviour. Pp. 419-468 in Heatwole, H., and B. K. Sullivan, eds. Amphibian Biology, Vol. 2. Social Behaviour. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.

Hamilton, H. L. 1941. The biological action of rotenone of fresh water animals. Proceedings of the Iowa Academy of Science 48:467-479.

Hammerson, G. A. 1982. Bullfrog eliminating leopard frogs in Colorado? Herpetological Review 13:115-116.

Hammerson, G. A. 1999. Amphibians and Reptiles in Colorado, 2nd ed. University Press of Colorado and Colorado Division of Wildlife, Niwot, Colorado. 484 pp.

Hecnar, S. J. 1995. Acute and chronic toxicity of ammonium nitrate fertilizer to amphibians from southern Ontario. Environmental Toxicology and Chemistry 14:2131-2137.

Hecnar, S. J., and R. T. M'Closkey. 1997a. The effects of predatory fish on amphibian species richness and distribution. Biological Conservation 79:123-131.

Hecnar, S. J., and R. T. M'Closkey. 1997b. Changes in the composition of a ranid frog community following bullfrog extinction. American Midland Naturalist 137:145-150.

Hecnar, S. J., and R. T. M'Closkey. 1998. Species richness patterns of amphibians in southwestern Ontario ponds. Journal of Biogeography 25:763-772.

Helgen, J., R. G. McKinnell, and M. C. Gernes. 1998. Investigation of malformed northern leopard frogs in Minnesota. Pp. 288-297 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

Hemesath, L. M. 1998. Iowa's Frog and Toad Survey, 1991-1994. Pp. 206-216 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

Hendricks, F. S. 1973. Intestinal contents of *Rana pipiens* Schreber (Ranidae) larvae. Southwestern Naturalist 18:99-101.

Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster. 1994. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D. C. 364 pp.

Heyer, W. R. 1994. Thread bobbins. Pp. 153-155 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D. C. 364 pp.

Hine, R. L., B. L. Les, B. F. Hellmich, and R. C. Vogt. 1975. Preliminary report on leopard frog (*Rana pipiens*) populations in Wisconsin. Wisconsin Department of Natural Resources Research Report No. 81:1-31.

Hine, R. L., B. L. Les, and B. F. Hellmich. 1981. Leopard frog populations and mortality in Wisconsin. Wisconsin Department of Natural Resources Technical Bulletin No. 122:1-139.

Hillis, D. M. 1988. Systematics of the *Rana pipiens* complex: Puzzle and paradigm. Annual Review of Ecology and Systematics 19:39-63.

Hillis, D. M., J. S. Frost, and D. A. Wright. 1983. Phylogeny and biogeography of the *Rana pipiens* complex: A biochemical evaluation. Systematic Zoology 32:132-143.

Holme, J. A., M. Refsnes, and E. Dybing. 1999. Possible carcinogenic risk associated with the production and use of creosote-treated wood. Tidsskrift for den Norske Laegeforening 119:2664-2666.

Hoppe, D. M. 2000. History of Minnesota frog abnormalities: Do recent findings represent a new phenomenon? Journal of the Iowa Academy of Science 107:86-89.

Howard, R. D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution 32:850-871.

Hupf, T. H. 1977. Natural histories of two species of leopard frogs, *Rana blairi* and *Rana pipiens,* in a zone of sympatry in northeastern Nebraska. Unpublished M. S. thesis, University of Nebraska, Lincoln. 125 pp.

Jaeger, R. G. 1980. Microhabitats of a terrestrial forest salamander. Copeia 1980:265-268.

Jaeger, R. G. 1994a. Transect sampling. Pp. 103-107 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D. C. 364 pp.

Jaeger, R. G. 1994b. Patch sampling. Pp. 107-109 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D. C. 364 pp.

Jaeger, R. G. and R. F. Inger. 1994. Quadrat sampling. Pp. 97-102 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D. C. 364 pp.

Jancovich, J. K., E. W. Davidson, J. F. Morado, B. L. Jacobs, and J. P. Collins. 1997. Isolation of a lethal virus from the endangered tiger salamander *Ambystoma tigrinum stebbinsi*. Diseases of Aquatic Organisms 31:161-167.

Johnson, T. R. 1998. Missouri toad and frog calling survey: The first year. Pp. 357-359 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

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

Johnson, P. T. J., K. B. Lunde, and A. R. Blaustein. 2001. *Ribeiroia ondatrae* (Trematoda: Digenea) infection induces severe limb malformations in western toads (*Bufo boreas*). Canadian Journal of Zoology 79:370

Kaplan, H. M., and J. G. Overpeck. 1964. Toxicity of halogenated hydrocarbon insecticides for the frog *Rana pipiens*. Herpetologica 20:163-169.

Kaplan, H. M., and S. S. Glaczenski. 1965. Hematological effects of organophosphate insecticides in the frog (*Rana pipiens*). Life Sciences 4:1213-1219.

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

Kendell, K. 2002. Northern leopard frog reintroduction: Year 3 (2001). Alberta Sustainable Resource Development, Fish and Wildlife Division, Alberta Species at Risk Report No. 42, Edmonton, Alberta. 45 pp.

Koch, E. D., and C. R. Peterson. 1995. Amphibians and Reptiles of Yellowstone and Grand Teton National Parks. University of Utah Press, Salt Lake City, Utah. 188 pp.

Krebs, C. J. 1999. Ecological Methodology, 2nd ed. Benjamin Cummings, Menlo Park California. 620 pp.

Kruse, K. C., and M. G. Francis. 1977. A predation deterrent in larvae of the bullfrog, *Rana catesbeiana*. American Fisheries Society Transactions 106:248-252.

Lamberti, G. A., S. V. Gregory, C. P. Hawkins, R. C. Wildman, L. R. Ashkenas, and D. M. Denicola. 1992. Plant-herbivore interactions in streams near Mt. St. Helens. Freshwater Biology 27:237-247.

Lamoureux, V. S., and D. M. Madison. 1999. Overwintering habitats of radio-implanted green frogs, *Rana clamitans*. Journal of Herpetology 33:430-435.

Landé, S. P., and S. I. Guttman. 1973. The effects of copper sulfate on the growth and mortality rate of *Rana pipiens* tadpoles. Herpetologica 29:22-27.

Lannoo, M. J., K. Lang, T. Waltz, and G. S. Phillips. 1994. An altered amphibian assemblage: Dickinson County, Iowa, 70 years after Frank Blanchard's survey. American Midland Naturalist 131:311-319.

Lannoo, M. J. 1998a. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

Lannoo, M. J. 1998b. Amphibian conservation and wetland management in the upper midwest: A catch-22 for the cricket frog? Pp. 330-339 in M. J. Lannoo, ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

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

Leonard, W. P., K. R. McAllister, and R.C. Friesz. 1999. Survey and assessment of northern leopard frog (*Rana pipiens*) populations in Washington State. Northwestern Naturalist 80:51-60.

Lepage, M., R. Courtois, C. Daigle, and S. Matte. 1997. Surveying calling anurans in Québec using volunteers. Pp. 128-140 in Green, D. M., ed. Amphibians in Decline: Canadian Studies of a Global Problem. Herpetological Conservation Number One. Society for the Study of Amphibians and Reptiles, St. Louis, Missouri. 338 pp.

Linder, G., and B. Grillitsch. 2000. Ecotoxicology of metals. Pp. 325-459 in D. W. Sparling, G. Linder, and C. A. Bishop, eds. Ecotoxicology of Amphibians and Reptiles. SETAC Press, Pensacola, Florida. 877 pp.

Linzey, D. W. 1967. Food of the leopard frog, *Rana p. pipiens*, in central New York. Herpetologica 23:11-17.

Linzey, D. W., and A. H. Wright. 1947. A synoptic key to the salientian eggs of the United States. American Midland Naturalist 37:179-222.

Long, L. E., L. S. Saylor, and M. E. Soule. 1995. A pH/UV-B synergism in amphibians. Conservation Biology 9:1301-1303.

Lynch, J. D. 1978. The distribution of leopard frogs (*Rana blairi* and *Rana pipiens*) (Amphibia, Anura, Ranidae) in Nebraska. Journal of Herpetology 12:157-162.

Madison, D. M. 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. Journal of Herpetology 31:542-552.

Madison, D. M., and L. Farrand. 1997. Habitat use during breeding and emigration in radio-implanted tiger salamanders, *Ambystoma tigrinum*. Copeia 1998:402-410.

Manion, J. J., and L. Cory. 1952. Winter kill of *Rana pipiens* in shallow ponds. Herpetologica 8:32.

Martof, B. 1953. Home range movements of the green frog, *Rana clamitans*. Ecology 34:529-543.

Mathews, K. R., and K. L. Pope. 1999. A telemetric study of the movement patterns and habitat use of *Rana muscosa*, the mountain yellow-legged frog, in a high-elevation basin in Kings Canyon National Park, California. Journal of Herpetology 33:615-624.

Maunder, J. E. 1997. Amphibians of Newfoundland and Labrador: Status changes since 1983. Pp. 93-99 in D. M. Green, ed. Amphibians in Decline: Canadian Studies of a Global Problem, Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri.

Maxell, B. A. 2000. Management of Montana's amphibians: A review of factors that may present a risk to population viability and accounts on the identification, distribution, taxonomy, habitat use, natural history, and the status and conservation of individual species. Report to USFS Region 1, Order Number 43-0343-0-0224. University of Montana, Wildlife Biology Program. Missoula, Montana. 161 pp.

McAlpine, D. F. 1997. Historical evidence does not suggest New Brunswick amphibians have declined. Pp. 117-127 in D. M. Green, ed., Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri.

McAlpine, D. F., and M. D. B. Burt. 1998. Helminths of bullfrogs, *Rana catesbeiana*, green frogs, *R. clamitans*, and leopard frogs, *R. pipiens*, in New Brunswick. Canadian Field Naturalist 112:50-68.

McAlpine, D. F., and T. G. Dilworth. 1989. Microhabitat and prey size among three species of *Rana* (Anura: Ranidae) sympatric in eastern Canada. Canadian Journal of Zoology 67:2244-2252.

McClelland, B. E., and W. Wilczynski. 1989. Release call characteristics of male and female *Rana pipiens*. Copeia 1989:1045-1049.

McCollum, S. A., and J. D. Leimberger. 1997. Predator-induced morphological changes in an amphibian: Predation by dragonflies affects tadpole shape and color. Oecologia 109:615-621.

McLeod, R., and J. E. Gates. 1998. Response of herpetofaunal communities to forest cutting and burning at Chesapeake Farms, Maryland. American Midland Naturalist 139:164-177.

Mennell, L. 1997. Amphibians in southwestern Yukon and northwestern British Columbia. Pp. 107-109 in D. M. Green, ed., Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri.

Merrell, D. J. 1963. Rearing tadpoles of the leopard frog, *Rana pipiens*. Turtox News 41:263-265.

Merrell, D. J. 1965. The distribution of the dominant Burnsi gene in the leopard frog, *Rana pipiens*. Evolution 19:69-85.

Merrell, D. J. 1968. A comparison of the estimated size and the "effective size" of breeding populations of the leopard frog, *Rana pipiens*. Evolution 22:274-283.

Merrell, D. J. 1969. Natural selection in a leopard frog population. Journal of the Minnesota Academy of Science 35:86-89.

Merrell, D. J. 1970. Migration and gene dispersal in *Rana pipiens*. American Zoologist 10:47-52.

Merrell, D. J. 1977. Life history of the leopard frog, *Rana pipiens*, in Minnesota. Bell Museum of Natural History Occasional Papers No. 15:1-23.

Merrell, D. J., and C. F. Rodell. 1968. Seasonal selection in the leopard frog, *Rana pipiens*. Evolution 22:284-288.

Meteyer, C. U., I. K. Loeffler, J. F. Fallon, K. A. Converse, E. Green, J. C. Helgen, S. Kersten, R. Levey, L. Eaton-Poole, and J. G. Burkhart. 2000. Hind limb malformations in free-living northern leopard frogs (*Rana pipiens*) from Maine, Minnesota, and Vermont suggest multiple etiologies. Teratology 62:151-171.

Mierzwa, K. S. 1998. Biogeography of Midwestern Amphibians. Pp. 24-30 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

Milius, S. 2000. New frog-killing disease may not be so new. Science News 157:133.

Miller, J. D. 1978. Observations on the diets of *Rana pretiosa*, *Rana pipiens*, and *Bufo boreas* from western Montana. Northwest Science 52:243-249.

Minton, S. A. 1998. Observations on Indiana amphibian populations: A Forty-five-year overview. Pp. 217-220 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

Morell, V. 1999. Are pathogens felling frogs? Science 284:728-731.

Mosimann, J. E., and G. B. Rabb. 1952. The herpetology of Tiber Reservoir Area, Montana. Copeia 1952:23-27.

Mossman, M. J., L. M. Hartman, R. Hay, J. R. Sauer, and B. J. Dhuey. 1998. Monitoring long-term trends in Wisconsin frog and toad populations. Pp. 169-198 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

Moriarty, J. J. 1998. Status of Amphibians in Minnesota. Pp. 166-168 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

Morin, P. J. 1983. Predation, competition, and the composition of larval anuran guilds. Ecological Monographs 53:119-138.

Mushinsky, H. R. 1985. Fire and the Florida sandhill herpetofaunal community: With special attention to responses of *Cnemidophorus sexlineatus*. Herpetologica 41:333-342.

Nash, R. F., G. G. Gallup, Jr., and M. K. McClure. 1970. The immobility reaction in leopard frogs (*Rana pipiens*) as a function of noise-induced fear. Psychonometric Science 21:155-156.

Noble, G. K., and L. R. Aronson. 1942. The sexual behavior of Anura: The normal mating pattern of *Rana pipiens*. Bulletin of the American Museum of Natural History 80:127-142.

Northern Prairie Wildlife Research Center. 1997. North American Reporting Center for Amphibian Malformations. Jamestown, North Dakota: North Prairie Wildlife Research Center Home Page. http://www.npwrc.usgs.gov/narcam (Version 12, April 2001).

Oldfield, B., and J. J. Moriarty. 1994. Amphibians and Reptiles Native to Minnesota. University of Minnesota Press, Minneapolis, Minnesota. 237 pp.

Orchard, S. A. 1992. Amphibian population declines in British Columbia. Pp. 10-13 in Bishop, C. A., K. E. Pettit, eds. Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy. Occasional Papers of the Canadian Wildlife Service No. 76. 120 pp.

Orr, L., J. Neumann, E. Vogt, and A. Collier. 1998. Status of northern leopard frogs, pickerel frogs and wood frogs, in Illinois. Pp. 83-90 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

Ouellet, M., J. Bonin, J. Rodrigue, J.-L. DesGranges, and S. Lair. 1997. Hindlimb deformities (ectromelia, ectrodactyly) in free-living anurans from agricultural habitats. Journal of Wildlife Diseases 33:95-104.

Pace, A. E. 1974. Systematic and biological studies of the leopard frogs (*Rana pipiens* Complex) of the United States. Miscellaneous Publications of the Museum of Zoology, University of Michigan, No. 148:1-140.

Parrish, J. B., D. J. Herman, and D. J. Reyher. 1996. A Century of Change in Black Hills Forest and Riparian Ecosystems. U.S. Forest Service Agricultural Experiment Station, U.S. Department of Agriculture. South Dakota State University. No. B722. 20 pp.

Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: The problem of separating human impacts from natural fluctuations. Science 253:892-895.

Pechmann, J. H. K., and H. M. Wilbur. 1994. Putting declining amphibian populations in perspective: Natural fluctuations and human impacts. Herpetologica 50:65-84.

Peterson, C. R. 1974. A Preliminary Report on the Amphibians and Reptiles of the Black Hills of South Dakota and Wyoming. Unpublished M. S. Thesis, University of Illinois at Urbana-Champaign, Illinois. 59 pp.

Peterson, C. R., and M. E. Dorcas. 1994. Automated data acquisition. Pp. 47-57 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D. C. 364 pp.

Petranka, J. W. 1994. Response to impact of timber harvesting on salamanders. Conservation Biology 8:302-304.

Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D. C. 587 pp.

Petranka, J. W., M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management 67:135-147.

Petranka, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology 7:363-370.

Phaneuf, D., J. L. DesGranges, N. Plante, and J. Rodrigue. 1995. Contamination of local wildlife following a fire at a polychlorinated biphenyls warehouse in St. Basile le Grand, Quebec, Canada. Archives of Environmental Contamination and Toxicology 28:145-153.

Porter, K. R., and D. E. Hakanson. 1976. Toxicity of mine drainage to embryonic and larval boreal toads (Bufonidae: *Bufo boreas*). Copeia 1976:327-331.

Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky, and K. D. Wells. 2001. Herpetology, 2nd ed. Prentice Hall, Upper Saddle River, New Jersey. 612 pp.

Pounds, J. A., and M. L. Crump. 1994. Amphibian declines and climate disturbance: The case of the golden toad and the harlequin frog. Conservation Biology 8:72-75.

Prudhoe, S., and R. A. Bray. 1982. Platyhelminth Parasites of the Amphibia. Oxford University Press, Oxford, United Kingdom. 217 pp.

Ramotnik, C. A., and N. J. Scott, Jr. 1988. Habitat requirements of New Mexico's endangered salamanders. Pp. 54-63 in Szaro, R. C., K. E. Severson, and D. R. Patton, eds. Management of Amphibians, Reptiles, and Mammals in North America. U. S. D. A. Forest Service General Technical Report RM-166. 458 pp.

Rand, A. S., and G. E. Drewry. 1994. Acoustic monitoring at fixed sites. Pp. 150-153 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D. C. 364 pp.

Raphael, M. G. 1988. Long-term trends in abundance of amphibians, reptiles, and mammals in douglas-fir forests of northwestern California. Pp. 23-31 in Szaro, R. C., K. E. Severson, and D. R. Patton, eds. Management of Amphibians, Reptiles, and Mammals in North America. U. S. D. A. Forest Service General Technical Report RM-166. 458 pp.

Rathbun, G. B., and T. G. Murphey. 1996. Evaluation of a radio-belt for ranid frogs. Herpetological Review 27:187-189.

Raymond, L. R., and L. M. Hardy. 1991. Effects of a clearcut on a population of the mole salamander, *Ambystoma talpoideum*, in an adjacent unaltered forest. Journal of Herpetology 25:509-512.

Reichel, J. D. 1996. Status of amphibians and reptiles in eastern Montana. Intermountain Journal of Sciences 2:57.

Relyea, R. A. 2001a. Morphological and behavioral plasticity of larval anurans in response to different predators. Ecology 82:523-540.

Relyea, R. A. 2001b. The relationship between predation risk and antipredator responses in larval anurans. Ecology 82:541-554.

Relyea, R. A., and E. E. Werner. 2000. Morphological plasticity in four larval anurans distributed along an environmental gradient. Copeia 2000:178-190.

Resetar, A. R. 1998. Locating historical information on amphibian populations. Pp. 379-384 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa. 507 pp.

Richards, C. M. 1958. The inhibition of growth in crowded *Rana pipiens* tadpoles. Physiological Zoology 31:138-151.

Richards, S. J., U. Sinsch, and R. A. Alford. 1994. Radio tracking. Pp. 155-158 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D. C. 364 pp.

Roberts, W. E. 1992. Declines in amphibian populations in Alberta. Pp.14-16 in Bishop, C. A., and K. E. Pettit, eds. Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy. Occasional Papers of the Canadian Wildlife Service No. 76. 120 pp.

Rome, L. C., E. D. Stevens, and H. B. John-Alder. 1992. The influence of temperature and thermal acclimation on physiological function. Pp. 183-205 in M. E. Feder and W. W. Burggren, eds. Environmental Physiology of the Amphibians. University of Chicago Press, Chicago.

Rudolph, D. C., and J. G. Dickson. 1990. Streamside zone width and amphibian and reptile abundance. Southwestern Naturalist 35:472-476.

Rumble, M. A., D. Willis, and B. E. Smith. In press. Wildlife, fish, and herpetofauna of created impoundments in the intermountain west. In Anderson, S., M. McKinstry, and W. Hubert, eds. Palustrine Habitats of the Intermountain West.

Russell, A. P., and A. M. Bauer. 1993. The Amphibians and Reptiles of Alberta. University of Alberta Press, Edmonton, Alberta. 264 pp.

Russell, K. R., D. H. Van Lear, and D. C. Guynn, Jr. 1999. Prescribed fire effects on herpetofauna: Review and Management implications. Wildlife Society Bulletin 27:374-384.

Ryan, R. A. 1953. Growth rates of some ranids under natural conditions. Copeia 1953:73-80.

Schlichter, L. C. 1981. Low pH affects the fertilization and development of *Rana pipiens* eggs. Canadian Journal of Zoology 59:1693-1699.

Scott, N. J., Jr., and B. D. Woodward. 1994. Surveys at breeding sites. Pp. 118-125 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D. C. 364 pp.

Seburn, C. N. L., D. C. Seburn, and C. A. Paszkowski. 1997. Northern leopard frog (*Rana pipiens*) dispersal in relation to habitat. Pp. 64-72 in Green, D. M., ed. Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, Herpetological Conservation Number One. St. Louis, Missouri. 338 pp.

Semlitsch, R. D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology 12:1113-1119.

Semlitsch, R. D., and J. R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 12:1129-1133.

Semlitsch, R. D. 2000a. Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64:615-631.

Semlitsch, R. D. 2000b. Size does matter: The value of small isolated wetlands. National Wetlands Newsletter, January-February 2000:5-13.

Sessions, S. K., R. A. Franssen, and V. L. Horner. 1999. Morphological clues from multilegged frogs: Are retinoids to blame? Science 284:800-802.

Sessions, S. K., and S. B. Ruth. 1990. Explanation for naturally occurring supernumerary limbs in amphibians. Journal of Experimental Zoology 254:38-457.

Sexton, O. J., C. A. Phillips, T. J. Bergman, E. B. Wattenberg, and R. E. Preston. 1998. Abandon not hope: Status of repatriated populations of spotted salamanders and wood frogs at the Tyson Research Center, St. Louis County, Missouri. Pp. 340-344 in Lannoo, M. J., ed. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City. 507 pp.

Sinsch, U. 1997. Postmetamorphic dispersal and recruitment of first breeders in a *Bufo calamita* metapopulation. Oecologia 112:42-47.

Smith, B. E., J. J. Kolbe, and R. S. Ferguson. 1996a. A herpetological survey of Wind Cave National Park, South Dakota. U. S. G. S./Biological Resources Division. Northern Prairie Science Center. 66 pp.

Smith, B. E., D. M. Browning, E. Taylor, R. S. Ferguson, and K. Yturralde. 1996b. Herpetofaunal surveys of the Fall River Ranger District, U. S. Forest Service, southwestern South Dakota and Badlands National Park. U. S. G. S./Biological Resources Division. Northern Prairie Science Center. 27 pp.

Smith, B. E., S. K. Ashton, and R. E. Baum. 1998. Herpetofaunal surveys on the Spearfish-Nemo District, Black Hills National Forest: Preliminary report and recommendations, 1998. Unpublished report submitted to the U. S. D. A. Forest Service, Black Hills National Forest, Spearfish-Nemo District. 27 pp.

Smith-Gill, S. J., and D. E. Gill. 1978. Curvilinearities in the competition equations: An experiment with ranid tadpoles. American Naturalist 112:557-570.

Sparling, D. W. 2000. Ecotoxicology of organic contaminants to amphibians. Pp. 461-494 in D. W. Sparling, G. Linder, and C. A. Bishop, eds. Ecotoxicology of Amphibians and Reptiles. SETAC Press, Pensacola, Florida. 877 pp.

Sparling, D. W., G. Linder, and C. A. Bishop, eds. 2000a. Ecotoxicology of Amphibians and Reptiles. SETAC Press, Pensacola, Florida. 877 pp.

Sparling, D. W., G. Linder, and C. A. Bishop. 2000b. The current status of amphibian and reptile ecotoxicological research. Pp. 1-13 in D. W. Sparling, G. Linder, and C. A. Bishop, eds. Ecotoxicology of Amphibians and Reptiles. SETAC Press, Pensacola, Florida. 877 pp.

Stebbins, R. C. 1985. A Field Guide to Western Reptiles and Amphibians, 2nd ed. Houghton Mifflin Company, Boston, Massachusetts. 337 pp.

Stebbins, R. C., and N. W. Cohen. 1995. A Natural History of Amphibians. Princeton University Press. Princeton, New Jersey. 316 pp.

Stebbins, R. C. 2003. A Field Guide to Western Reptiles and Amphibians, 3rd ed. Houghton Mifflin Company, Boston, Massachusetts.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18-30.

USDA Forest Service. 1994. FSM 5670 R2 Supplement No. 2600-94-2; Region 2 Sensitive Species List. USDA Forest Service, Rocky Mountain Region, Denver, Colorado.

U. S. D. A. Forest Service. 1997. Black Hills National Forest Land and Resource Management Plan. Custer, South Dakota.

USDA Forest Service. 1999. Northern Region Sensitive Species List. USDA Forest Service, Northern Region, Missoula, MT. URL http:// www.fs.fed.us/r1/tes_index.html

U.S. Environmental Protection Agency. 2001. Office of Pesticide Programs Homepage. http://www.epa.gov/pesticides/. (Updated May 18, 2001).

Ultsch, G. R., T. E. Graham, and C. E. Crocker. 2000. An aggregation of overwintering leopard frogs, *Rana pipiens*, and common map turtles, *Graptemys geographica*, in northern Vermont. Canadian Field-Naturalist 114:314-315.

Wassersug, R. J., and K. Hoff. 1985. Kinematics of swimming in anuran larvae. Journal of Experimental Biology 119:1-30.

Waye, H. L. 2001. Teflon tubing as radio transmitter belt material for northern leopard frogs (*Rana pipiens*). Herpetological Review 32:88-89.

Wells, K. D. 1977. The social behaviour of anuran amphibians. Animal Behaviour 25:666-693.

Wells, K. D. 1978. Territoriality in the green frog (*Rana clamitans*): Vocalizations and agonistic behaviour. Animal Behaviour 26:1051-1063.

Welsh, H. H., Jr., and A. J. Lind. 1995. Habitat correlates of the Del Norte salamander, *Plethodon elongatus*, in northwestern California. Journal of Herpetology 29:198-210.

Welsh, H. H., Jr., and L. M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: A case study from California's redwoods. Ecological Applications 8:1118-1132.

Werner, E. E., and K. S. Glennemeier. 1999. Influence of forest canopy cover on breeding pond distributions of several amphibian species. Copeia 1999:1-12.

Werner, J. K., J. Weaselhead, and T. Plummer. 1999. The accuracy of estimating eggs in anuran egg masses using weight or volume measurements. Herpetological Review 30:30-31.

Whitaker, J. O., Jr. 1961. Habitat and food of mousetrapped young *Rana pipiens* and *Rana clamitans*. Herpetologica 17:174-179.

Wilbur, H. M. 1997. Experimental ecology of food webs: Complex systems in temporary ponds. Ecology 78:2279-2302.

Williamson, J. E., and T. S. Hayes. 2000. Water-quality characteristics for selected streams in Lawrence County, South Dakota, 1988-92. Water Resources Investigations Report 00-4220. 137 pp.

Woodward, B. D. 1982. Tadpole competition in a desert anuran community. Oecologia 54:96-100.

Woodward, B. D. 1983. Predator-prey interactions and breeding-pond use of temporary-pond species in a desert anuran community. Ecology 64:1549-1555.

Wright, A. H., and A. A. Wright. 1949. Handbook of Frogs and Toads. Comstock Publishing. Ithaca, New York. 640 pp.

Wright, A. H. 1914. North American Anura: Life-histories of the Anura of Ithaca, New York. Carnegie Institution, Washington, Publication 197:1-98.

Wyman, R. L., ed. 1991. Global Climate Change and Life on Earth. Chapman and Hall, New York.

Zimmerman, B. 1994. Audio strip transects. Pp. 92-97 in Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D. C. 364 pp.