Spring 2012

A CONCEPTUAL MODEL TO FACILITATE AMPHIBIAN CONSERVATION IN THE NORTHERN GREAT PLAINS

David M. Mushet
Northern Prairie Wildlife Research Center, dmushet@usgs.gov

Ned H. Euliss Jr.
U.S. Geological Survey, ceuliss@usgs.gov

Craig A. Stockwell
North Dakota State University - Main Campus, craig.stockwell@ndsu.edu

Great Plains Research 22 (Spring 2012):45–58
2012 Published by the Center for Great Plains Studies, University of Nebraska–Lincoln

A CONCEPTUAL MODEL TO FACILITATE AMPHIBIAN CONSERVATION IN THE NORTHERN GREAT PLAINS

David M. Mushet

U.S. Geological Survey
Northern Prairie Wildlife Research Center
8711 37th Street SE
Jamestown, ND 58401
dmushet@usgs.gov
and
Environmental and Conservation Science Program
North Dakota State University
Fargo, ND 58105

Ned H. Euliss, Jr.

U.S. Geological Survey
Northern Prairie Wildlife Research Center
8711 37th Street SE
Jamestown, ND 58401
ceuliss@usgs.gov

and

Craig A. Stockwell

Department of Biological Sciences and Environmental and Conservation Science Program
North Dakota State University
Fargo, ND 58105
craig.stockwell@ndsu.edu

ABSTRACT—As pressures on agricultural landscapes to meet worldwide resource needs increase, amphibian populations face numerous threats including habitat destruction, chemical contaminants, disease outbreaks, wetland sedimentation, and synergistic effects of these perturbations. To facilitate conservation planning, we developed a conceptual model depicting elements critical for amphibian conservation in the northern Great Plains. First, we linked upland, wetland, and landscape features to specific ecological attributes. Ecological attributes included adult survival; reproduction and survival to metamorphosis; and successful dispersal and recolonization. Second, we linked ecosystem drivers, ecosystem stressors, and ecological effects of the region to each ecological attribute. Lastly, we summarized information on these ecological attributes and the drivers, stressors, and effects that work in concert to influence the maintenance of viable and genetically diverse amphibian populations in the northern Great Plains. While our focus was on the northern Great Plains, our conceptual model can be tailored to other geographic regions and taxa.

Key Words: amphibian conservation, adaptive management, conceptual models, ecological attributes, ecological effects, ecosystem drivers, ecosystem stressors

INTRODUCTION

Amphibian populations have been declining worldwide largely due to anthropogenic habitat alteration (Blaustein and Wake 1990; Wyman 1990; Pechmann et al. 1991; Alford and Richards 1999; Kiesecker et al. 2001; Green 2003). In the northern Great Plains, habitat alteration has consisted primarily of wetland and grassland conversion to cropland. Approximately half the wetlands in the northern Great Plains have been lost (Tiner 1984; Dahl 1990) and 34% of the upland habitats have been

Manuscript received for review, March 2011; accepted for publication, August 2011.

converted to agricultural production (Euliss et al. 2006). Conversely, over 2,200,000 ha of wetland and grassland habitats have been restored in the northern Great Plains (Gleason et al. 2008), but many of these restored habitats are vulnerable for conversion back to agricultural production due to rising commodity prices. In order to conserve amphibian populations within agricultural landscapes, we need a better understanding of habitats important to amphibian populations in the northern Great Plains. For amphibians, these habitats consist principally of wetland, upland, and landscape features that influence a species' viability through survival, reproduction, and successful dispersal.

Conceptual ecological models are effective tools for summarizing and organizing our current understanding of ecosystem structure and function (Heemskerk et al. 2003). Through the use of illustrations, conceptual models provide a means of communicating scientific thought by visualizing the linkages among major ecosystem drivers and stressors, the ways they affect ecological outcomes, and their relationship to specific habitat components that can be purposely manipulated by management. Hence, conceptual models are not ends in themselves but are effective for developing conservation plans or establishing new policy. Specifically, conceptual models can aid communication, inquiry, and consensus building among scientists, managers, policy makers, and a diverse public (Maddox et al. 1999; Ogden et al. 2005). As an example, Ogden et al. (2005) introduce a set of conceptual models as a tool to facilitate efforts to design and assess the Everglades restoration program. To facilitate amphibian conservation and management in the northern Great Plains, we developed a similar conceptual model to better inform decision makers' conservation plans for the region's amphibian populations. Our model links important ecosystem drivers, ecosystem stressors, ecological effects, and ecological attributes (Fig. 1) influencing amphibian population viability and genetic diversity in the northern Great Plains.

To minimize semantic confusion, we followed Ogden et al. (2005) in defining ecosystem drivers, stressors, effects, and attributes. They define *ecosystem drivers* as major natural and anthropogenic forces occurring outside a system that have large-scale influence on that system. For instance, drivers of amphibian populations in the northern Great Plains are principally associated with continental and regional climate cycles, and economic or political factors that encourage or discourage habitat alteration. *Ecosystem stressors* are changes brought about by the drivers that cause changes in physical, chemical, or biotic components of an ecosystem. Droughts, tillage of soils, wetland drainage, and use of agrichemicals are examples of typical ecosystem stressors faced by amphibian populations in the northern Great Plains. *Ecological effects* are physical, chemical, or biological responses to the stressors. As an example, increased runoff, increased sedimentation, altered water depths, and altered plant communities can all be ecological effects of soil tillage (an ecosystem stressor). Lastly, *ecological attributes* are the affected components of an ecosystem that can be linked to specific processes important for system sustainability. Thus, in the example above, the effects of tillage can result in reduced dispersal and recolonization success. This ecological attribute influences the viability and genetic diversity of amphibian populations.

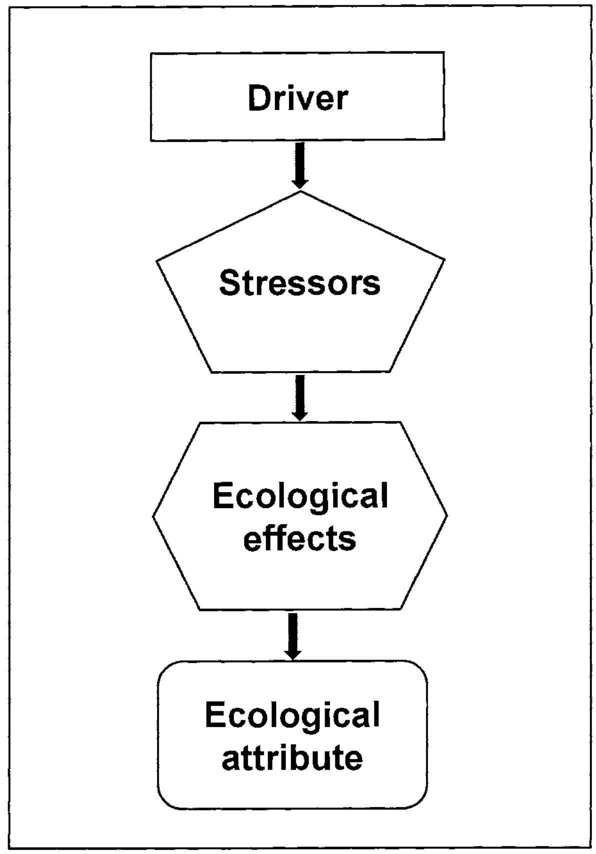

Figure 1. Simplified diagram depicting linkages between a driver and attribute through stressors and their ecological effects (modified from Ogden et al. 2005).

MODEL DESIGN AND METHODS

Tradeoffs between model generality and model realism affect the ability of a single model to adequately describe an entire system or even a part of a system (Maddox et al. 1999). The generality needed to make a model applicable to an entire region would by necessity focus on broad-scale ecosystem drivers while providing few details of intricate connections. However, to obtain realism, considerable details are needed to identify important connections. Here, we attempted to find a compromise between model generality and realism through use of a two-stage process. First we used existing literature to develop a generalized model that identifies key habitat components and ecological attributes affecting amphibian populations in the northern Great Plains (Fig. 2). Using the ecological attributes as end points, we then defined linkages to major natural and anthropogenic ecosystem drivers through the identification of ecosystem stressors and their ecological effects. We organized these drivers, stressors, effects, and ecological attributes into a second, more detailed model allowing for the visualization of important linkages (Fig. 3). By linking major natural and anthropogenic drivers to key ecological attributes responsible for sustaining diverse amphibian populations in the northern Great Plains, we obtained a clearer understanding of the effects of driver-induced stressors and thus potential impacts on amphibian populations.

HABITAT COMPONENTS IMPORTANT TO NORTHERN GREAT PLAINS AMPHIBIANS

Conditions of wetlands and uplands, and the spatial arrangement of wetlands and uplands at the landscape scale, exert a synergistic influence on amphibian conservation in the northern Great Plains (Fig. 2). Amphibians use wetlands primarily for reproduction. Within wetlands, survival of eggs and larvae to metamorphosis is necessary for continued persistence in an area. However, these breeding wetlands are not spatially independent, and the production of dispersers is needed to maintain viable (Semlitsch 2000) and genetically diverse populations (Wilbur 1980). Water quality, hydroperiod, water depth, and biotic interactions (i.e., predation, competition, parasitism, and disease) affect reproduction and survival of amphibians in the wetland habitat (Semlitsch 2000).

Upland habitats contribute to the survival of adults through summer months. Important habitat components of uplands include vegetative cover, condition of substrates, and the invertebrate food resources they provide (Semlitsch 2000). Amphibian survival through winter is dependent upon components of overwintering habitat within wetlands (e.g., water depth) or uplands (e.g., insulation provided by snow or vegetative biomass), according to which amphibian species is being considered (Lannoo 2005).

At a landscape scale, density and diversity of suitable wetland habitats and the condition of the habitats between wetlands significantly affect dispersal and recolonization success (Semlitsch 2000). Thus, wetland, upland, overwintering, and landscape components can be linked to ecological attributes including reproduction and survival to metamorphosis, survival of adults, and successful dispersal and recolonization (Fig. 2).

Wetland Habitats

Amphibians of the northern Great Plains use wetland habitats primarily for mating, egg survival, and larval growth. To maintain viable amphibian populations, adequate numbers of juveniles must be produced to sustain adult breeding populations, rescue local populations, and recolonize areas where populations have become extirpated (Gill 1978). Within wetlands, hydroperiod and biotic interactions (i.e., predation, competition, parasitism, and disease) work in concert to influence the numbers of juveniles produced (Pechmann et al. 1989; Semlitsch et al. 1996).

Both extremely temporary wetlands (i.e., those with hydroperiods of less than 30 days) and permanent wetlands (i.e., those with hydroperiods greater than 1 year) are used by fewer amphibian species than wetlands with intermediate hydroperiods (Heyer et al. 1975; Wilbur 1980). If wetlands dry too quickly, only species with rapid rates of metamorphosis can occur. Additionally, inter- and intraspecific competition for food resources can reduce larval developmental rates, thereby lengthening the aquatic portion of life cycles and increasing vulnerability to desiccation in short-hydroperiod wetlands (Collins and Cheek 1983; Wilbur 1987; Newman 1987; Pfennig 1990; Wilbur and Fauth 1990). Likewise, if a wetland is too permanent, it can become populated with predators (especially fish), which can reduce or eliminate larvae of species that lack antipredator traits (Caldwell et al. 1980; Morin 1986; Kats et al. 1988; Tyler et al. 1998). The diversity and abundance of amphibians in and around wetlands can be greatly impacted by either increasing or decreasing the number of days a wetland holds water (Pechmann et al. 1989).

Wetland water quality can also have a significant impact on amphibian population processes, including egg development and larval survival (Boyer and Grue 1995). For instance, increased sedimentation rates or importation of chemical contaminants can affect amphibian egg survival, larval growth, and successful metamorphosis of young-of-the-year (Boyer and Grue 1995). In agricultural

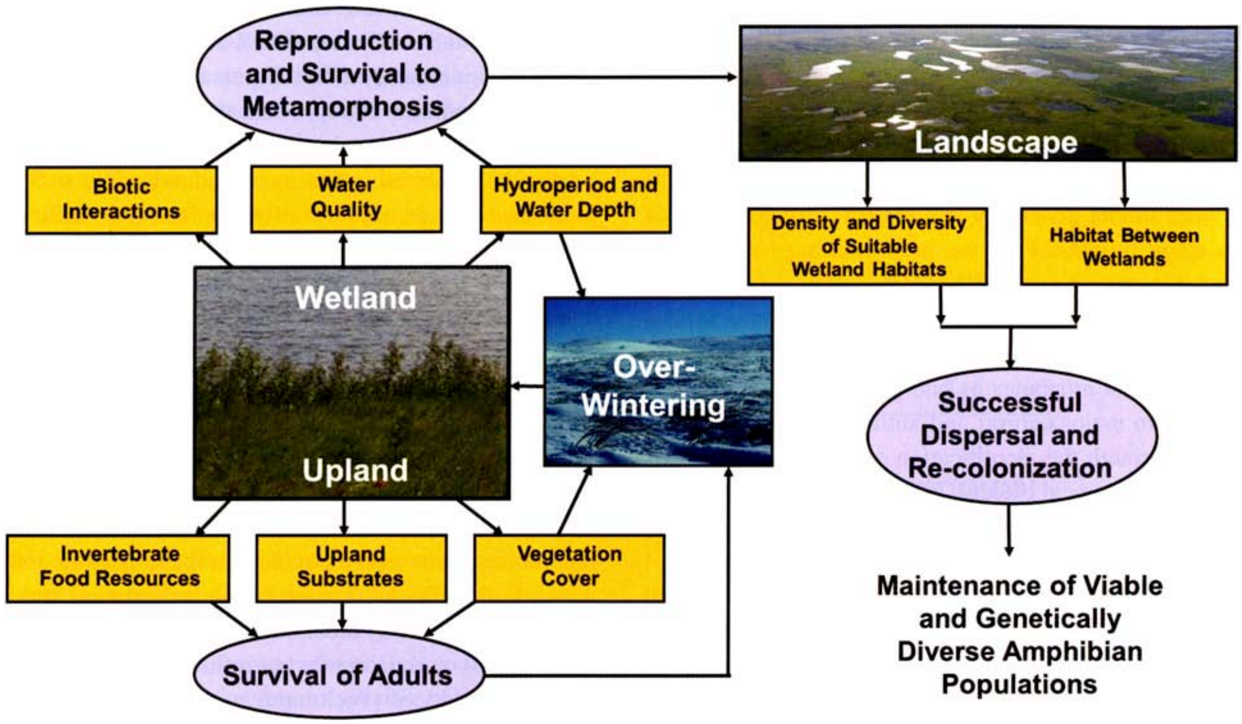

Figure 2. A generalized model depicting connections between habitats (photos), key life-history attributes (ovals), and ecosystem components (rectangles). These lead to maintenance of viable and genetically diverse populations of amphibians in the northern Great Plains.

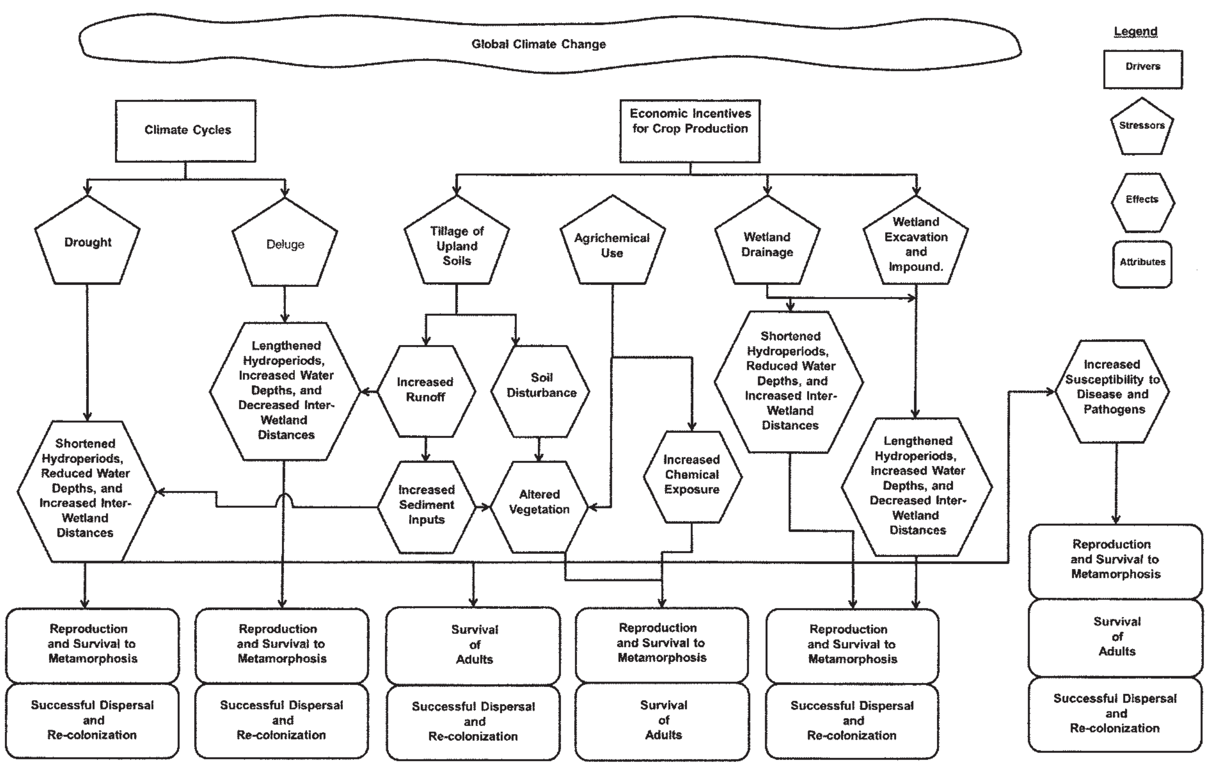

Figure 3. A conceptual model relating key drivers to ecological attributes important to amphibians in the northern Great Plains. Global climate change has the potential to affect both major drivers and therefore all stressors, effects, and life-history attributes. Thus, it is displayed as a cloud overarching the entire model.

areas such as the northern Great Plains, water quality can be an especially contentious issue (e.g., Hayes 2004) due to the potential negative impacts of agrichemicals on water quality and the dependency of the region's agricultural productivity on the use of vast quantities of these chemicals. Further, synergistic interactions of hydroperiod, predation, competition, and water quality can play an important role in amphibian population dynamics, persistence, and community structure (Wellborn et al. 1996; Semlitsch 2000).

Upland Habitats

With the exception of mudpuppies (*Necturus maculosus*), all amphibians of the northern Great Plains have complex life cycles that require both aquatic and terrestrial habitats (Wilbur 1980). Juveniles and adults live in the terrestrial habitat for much of the year (Madison 1997; Semlitsch 1998), where they feed on rich invertebrate food resources found in the upland vegetation (Stebbins and Cohen 1995). Survival in terrestrial habitats is key to ensuring viable populations (Semlitsch 2000). Many agricultural production activities impact uplands and thus adult survival probability (Gray et al. 2004a).

Amphibians can be directly exposed to harmful levels of agricultural pesticides in terrestrial habitats (Semlitsch 2000). Additionally, pesticides can directly affect both native plant and invertebrate communities by killing both target and nontarget species, altering natural food web dynamics important to amphibians. Soil cultivation can reduce live and detrital vegetation that functions as foraging, retreat, and burrow sites for amphibians (Dodd 1996; deMaynadier and Hunter 1998; Herbeck and Larsen 1999; Naughton et al. 2000). Further, cultivation can alter wetland habitats through increased sedimentation (Gleason and Euliss 1998) and water-level fluctuations (Euliss and Mushet 1996).

Overwintering Habitats

Winters in the northern Great Plains deserve special attention because overwintering strategy is a primary factor influencing amphibian distribution and abundance. To overwinter in the northern Great Plains, amphibians rely primarily on behavioral avoidance or physiological mechanisms. Species that behaviorally avoid freezing can be further subdivided into two groups, burrowers and underwater overwinterers. Burrowers, which include the plains spadefoot (*Spea bombifrons*), all the region's toad species (*Anaxyrus* spp.), and tiger salamanders (*Ambystoma* spp.), avoid freezing conditions by burrowing below the frost line in upland habitats (Lannoo 2005). In addition to digging their own burrows, some species have been recorded making use of preexisting burrows where available (e.g., Kolbe et al. 2002).

Amphibians that overwinter underwater avoid freezing temperatures by moving to deep water bodies that do not solidly freeze. The northern leopard frog (*Lithobates pipiens*) overwinters underwater in the northern Great Plains. However, ice thicknesses can approach 1 m in midwinter (Barica 1979), making shallow wetlands unsuitable because they freeze solid to the substrate in most winters. The distribution and abundance of suitable overwintering sites for northern leopard frogs can have a marked influence on the distribution of this species.

Lastly, some amphibian species (e.g., wood frogs [*Lithobates sylvatica*], boreal chorus frogs [*Pseudacris maculata*]) rely primarily on physiological means to survive winters (for a review see Storey and Storey 1992). Freeze-tolerant species transport sugars, primarily from their livers, into cells throughout their bodies, which prevents the destructive and lethal formation of ice crystals within cells, even while the extracellular fluids surrounding cells freeze solidly (Lee et al. 1992). The ability of the wood frog to not only resist but also tolerate freezing has allowed this species to occur in areas farther north than any other North American amphibian species (Lannoo 2005).

Landscape Characteristics

At the landscape scale, amphibians often can be characterized as exhibiting a metapopulation structure. Amphibian metapopulations are influenced by the number of juveniles dispersing and the probability that an individual will successfully reach and reproduce in a new breeding habitat (Hanski and Gilpin 1991; Sjögren 1991; Gibbs 1993). However, metapopulation spatial structure can be impacted by wetland drainage, which has substantially reduced the number and density of wetlands in agricultural landscapes (Tiner 1984; Dahl 1990; Dahl and Johnson 1991; Findlay and Houlahan 1997; Knutson et al. 1999; Kolozsvary and Swilhart 1999; Lehtinen et al. 1999; Gray et al. 2004b). Conservation programs that increase the number and landscape connectivity of wetlands are critical for conserving sustainable metapopulations. Increases in wetland numbers ultimately reduce interwetland distances, thereby increasing the likelihood for successful dispersal. Successful dispersal is especially important as populations frequently become extirpated due to persistent drought or localized climate variation (Dodd 1993; Semlitsch et al. 1996; Lannoo 1998).

Understanding the spatial and temporal dynamics of amphibian metapopulations is critical to evaluating how populations respond to anthropogenic as well as natural disturbance. In most amphibian metapopulation studies, the breeding pond is considered as the basic spatial unit used to delineate subpopulations of the larger metapopulation (e.g., Gill 1978; Sjögren 1991; Sjögren-Gulve 1994; Edenhamn 1996; Hecnar and M'Closkey 1996; Skelly and Meir 1997; Trenham 1998). Interpopulation movement, population dynamics, and genetic structure are then assessed based on the delineated subpopulations. However, this "ponds-as-patches" view of amphibian metapopulations may present an oversimplification of amphibian spatial dynamics that can lead us to lose focus on other habitat components critical to amphibian conservation and metapopulation dynamics (Marsh and Trenham 2001). The adults of most pond-breeding amphibians spend the majority of their lives away from breeding ponds in terrestrial habitats (Wilbur 1984). Additionally, some amphibian species use different wetland types over the course of their life cycles. Aggregations of breeding adults at individual ponds may not represent distinct subpopulations (Marsh and Trenham 2001), and thus, breeding ponds may not be the spatial unit best suited for evaluating metapopulation dynamics.

Terrestrial habitat between wetlands also is a key habitat component influencing juvenile dispersal success (Semlitsch 2000). Although little information is available on the dispersal of amphibians through terrestrial habitats, it is likely that implementation of conservation plans that maintain continuous natural habitat cover or corridors between neighboring wetlands would reduce risks to predation, desiccation, and starvation of dispersers. In addition, the spatial distribution of overwintering habitat can be important. For example, wetlands that do not freeze solidly are critical to overwintering northern leopard frogs, especially during drought, when water depths are reduced. The spatial distribution of such "drought refugia" can affect population dynamics of this species for several years following droughts (Mushet 2010).

DRIVERS, STRESSORS, AND EFFECTS

In the northern Great Plains, major drivers affecting amphibian populations include climate cycles and economic incentives for crop production. These drivers can be linked to ecological attributes important to the maintenance of viable and genetically diverse amphibian populations through ecosystem stressors and their ecological effects (Fig. 3). Here we list ecosystem stressors tied to these major drivers and provide details on their ecological effects on amphibians.

Interannual Climate Variation

In the northern Great Plains, 10- to 20-year precipitation cycles include periods of drought (Woodhouse and Overpeck 1998) alternating with periods of average or above average rainfall (Duvick and Blasing 1981; Karl and Koscielny 1982; Diaz 1983; Karl and Riebsame 1984; Diaz 1986; Winter and Rosenberry 1998). During years of drought, wetlands in the northern Great Plains have severely shortened hydroperiods resulting in decreased wetland water depths and in some cases complete desiccation of wetlands. During persistent periods of above-average precipitation, wetlands become more permanent and fish may become established, resulting in degradation of their value as amphibian breeding sites (Semlitsch 2000). Most wetlands in the northern Great Plains were historically fish-free due to seasonally ephemeral water conditions, cyclical droughts, isolation from other wetland and riverine systems, and extreme temperatures that froze wetlands solid during winter (Peterka 1989). However, consolidation drainage, excavation of dugouts within wetlands for cattle watering, connection of wetlands through artificial drainage networks, and extended periods of above-normal precipitation all have led to more favorable conditions for fish in many of the region's wetlands. Further, active movement of fish into and among wetlands by commercial bait dealers and fishery managers has greatly expanded the presence of fish within the region's wetlands. Predatory fish feed directly upon amphibian larvae, many of which lack natural defenses to predators given the fishless habitats in which they evolved (Kats et al. 1988). Additionally, planktivorous fish can reduce the abundance of large filter-feeding invertebrates in lakes, leading to turbid waters (Spencer and King 1984; Hanson and Butler 1990) that slow the growth of submerged hydrophytes (Hanson and Butler 1990). These hydrophytes provide structure for epiphytic algae, the food base for anuran larvae. Thus, amphibian assemblages have been found to vary greatly between wetlands with and without fish (Kats et al. 1988; Hecnar and M'Closkey 1996).

Wetland Drainage

Wetland drainage in the northern Great Plains can have ecological effects similar to those expressed during periods of natural drought (i.e., significantly reducing hydroperiod length, often to the point that the wetlands can no longer provide for reproduction of amphibians). However, wetland drainage can also effectively lengthen the hydroperiod of lower-elevation terminal wetlands into which other wetlands have been drained, potentially mimicking the ecological effects expressed during natural periods of abundant precipitation (Fig. 3). Additionally, the increased connectivity among wetlands due to the creation of artificial drainage networks allows for the increased movement of aquatic organisms, including fish, among wetlands, having potential negative impacts on amphibians. Thus, when we consider the effects of wetland drainage on amphibians of the northern Great Plains, we must also take into account not only the loss of wetlands from drainage but also the effect of drainage water on wetlands receiving it and also the increased interconnectivity among wetlands.

Tillage of Upland Soils

Conversion of grasslands to agriculturally productive croplands in the northern Great Plains has fundamentally changed the nature of the landscape in which the region's amphibians exist. For example, the dominance of agriculture has resulted in an increase in the import of sediments from surrounding uplands into wetland basins (Adomaitis et al. 1967; Martin and Hartman 1987; Gleason 1996; Gleason and Euliss 1998; Gleason 2001). This chronic filling of wetlands has resulted in altered water depths and storage volumes (Gleason and Euliss 1998; Gleason 2001). Chronic reduction in depth has effectively shortened the hydroperiod and as a consequence has reduced the number and distribution of overwintering refuge sites for the northern leopard frog. Sedimentation has been shown to influence the composition of the plant and invertebrate communities (Jurik et al. 1994; Wang et al. 1994; Gleason and Euliss 1998; Gleason et al. 2003), which can alter food web dynamics important to amphibians (Stebbins and Cohen 1995).

Agrichemical Use

Amphibian populations of the northern Great Plains are affected by both inorganic and organic contaminants. Rouse et al. (1999) reported that nitrate in concentrations found in many surface waters is one of the most widespread contaminant threats to North American amphibians. Nitrogen from nitrogen-based fertilizers and livestock waste accumulates in wetlands (Goolsby et al. 1991) where it typically occurs in the form of nitrate. Nitrate at concentrations found in many agricultural wetlands (>1 mg/L) has been shown to cause both acute and toxic effects in amphibians (Berger 1989; Baker and Waights 1993, 1994; Bishop et al. 1999). Agricultural fertilization can also lead to the accumulation of phosphates in wetlands, which can affect amphibians by enhancing snail populations, the intermediate hosts of many amphibian parasites.

Amphibians are also often exposed to a diverse array of organic agricultural pesticides, which can have significant effects on amphibian populations (Bishop 1992; Hall and Henry 1992; Berrill et al. 1993, 1997; Smith 2001; Hayes 2004; Howe et al. 2004; Relyea 2005a, 2005b) and their aquatic food resources (Relyea 2005a, 2009). Studies have shown even extremely low concentrations of pesticides such as atrazine can have important effects on amphibians (e.g., 0.1 ppb for atrazine, Hayes et al. 2003). Additionally, multiple agricultural chemicals can act synergistically in aquatic environments (Howe et al. 1998; Relyea 2004a, 2009), and these chemicals can also act synergistically with predatory stress (Boone and Semlitsch 2001; Relyea 2004b; Rohr et al. 2006). Given these ecological effects, conservation efforts should include mechanisms for reducing exposure of amphibians to these chemicals.

Wetland Excavation and Impoundment

In efforts to increase the agricultural and waterfowl productivity of drier portions of the northern Great Plains in the west, thousands of wetlands with relatively long hydroperiods have been created primarily by damming low-order surface flows (Ruwaldt et al. 1979; Willis 2001) or excavating existing wetlands (Euliss and Mushet 2004) (Fig. 4). Excavated and impounded wetlands often are stocked with predatory fish that can have a negative impact on amphibian communities. As with natural climate cycles and wetland drainage, wetlands that are excavated or impounded will have altered hydroperiods, which in turn can either favor or disfavor certain amphibian species (Fig. 3). As an example, Euliss and Mushet (2004) documented an increase in the distribution and abundance of tiger salamanders across western North Dakota in response to altered wetland hydroperiods. However, increases in this and other predatory species (e.g., predatory aquatic insects) have the potential to negatively affect amphibian species adapted to the naturally short hydroperiods of this region. Additionally, natural barriers that once existed in the form of great distances between permanent water sources may have been broken down by the abundance of newly created water sources on the region's landscape.

Figure 4. A natural wetland habitat (top) and an excavated and impounded wetland (bottom) in western North Dakota.

DISEASE AND PATHOGENS

All the ecosystem stressors and ecological effects discussed above can contribute to increased susceptibility of amphibians to disease and pathogens (Fig. 3). Infectious disease such as *Ranavirus* (Hyatt et al. 2000) and chytrid fungus (*Batrachochytrium dendrobatidis*) (Annis et al. 2004) is one of the contributing factors to worldwide declines of amphibian populations (Crawshaw 1992; Daszak et al. 1999; Collins et al. 2001; Kiesecker et al. 2001; Collins et al. 2003). *Ranavirus* is a lethal pathogen that affects both amphibians and fish, and therefore it has been suggested that fish may serve as reservoirs for amphibian viruses of this genus (Bollinger et al. 1999). Once established in an amphibian population, *Ranavirus* can persist through intraspecific reservoirs in the absence of fish (e.g., terrestrial adult amphibians may serve as a reservoir reinfecting larval populations in wetlands) and cause recurrent die-offs (Brunner et al. 2004). *Ranavirus* outbreaks have been implicated in several large-scale die-offs of tiger salamanders, northern leopard frogs, and wood frogs in the northern Great Plains (Bollinger et al. 1999; National Wildlife Health Center 2001; Green et al. 2002).

CLIMATE CHANGE

Global climate change adds a new dimension of complication affecting multiple aspects of the conservation and management of amphibians in the northern Great Plains. Climate change will likely affect all the drivers, stressors, effects, and ecological attributes previously discussed (Fig. 3). For instance, extended droughts are expected under various climate change models (Schneider et al. 2007), which will likely result in severely reduced numbers of drought refugia for the northern leopard frog. Thus, climate change scenarios should also be considered by researchers, policy makers, and managers as they examine management practices that could impact amphibian populations. Will key habitat components shift in location or function due to changing frequency of severe events (Johnson et al. 2005; Neimuth et al. 2010)? How will changes in precipitation patterns affect hydroperiods of amphibian breeding wetlands (Johnson et al. 2010)? Will warmer temperatures allow additional diseases to become established in the northern Great Plains? These are just a few of the questions that will need to be considered, and any conservation plan developed for amphibians in the region or elsewhere should address adaptive mechanisms for dealing with the largely unknown effects of a changing climate. Only through the use of conservation plans that have mechanisms for detecting and adapting actions to changing environmental conditions can these plans provide for the persistence of populations given uncertain environmental futures.

CONCLUSIONS

The conversion of the northern Great Plains to support agricultural production has great implications for the conservation of the region's amphibians. The majority of the land within the northern Great Plains is privately owned and managed, and thus in most cases monetary decisions drive the decision-making process. While changes associated with dynamic commodity markets may seem daunting to the manager charged with the task of maintaining or improving amphibian populations, the conceptual models described here reveal significant opportunities to influence vast tracts of the landscape through the implementation of federal and state conservation programs. In short, conservation programs on private lands are critical in amphibian conservation efforts in the northern Great Plains. As an example, the Conservation Reserve Program (CRP) of the U.S. Department of Agriculture (USDA) Farm Service

Agency helps to maintain perennial cover on 2.5 million acres of land in North Dakota alone. This incentive to return croplands to grasslands stops the tillage of soils in areas enrolled in the program and greatly reduces agrichemical usage. An examination of linkages identified in Figure 3 shows that in addition to the positive benefits of reduced sediment inputs into wetland habitats and reduced exposure of amphibians to chemicals, changing the upland plant community from annual crops to perennial vegetation creates intact upland habitat for foraging adult and dispersing juvenile amphibians, and provides numerous options for amphibians seeking overwinter cover. However, further examination of this model also reveals that halting the tillage of upland soils may lead to a decrease in runoff water entering wetland basins. Thus, if sediment inputs have been substantial prior to restoration, returning uplands surrounding a wetland to grassland may result in substantial drying of that wetland. Such a scenario was documented by van der Kamp et al. (1999) when wetlands within an area were unintentionally dried as a result of converting croplands to perennial grasslands. Thus, if maintaining water depth for a particular species is identified as a management goal (e.g., to maintain overwintering habitat for northern leopard frogs), a manager may need to consider the removal of excessive accumulations of sediments from wetlands to mitigate for decreased water inputs. Returning degraded wetlands to their original depths through sediment removal would also help restore original hydroperiods, another effect identified by an examination of our model (Fig. 3).

The conceptual models described here are designed to facilitate conservation of viable and genetically diverse amphibian populations in the northern Great Plains by helping to focus communication among scientists, managers, and policy makers through the visual depiction of linkages between major system drivers, stressors, effects, and ecological attributes important to the region's amphibians. Our models also highlight the need to consider multiple factors and their linkages in efforts to conserve amphibian populations in the region. Given that the needs of amphibians vary by species, care should be taken to identify potential and synergistic effects on multiple species. Conceptual models such as those presented here can facilitate these efforts. Additionally, identification of ecosystem drivers and stressors and their effects on ecological attributes of amphibians will enhance our ability to allow for changes in conservation and management actions in response to an uncertain future.

ACKNOWLEDGMENTS

We greatly appreciate support received for this effort from the U.S. Department of Agriculture's Natural Resources Conservation Service Conservation Effects Assessment Project (CEAP–Wetlands). We also thank Sharon Kahara and Robert Newman for providing helpful reviews of earlier versions of this manuscript.

REFERENCES

Adomaitis, V.A., H.A. Kantrud, and J.A. Shoesmith. 1967. Some chemical characteristics of aeolian deposits of snow-soil on prairie wetlands. *Proceedings of the North Dakota Academy of Science* 21:65–69.

Alford, R.A., and S.J. Richards. 1999. Global amphibian declines: A problem in applied ecology. *Annual Review of Ecology and Systematics* 30:133–65.

Annis S.L., F.P. Dastoor, H. Ziel, P. Daszak, and J.E. Longcore. 2004. A DNA-based assay identifies *Batrachochytrium dendrobatidis* in amphibians. *Journal of Wildlife Diseases* 40:420–28.

Baker, J.M., and V. Waights. 1993. The effects of sodium nitrate on the growth and survival of toad tadpoles (*Bufo bufo*) in the laboratory. *Herpetology Journal* 3:147–48.

Baker, J.M., and V. Waights. 1994. The effects of nitrate on tadpoles of the tree frog (*Litoria caerulea*). *Herpetology Journal* 4:106–8.

Barica, J. 1979. *Some Biological Characteristics of Plains Aquatic Ecosystems and Their Effect on Water Quality.* 1979 PARC Symposium, Regina, SK, Canada.

Berger, L. 1989. Disappearance of amphibian larvae in the agricultural landscape. *Ecology International Bulletin* 17:65–73.

Berrill, M., S. Bertram, and B. Pauli. 1997. Effects of pesticides on amphibian embryos and larvae. *Herpetological Conservation* 1:233–45.

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* 12:525–39.

Bishop, C.A. 1992. The effects of pesticides on amphibians and the implications for determining causes of declines in amphibian populations. *Canadian Wildlife Service, Occasional Paper* 76:67–70.

Bishop, C.A., N.A. Mahoney, J. Struger, P. Ng, and K.E. Pettit. 1999. Anuran development, density and diversity in relation to agricultural activity in the Holland River watershed, Ontario, Canada

(1990–1992). *Environmental Monitoring and Assessment* 59:21–43.

Blaustein, A.R., and D.B. Wake. 1990. Declining amphibian populations: a global phenomenon? *Trends in Ecology and Evolution* 5:203–4.

Bollinger, T.K., J. Mao, D. Schock, R.M. Brigham, and V.G. Chinchar. 1999. Pathology, isolation, and preliminary molecular characteristics of a novel Iridovirus from tiger salamanders in Saskatchewan. *Journal of Wildlife Diseases* 35:413–29.

Boone, M.D., and R.D. Semlitsch. 2001. Interactions of an insecticide with larval density and predation in experimental amphibian communities. *Conservation Biology* 15:228–38.

Boyer, R. and C.E. Grue. 1995. The need to develop water quality criteria for frogs. *Environmental Health Perspectives* 103:352–57.

Brunner, J.L., D.M. Schock, E.W. Davidson, and J.P. Collins. 2004. Intraspecific reservoirs: complex life history and the persistence of a lethal ranavirus. *Ecology* 560–66.

Caldwell, J.P., J.H. Thorp, and T.O. Jervey. 1980. Predator-prey relationships among larval dragonflies, salamanders, and frogs. *Oecologia* 46:285–89.

Collins, J.P., J.L. Brunner, V. Miera, M.J. Parris, D.M. Schock, and S. Storfer. 2003. Ecology and evolution of infectious diseases. In *Amphibian Conservation,* ed. R. Semlitsch, 137–51. Smithsonian Institution Press, Washington, DC.

Collins, J.P., and J.E. Cheek. 1983. Effect of food and density on development of typical and cannibalistic salamander larvae in *Ambystoma tigrinum nebulosum. American Zoologist* 23:77–84.

Collins, J.P., N. Cohen, E.W. Davidson, J. Longcore, and A. Storfer. 2001. Global amphibian declines: An interdisciplinary research challenge for the 21st century. In *Status and Conservation of US Amphibians,* vol. 1: *Conservation Essays,* ed. M.J. Lannoo, 43–52. University of California Press, Berkeley.

Crawshaw, G.J. 1992. The role of disease in amphibian decline. *Canadian Wildlife Service Occasional Paper* 76:60–62.

Dahl, T.E. 1990. *Wetland Losses in the United States, 1780's to 1980's.* US Department of the Interior, Fish and Wildlife Service, Washington, DC.

Dahl, T.E., and C.E. Johnson. 1991. *Status and Trends of Wetlands in the Coterminous United States, Mid-1970's to Mid-1980's.* US Department of the Interior, Fish and Wildlife Service, Washington, DC.

Daszak, P., L. Berger, A.A. Cunningham, A.D. Hyatt, D.E. Grees, and R. Speare. 1999. Emerging infectious diseases and amphibian population declines. *Emerging Infectious Diseases* 5:735–48.

deMaynadier, P.G., and M.L. Hunter, Jr. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology* 12:340–52.

Diaz, H.F. 1983. Some aspects of major dry and wet periods in the contiguous United States, 1895–1981. *Journal of Climate and Applied Meteorology* 22:3–16.

Diaz, H.F. 1986. An analysis of twentieth century climate fluctuations in northern North America. *Journal of Climate and Applied Meteorology* 25:1625–57.

Dodd, C.K., Jr. 1993. Cost of living in an unpredictable environment: the ecology of striped newts *Notophthalmus perstriatus* during a prolonged drought. *Copeia* 1993:605–14.

Dodd, C.K., Jr. 1996. Use of terrestrial habitats by amphibians in the sandhill uplands of north-central Florida. *Alytes* 14:42–52.

Duvick, D.N., and T.J. Blasing. 1981. A dendroclimatic reconstruction of annual precipitation amounts in Iowa since 1680. *Water Resource Research* 17:1183–89.

Edenhamn, P. 1996. *Spatial Dynamics of the European Tree Frog (Hyla arborea L.) in a Heterogeneous Landscape.* PhD diss., Uppsala University, Uppsala, Sweden.

Euliss, N.H., Jr., and D.M. Mushet. 1996. Water-level fluctuations in wetlands as a function of landscape condition in the prairie pothole region. *Wetlands* 16:587–93.

Euliss, N.H., Jr., and D.M. Mushet. 2004. Impacts of water development on aquatic macroinvertebrates, amphibians, and plants in wetlands of a semi-arid landscape. *Aquatic Ecosystem Health and Management* 7:73–84.

Euliss, N.H., Jr., R.A. Gleason, A. Olness, R.L. McDougal, H.R. Murkin, R.D. Robarts, R.A. Bourbonniere, and B.G. Warner. 2006. North American prairie wetlands are important nonforested land-based carbon storage sites. *Science of the Total Environment* 361:179–88.

Findlay, C.S., and J. Houlahan. 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. *Conservation Biology* 11:1000–1009.

Gibbs, J.P. 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. *Wetlands* 13:25–31.

Gill, D.E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecological Monographs* 48:145–66.

Gleason, R.A. 1996. *Influence of Agricultural Practices on Sedimentation Rates, Aquatic Invertebrates, and Bird-use in Prairie Wetlands*. Master's thesis, Humboldt State University, Arcata, CA.

Gleason, R.A. 2001. *Invertebrate Egg and Plant Seed Banks in Natural, Restored, and Drained Wetlands in the Prairie Pothole Region (USA) and Potential Effects of Sedimentation on Recolonization of Hydrophytes and Aquatic Invertebrates*. PhD diss., South Dakota State University, Brookings, SD.

Gleason, R.A., and N.H. Euliss, Jr. 1998. Sedimentation of prairie wetlands. *Great Plains Research* 8:97–112.

Gleason, R.A., N.H. Euliss, Jr., D.E. Hubbard, and W.G. Duffy. 2003. Effects of sediment load on emergence of aquatic invertebrates and plants from wetland soil egg and seed banks. *Wetlands* 23:26–34.

Gleason, R.A., M.K. Laubhan, and N.H. Euliss, Jr., ed., 2008. *Ecosystem Services Derived from Wetland Conservation Practices in the United States Prairie Pothole Region with an Emphasis on the US Department of Agriculture Conservation Reserve and Wetlands Reserve Programs*. US Geological Professional Paper 1745, Reston, VA.

Goolsby, D.A., R.H. Coupe, and D.J. Markovchick. 1991. *Distribution of Selected Herbicides and Nitrate in the Mississippi River and its Major Tributaries*. Report No. 91-4163, US Geological Survey, Denver.

Gray, M.J., L.M. Smith, and R. Brenes. 2004a. Effects of agricultural cultivation on demographics of Southern High Plains amphibians. *Conservation Biology* 18:1368–77.

Gray, M.J., L.M. Smith, and R.I. Leyva. 2004b. Influence of agricultural landscape structure on a Southern High Plains, USA, amphibian assemblage. *Landscape Ecology* 19:719–29.

Green, D.E., K.A. Converse, and A.K. Schrader. 2002. Epizootiology of sixty-four amphibian morbidity events in the USA, 1996–2001. *Annals of the New York Academy of Sciences* 969:323–39.

Green, D.M. 2003. The ecology of extinction: Population fluctuation and decline in amphibians. *Biological Conservation* 111:331–43.

Hall, R.J., and P.P. Henry. 1992. Assessing effects of pesticides on amphibians and reptiles: status and needs. *Herpetological Journal* 2:65–71.

Hanski, I., and M.E. Gilpin. 1991. *Metapopulation Dynamics*. Academic Press, London.

Hanson, M.A., and M.G. Butler. 1990. Early responses of plankton and turbidity to bioaccumulation in a shallow prairie lake. *Hydrobiologia* 200/201:317–27.

Hayes, T.B. 2004. There is no denying this: Defusing the confusion about Atrazine. *BioScience* 54:1138–49.

Hayes, T.B., K. Haston, M. Tsui, A. Hoang, C. Haeffele, and A. Vonk. 2003. Atrazine-induced hermaphroditism at 0.1 ppb in American leopard frogs (*Rana pipiens*): Laboratory and field evidence. *Environmental Health Perspectives* 111:568–75.

Hecnar, S.J., and R.T. M'Closkey. 1996. The effects of predatory fish on amphibian species richness and distribution. *Biological Conservation* 79:123–31.

Heemskerk, M., K. Wilson, and M. Pavao-Zuckerman. 2003. Conceptual models as tools for communication across disciplines. *Conservation Ecology* 7:8. http://www.consecol.org/vol7/iss3/art8/.

Herbeck, L.A., and D.R. Larsen. 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark forests. *Conservation Biology* 13:623–32.

Heyer, W.R., R.W. McDiarmid, and D.L. Weigmann. 1975. Tadpoles, predation, and pond habitats in the tropics. *Biotropica* 7:100–111.

Howe, C.M., M. Berrill, B.D. Pauli, C.C. Helbing, K. Werry, and N. Veldhoen. 2004. Toxicity of Glyphosate-based pesticides to four North American frog species. *Environmental Toxicology and Chemistry* 23:1928–38.

Howe, G.E., R. Gillis, and R.C. Mowbray. 1998. Effect of chemical synergy and larval stage on the toxicity of atrazine and alachlor to amphibian larvae. *Environmental Toxicology and Chemistry* 17:519–25.

Hyatt, A.D., A.R. Gould, Z. Zupanivic, A. Cunningham, S. Hengstberger, R.J. Whittington, J. Kattenbely, and B.E.H. Coupar. 2000. Comparative studies of amphibian and piscine iridoviruses. *Archives of Virology* 145:301–31.

Johnson, W.C., B.V. Millett, T. Gilmanov, R.A. Voldseth, G.R. Guntenspergen, and D.E. Naugle. 2005. Vulnerability of northern prairie wetlands to climate change. *Bioscience* 55:863–72.

Johnson, W.C., B. Werner, G.R. Guntenspergen, R.A. Voldseth, B. Millett, D.E. Naugle, M. Tulbure, R.W.H. Carroll, J. Tracy, and C. Olawsky. 2010.

Prairie wetland complexes as landscape functional units in a changing climate. *Bioscience* 60:128–40.

Jurik, T.W., S.-C. Wang, and A.G. van der Valk. 1994. Effects of sediment load on seedling emergence from wetland seed banks. *Wetlands* 14:159–65.

Karl, T.R., and A.J. Koscielny. 1982. Drought in the United States: 1895–1981. *Journal of Climatology* 2:313–29.

Karl, T.R., and W.E. Riebsame. 1984. The identification of 10 to 20 year temperature and precipitation fluctuations in the contiguous United States. *Journal of Climate and Applied Meteorology* 23:950–66.

Kats, L.B., J. Petranka, and A. Sih. 1988. Antipredator defenses and the persistence of amphibian larvae with fishes. *Ecology* 69:1865–70.

Kiesecker, J.M., A.R. Blaustein, and L.K. Belden. 2001. Complex causes of amphibian population declines. *Nature* 410:681–84.

Knutson, M.G., J.R. Sauer, D.A. Olsen, M.J. Mossman, L.M. Hemesath, and M.J. Lannoo. 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, USA. *Conservation Biology* 13:1437–46.

Kolbe, J.J., B.E. Smith, and D.M. Browning. 2002. A large aggregation of tiger salamanders (*Ambystoma tigrinum melanostictum*) at a black-tailed prairie dog (*Cynomys ludovicianus*) town in southwestern South Dakota. *Herpetological Review* 33:95–99.

Kolozsvary, M.B., and R.K. Swilhart. 1999. Habitat fragmentation and the distribution of amphibians: patch and landscape correlates in farmland. *Canadian Journal of Zoology* 77:1288–99.

Lannoo, M.J., ed. 1998. *Status and Conservation of Midwestern Amphibians*. University of Iowa Press, Ames.

Lannoo, M.J., ed. 2005. *Amphibian Declines: The Conservations Status of United States Species*. University of California Press, Berkeley.

Lee, R.E., Jr., J.P. Costanzo, E.C. Davidson, and J.R. Layne, Jr. 1992. Dynamics of body water during freezing and thawing in a freeze-tolerant frog *(Rana sylvatica). Journal of Thermal Biology* 17:263–66.

Lehtinen, R.M., S.M. Galatowitsch, and J.R. Tester. 1999. Consequences of habitat loss and fragmentation for wetland amphibian assemblages. *Wetlands* 19:1–12.

Maddox, G.D., K.E. Poiani, and R.E. Unnasch. 1999. Evaluating management success: Using ecological models to ask the right monitoring questions. In *The Ecological Stewardship Project: A Common Reference for Ecosystem Management*, ed. N. Johnson, 563–84. Elsevier Science, Oxford.

Madison, D.M. 1997. The emigration of radio-implanted spotted salamanders, *Abmystoma maculatum*. *Journal of Herpetology* 31:542–52.

Marsh, D.M., and P.C. Trenham. 2001. Metapopulation dynamics and amphibian conservation. *Conservation Biology* 15:40–49.

Martin, D.B., and W.A. Hartman. 1987. The effect of cultivation on sediment and deposition in prairie pothole wetlands. *Water, Air, and Soil Pollution* 34:45–53.

Morin, P.J. 1986. Interactions between intraspecific competition and predation in an amphibian predator-prey system. *Ecology* 67:713–20.

Mushet, D.M. 2010. *From Earth-Observing Space Satellites to Nuclear Microsatellites: Amphibian Conservation in the Northern Great Plains*. PhD diss., North Dakota State University, Fargo.

National Wildlife Health Center. 2001. *Amphibian Diseases*. NWHC Information Sheet. US Geological Survey, Madison, WI.

Naughton, G.P., C.B. Henderson, K.R. Foresman, and R.L. McGraw II. 2000. Long-toed salamanders in harvested and intact Douglas-fir forests of western Montana. *Ecological Applications* 10:1681–89.

Neimuth, N.D., B. Wangler, and R.E. Reynolds. 2010. Spatial and temporal variation in wet area of wetlands in the prairie pothole region of North Dakota and South Dakota. *Wetlands* 30:1053–64.

Newman, R.A. 1987. Effects of density and predation on *Scaphiopus couchi* tadpoles in desert ponds. *Oecologia* 71:301–7.

Ogden, J.C., S.M. Davis, K.J. Jacobs, T. Barnes, and H.E. Fling. 2005. The use of conceptual ecological models to guide ecosystem restoration in south Florida. *Wetlands* 25:795–809.

Pechmann, J.H.K., D.E. Scott, J.W. Gibbons, and R.D. Semlitsch. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. *Wetlands Ecology and Management* 1:3–11.

Pechmann, J.H.K., D.E. Scott, R.D. Semlitsch, J.P. Caldwell, L.J. Vitt, and J. Whitfield Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253:892–95.

Peterka, J.J. 1989. Fishes in northern prairie wetlands. In *Northern Prairie Wetlands*, ed. A. van der Valk, 302–15. Iowa State University Press, Ames.

Pfennig, D.W. 1990. The adaptive significance of an environmentally-cued developmental switch in an anuran tadpole. *Oecologia* 85:101–7.

Relyea, R.A. 2004a. Predator cues and pesticides: A double dose of danger for amphibians. *Ecological Applications* 13:1515–21.

Relyea, R.A. 2004b. Synergistic impacts of malathion and predatory stress on six species of North American tadpoles. *Environmental Toxicology and Chemistry* 23:1080–84.

Relyea, R.A. 2005a. The impact of insecticides and herbicides on the biodiversity and productivity of aquatic communities. *Ecological Applications* 15:618–27.

Relyea, R.A. 2005b. The lethal impact of Roundup on aquatic and terrestrial amphibians. *Ecological Applications* 15:1118–24.

Relyea, R.A. 2009. A cocktail of contaminants: How mixtures of pesticides at low concentrations affect aquatic communities. *Oecologia* 159:363–76.

Rohr, J., J. Kerby, and A. Sih. 2006. Community ecology as a framework for predicting contaminant effects. *Trends in Ecology and Evolution* 21:606–13.

Rouse, J.D., C.A. Bishop, and J. Struger. 1999. Nitrogen pollution: An assessment of its threat to amphibian survival. *Environmental Health Perspectives* 107:799–803.

Ruwaldt, J.J., L.D. Flake, and J.M. Gates. 1979. Waterfowl pair use of natural and man-made wetlands in South Dakota. *Journal of Wildlife Management* 43:375–83.

Schneider, S.H., S. Semenov, A. Patwardhan, I. Burton, C.H.D. Magadza, M. Oppenheimer, A.B. Pittock, A. Rahman, J.B. Smith, A. Suarez and F. Yamin. 2007. Assessing key vulnerabilities and the risk from climate change. In *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change,* ed. M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden, and C.E. Hanson, 779–810. Cambridge University Press, Cambridge.

Semlitsch, R.D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conservation Biology* 12:1113–19.

Semlitsch, R.D. 2000. Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* 64:615–31.

Semlitsch, R.D., D.E. Scott, J.H.K. Pechmann, and J.W. Gibbons. 1996. Structure and dynamics of an amphibian community: Evidence from a 16-year study of a natural pond. In *Long-term Studies of Vertebrate Communities,* ed. M.L. Cody and J.A. Smallwood, 217–48. Academic Press, San Diego.

Sjögren, P. 1991. Extinction and isolation gradients in metapopulations: The case of the pool frog (*Rana lessonae*). *Biological Journal of the Linnean Society* 42:135–47.

Sjögren-Gulve, P. 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. *Ecology* 75:1357.

Skelly, D.K., and E. Meir. 1997. Rule-based models for evaluating mechanisms of distributional change. *Conservation Biology* 11:531–38.

Smith, G.R. 2001. Effects of acute exposure to a commercial formulation of Glyphosate on the tadpoles of two species of anurans. *Bulletin of Environmental Contamination and Toxicology* 67:483–88.

Spencer, C.N., and D.L. King. 1984. Role of fish in regulation of plant and animal communities in eutrophic ponds. *Canadian Journal of Fisheries and Aquatic Science* 41:1851–55.

Stebbins, R.C., and N.W. Cohen. 1995. *A Natural History of Amphibians*. Princeton University Press, Princeton, NJ.

Storey, K.B., and J.M. Storey. 1992. Natural freeze tolerance in ectothermic vertebrates. *Annual Review of Physiology* 54:619–37.

Tiner, R.W. 1984. *Wetlands of the United States: Current Status and Recent Trends*. US Fish and Wildlife Service, Washington, DC.

Trenham, P.C. 1998. *Demography, Migration and Metapopulation Structure of Pond Breeding Salamanders*. PhD diss., University of California, Davis.

Tyler, T., W.J. Liss, L.M. Ganio, G.L. Larson, R. Hoffman, E. Deimling, and G. Lomnicky. 1998. Interaction between introduced trout and larval salamanders (*Ambystoma macrodactylum*) in high-elevation lakes. *Conservation Biology* 12:94–105.

van der Kamp, G., W.J. Stolte, and R.G. Clark. 1999. Drying out of small prairie wetlands after conversion of their catchments from cultivation to permanent brome grass. *Hydrological Sciences* 44:387–97.

Wang, S.-C., T.W. Jurik, and A.G. van der Valk. 1994. Effects of sediment load on various stages in the life and death of cattail (*Typha* x *glauca*). *Wetlands* 14:166–73.

Wellborn, G.A., D.K. Skelly, and E.E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* 27:337–63.

Wilbur, H.M. 1980. Complex life cycles. *Annual Review of Ecology and Systematics* 11:67–93.

Wilbur, H.M. 1984. Complex lifecycles and community organization in amphibians. In *A New Ecology: Novel Approaches to Interactive Systems,* ed. P.W. Price, C.N. Slobodchikoff, and W.S. Gaud, 195–224. Wiley, New York.

Wilbur, H.M. 1987. Regulation of structure in complex systems: experimental temporary pond communities. *Ecology* 68:1437–52.

Wilbur, H.M., and J.E. Fauth. 1990. Experimental aquatic food webs: Interactions between two predators and two prey. *American Naturalist* 135:176–204.

Willis, K. 2001. 73 new wetlands created in southwestern North Dakota. *Birdscapes* 2001 (Fall): 12.

Winter, T.C., and D.O. Rosenberry. 1998. Hydrology of prairie pothole wetlands during drought and deluge: A 17-year study of the Cottonwood Lake wetland complex in North Dakota in the perspective of longer term measured and proxy hydrological records. *Climatic Change* 40:189–209.

Woodhouse, C.A., and J.T. Overpeck. 1998. 2000 years of drought variability in the central United States. *Bulletin of the American Meteorological Society* 79:2693–2714.

Wyman, R.L. 1990. What's happening to the amphibians. *Conservation Biology* 4:350–52.