Invited Paper:

PRINCIPLES FOR MANAGEMENT OF AQUATIC-BREEDING AMPHIBIANS

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Abstract: Coordinated efforts by ecologists and natural resource managers are necessary to balance the conservation of biological diversity with the potential for sustained economic development. Because some amphibians have suffered world-wide declines during the last 20 years, it is important to consider biologically based management strategies that will preserve local and regional populations. This paper provides a brief overview of potential threats to local and regional populations, the state of knowledge on population and landscape processes, and the critical elements needed for an effective management plan for amphibians. Local population dynamics and ecological connectivity of amphibian metapopulations must be considered in effective management plans. There are 3 critical factors to consider in a management plan (1) the number or density of individuals dispersing from individual wetlands, (2) the diversity of wetlands with regard to hydroperiod, and (3) the probability of dispersal among adjacent wetlands or the rescue and recolonization of local populations. Wetland losses reduce the total number of sites where pond-breeding amphibians can reproduce and recruit juveniles into the breeding population. Loss of small, temporary wetlands (<4.0 ha) may be especially harmful to amphibians because of their abundance and high species diversity. Alteration of wetlands, particularly hydrologic cycles, can severely impair completion of larval metamorphosis through either early pond drying (if hydroperiod is shortened) or through increased predation (if hydroperiod is lengthened or connections made with fish-infested lakes, rivers, or canals). Wetland loss also increases the distance between neighboring wetlands that is critical to metapopulation source-sink processes. Reduction in wetland density reduces the probablity that populations will be rescued from extinction by nearby source populations. Local populations cannot be considered independent of source-sink processes that connect wetlands at the landscape or regional level. Further, the fragmentation of natural habitats from timber harvesting, agriculture, roads, drainage canals, or urban development impedes or prevents dispersal and decreases the probability of wetland recolonization. If our goal is to maintain or enhance present levels of amphibian diversity, then resource managers must incorporate critical elements into plans that protect population and landscape processes thereby maintaining viable populations and communities of amphibians.

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Over the past decade amphibians have been the focus of increasing concern because of reported population declines (Barinaga 1990). Current evidence indicates that some amphibians may be experiencing population declines, range constrictions, or extinctions that appear to be related to impacts at local, regional, and possibly global scales (Wake 1998, Alford and Richards 1999). Although most biologists agree that local habitat destruction (filling and draining of wetlands, channelization of streams, creation of impoundments, forest fragmentation) are major factors causing declines, recent evidence suggests that disease and pathogens, global climate change, invasive species, chemical contamination, and commercial trade also are real threats (Blaustein et al. 1994*a*, Dodd 1997, Lips 1998, Wake 1998, Alford and Richards 1999, Carey et al. 1999). We also know that amphibian breeding populations, and hence larval populations, naturally undergo wide fluctuations in number thereby making them especially sensitive to stochastic events (Berven 1990, Pechmann et al. 1991). Further, there is general agreement that any of these factors can be synergistic, allowing subtle or undetectable effects of any single factor to be exacerbated to harmful levels by another factor. Thus, in combination these factors may result in reduced viability of populations and account for some observed declines. Be-

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Table 1. Checklist of questions to help determine management goals and to develop effective management plans for amphibian conservation.

Question
What species currently inhabit your region?
What was the historical species richness and relative abundance of amphibians in your region?
What are the primary causes of amphibian declines or threats to amphibian populations in your region?
Which amphibian species or breeding habitats are most severely threatened in your region?
What amphibian species can your site currently, or potentially support?
How can your site best be managed to contribute to amphibian conservation at a local or regional level?
What are the land-use activities within and surrounding your site?
What, if any, management practices are currently used on your site?
Are current management practices compatible with managing amphibians?
What, if any, management practices are your neighbors engaged in?
How can management efforts be coordinated with other landowners, neighboring jurisdictions, or agencies?

cause of these threats, sound principles upon which to base management plans for different ecosystems, amphibian communities, or species are essential if we are to conserve amphibian diversity in the face of continuing economic development and a growing human population.

One of the positive outcomes of recent concerns has been the shift in emphasis by many amphibian ecologists toward conservation and management issues. Such shifts have recently produced a better understanding of individual effects and integrated knowledge of landscape processes. Improved knowledge and understanding, in turn, contribute to development of biologically-based management plans (Semlitsch 1998, Werner and Glennemier 1999, deMaynadier and Hunter 1999, Carey et al. 1999, Herbeck and Larsen 1999, Skelly et al. 1999). Effective conservation plans will result from combining the efforts of population, community, and landscape ecologists with those of natural resource managers and policymakers. The principles I discuss here for amphibian management strive to present such an interdisciplinary approach and should serve both to meet many of the immediate needs for species conservation and act as a template for revised plans as new biological information becomes available. Thus, my goal is to provide the basic principles needed to develop biologically-based management plans to conserve amphibians in any region.

Any management plan that is specifically designed for local species, threats, and current land-use practices must begin with a series of questions that can be used to set goals and develop a plan (Table 1). I suggest that readers first become familiar with the basic questions from Table 1 to understand how their situation is impacted by the points raised in the sections that follow. The paper is organized in 3 parts: a brief overview of known threats to local and regional populations, state of knowledge of population and landscape processes, and the critical elements of an effective management plan. Much of the research reported here was conducted at a limited number of locations (but at local or regional scales) and for a subset of species. Many results are based on studies of pond-breeding species, especially in North America, with few examples of stream or tropical species. However, results appear robust, and it is not unreasonable to suggest that inferences can be made on a more global scale as well as extend to other taxonomic groups such as stream-breeding and tropical species that are likely suffering similar threats. Clearly, more basic data on life history requirements and population biology, especially long-term trends, are needed for many species. However, most of the critical elements required to begin managing amphibians are known.

THREATS TO LOCAL AND REGIONAL POPULATIONS

Habitat Destruction and Alteration

Most amphibians depend on both aquatic and terrestrial habitats to complete their life cycle. Careful management of these habitats at population and landscape levels is critical to maintain viable populations and regional diversity. However, both habitats have been heavily impacted by human use, and these impacts are likely the primary cause of reported species declines (Blaustein et al. 1994*a*, Dodd 1997).

The filling and drainage of wetlands for agriculture, timber harvest, and housing development can have a negative impact on amphibian breeding sites. Loss of wetlands reduces the number and density of breeding sites, thereby diminishing the capacity to maintain local and regional species populations. For example, approximately 53% of original wetlands in the United States alone have been lost to human development during the last 200 years (Dahl 1990). Efforts to prevent further loss of wetlands (Protection of Wetlands, Executive Order 11990) has helped large wetlands but offers little or no protection to small, isolated wetlands (temporary or seasonal wetlands <4.0 ha; Kaiser 1998) that can easily be filled or drained with little consequence (U.S. Army Corps of Engineers, Permit 404) or even overlooked because of lower detection limits on aerial photographs (~0.2 ha). Unfortunately, these abundant, small wetlands support a diverse array of amphibian species, produce large numbers of metamorphosing juveniles, and can function as stepping stones for dispersal and recolonization of extinct populations (Moler and Franz 1987, LaClaire and Franz 1990, Semlitsch and Bodie 1998).

Clearing of terrestrial habitats (forests, grasslands) for agriculture, industry, and urban use also can change the ability of aquatic and terrestrial habitats to support native species. For example, many forests that were once continuous between adjacent aquatic breeding sites are now fragmented or periodically disturbed by timber harvesting, crop production, or housing developments. Such modifications to the terrestrial environment can reduce some amphibian populations (Ash 1988, 1997; Hecnar and M'Closkey 1996). Deforestation eliminates shade, increases surface temperature, disrupts soil structure, and reduces soil moisture making these areas inhospitable or less suitable for many species, especially salamanders (Spotila 1972, Corn and Bury 1989). Additional negative effects of logging operations include removal of coarse woody debris, compaction of soil, sedimentation of aquatic habitats from logging roads, mechanical disturbance of leaf litter used for surface refuges or that support invertebrate prey; use of herbicides or insecticides that can directly impact amphibians or their invertebrate prey; and ditching that can alter the hydroperiod of local breeding ponds (Sharitz and Gibbons 1982, Corn and Bury 1989, Bishop 1992, deMaynadier and Hunter 1995, Dodd 1997). In addition, logging can potentially disrupt breeding migrations (Raymond and Hardy 1991), suggesting that dispersal which is important to rescue or recolonization of adjacent breeding sites may be impaired.

Global Climate Change

Global climate changes caused by the accumulation of greenhouse gases and reduction of the ozone layer are now being linked to species declines and raise serious questions about the future of amphibians in areas of high vulnerability, particularly species with specialized habitat requirements. Two factors of primary concern have been identified (1) alteration of rainfall and temperature patterns, and (2) increases in ultraviolet (UV-B) radiation. The increase in frequency and severity of El Nino-southern oscillation events has been closely related to negative impacts on diverse biotic systems world wide (e.g., bird communities, Grant and Grant 1996; reef fish assemblages, Holbrook and Schmitt 1996). Because of the strong dependence of amphibians on moisture for reproduction, any reductions or regional shifts in rainfall patterns could negatively impact reproductive success. Several studies have now linked changes in rainfall pattern, regional droughts, and general disruption of weather patterns to reduced success and population declines (Pounds and Crump 1994, Laurance et al. 1996, Donnelly and Crump 1998, Lips 1998). In addition, the direct alteration of habitats via changing climate (e.g., changes in the geographic or altitudinal distribution of vegetation, lowering of the water table) may place some species with specialized requirements or narrow tolerances at increased risk of extinction (e.g., spring- or cave-adapted species, montane terrestrial species; Dodd 1997).

Similarly, the increase in ultraviolet (UV-B) radiation has been shown to reduce survival and hatching success, and negatively impact development and growth of some amphibians, especially those inhabiting montane regions (Blaustein et al. 1994*b*, Hays et al. 1996). More importantly, species comparisons show that photolyase activity (UV-B damage repair enzyme) is lowest in declining species and highest in nondeclining species (Blaustein et al. 1994*b*). Increasing UV-B levels also exacerbates factors such as chemical contaminants (e.g., photoactivation and increased toxicity of an insecticide, Zaga et al. 1998), low pH (Long et al. 1995), and susceptibility to disease and pathogens (reduced immune function, Carey et al. 1999).

Chemical Contamination

It is important to consider that many amphibians encounter chemical contamination in both terrestrial and aquatic environments. Chemical application to agricultural fields, golf courses, and forests directly may expose terrestrial juveniles and adults to harmful levels of herbicides and insecticides. Furthermore, because freshwater environments are the ultimate sink for most chemical contaminants regardless of their source (e.g., agriculture or industry, Anderson and D'Apollonia 1978), larval amphibians also are likely exposed.

Although a number of chemical compounds have been reported to be toxic to amphibians (Harfenist et al. 1989), until recently, few ecotoxicological studies have focused on amphibians (Hall and Henry 1992). Although there is speculation that chemical contamination may be partially to blame for declines (Barinaga 1990, Blaustein and Wake 1990, Wake 1998) by disrupting growth, reproduction, and behavior (Bishop 1992), direct evidence of population declines due to contamination is rare. One of the primary reasons for the difficulty in linking chemical contamination to amphibian declines has been the lack of evidence of direct mortality due to chemical exposure. However, research has focused only recently on sublethal effects because these concentrations mimic natural exposure under field conditions. Laboratory studies using sublethal field concentrations clearly demonstrate reductions in growth and development, and abnormal feeding and swimming behavior that may ultimately contribute to population declines without evidence of mass mortality.

Both organic and inorganic chemicals have a great potential to impact amphibians (Rand 1995). Nitrates and ammonia can enter the environment as run-off from fertilized crop lands, golf courses, or feed lots. Concentrations can reach high levels in ponds within agricultural landscapes and cause direct mortality and reduced growth (Baker and Waights 1994). Pesticides are the predominant organic chemical that enter amphibian habitats. All insecticides are neurotoxins and do not necessarily break down quickly, but instead are sequestered either in sediments or animal tissue (i.e., bioconcentration). Contrary to what is often asserted in the literature, amphibian larvae appear to be less sensitive to pesticides than other aquatic organisms such as fish and aquatic insects (Mayer and Ellerseick 1986). Additionally, amphibians can bioconcentrate organophosphate compounds to levels much higher than more sensitive organisms (Hall and Kolbe 1980). This may have significant implications for predators that feed on amphibians. Organophosphates have been shown to cause numerous malformations, reduce development and growth, alter feeding and swimming behavior, and cause direct mortality. Lastly, while some organochlorines like DDT are no longer released into the environment in the United States, use of these chemicals continues in developing countries, especially in tropical regions without stringent laws or guidelines, and may be an important factor for tropical species.

Abiotic factors such as pH and temperature can pose a direct threat to amphibians when normal values are exceeded, and also influence toxicity of other contaminants (Pierce 1985, Freda 1986, Vertucci and Corn 1996, Boone and Bridges 1999). For example, amphibian eggs often fail to hatch (Dunson and Connell 1982), and larvae decrease swimming function (Andren et al. 1988, Freda and Taylor 1992) or suffer direct mortality in acidic conditions (lower than pH 5.0; Leftwich and Lilly 1992). Further, acidic waters often contain toxic levels of metals such as aluminum, cadmium, copper, iron, lead, and zinc (Freda 1991). Aluminum, the metal most commonly associated with decreased pH, reduces tadpole survival (Clark and Hall 1983, Bradford et al. 1994, Horne and Dunson 1995, Jung and Jagoe 1995). Metals (e.g., lead and copper) may also reach high levels in aquatic areas associated with mining.

Disease and Pathogens

Some reports of mass mortality of amphibians in relatively pristine areas of the world have now been linked to infectious diseases (Carey et al. 1999) thereby leading to the suggestion that pathogens are responsible for some species declines (Carey 1993, Laurance et al. 1996, Lips 1998). There appear to be 2 patterns of mortaility emerging: 1 geographically widespread, and the other localized. In the first pattern, mortality is geographically widespread, populations experience 50–100% mortality, declines are more pronounced at higher elevations or in cooler regions, only some species and principally metamorphosed terrestrial stages are affected. This pattern is attributed to fungal pathogens (a parasitic chytrid fungus; Carey et al. 1999). In the second pattern mortality is localized, all stages and species are affected, and outbreaks occur frequently in areas disturbed by humans and at high amphibian densities. This pattern is attributed to an iridovirus infection (Carey et al. 1999). What makes both these pathogens so significant to management issues is that they interact with other factors and have likely contributed to the susceptibility of various species or populations to other threats. For example, it is thought that environmental stress due to chemical contamination, increased temperature, drought, or increased UV-B could diminish the immune system. Further, human activities such as stocking infected fish may introduce pathogens to new locations; and, alteration of the environment might disturb natural communities of microorganisms, thereby allowing rare pathogens to increase in number (Carey et al. 1999).

Invasive Species

Numerous concerns have been raised about the negative impact of invasive species on native amphibians. Of particular concern are the stocking of predatory fish, range expansion and introduction of bullfrogs (*Rana catesbeiana*), and the introduction of exotic species such as marine toads (*Bufo marinus*), Cuban treefrogs (*Osteopilus septentrionalis*), and fire ants (*Solenopsis invicta*; Dodd 1997). Fish are considered the most critical and wide-spread problem because they can be both competitors and predators of amphibian larvae (Bristow 1991, Semlitsch 1987). Fish can affect species distributions among ponds (Moler and Franz 1987, Bradford 1989, Bronmark and Edenhamm 1994, Skelly 1996, Azevedo-Ramos et al. 1999), and have been linked to amphibian declines in the western U.S. (Hayes and Jennings 1986, Bradford 1989, Bradford and Graber 1993). Fish problems include introduction of native and exotic fish into amphibian ponds for commercial or sport fishing. Bullfrogs also have been shown to negatively affect local amphibian species through competition and predation, especially in the western United States and Europe where they have only recently been introduced (Hayes and Jennings 1986, Stumpel 1992, Kupferberg 1995, Kiesecker and Blaustein 1997, Lawler et al. 1999). Although the impact of other exotic species on native amphibians is unknown, one species, fire ants, may be worth studying in the southern United States because they are abundant around wetlands (personal observation) and have been reported to prey upon newly metamorphosed Houston toads (*Bufo houstonensis*; Freed and Neitman 1988). Finally, some have argued that increased abundance of raccoons (*Procyon lotor*), armadillos (*Dasypus* spp.), cattle egrets (*Bubulcus ibis*), feral hogs (*Sus scrofa*), or any predator species that may consume amphibians (larvae or adults) or alter habitat can also be considered a problem and should be monitored (Garrott et al. 1993, Goodrich and Buskirk 1995, Dodd 1997).

Commercial Exploitation

The commercial trade in amphibians is a great concern for natural populations and communities for several reasons. First, the direct impact of commercial or illegal collecting may remove a large portion of breeding adults and reduce the capacity of populations to sustain themselves. For example, Oza (1990) reported in the period prior to the 1990s, 200 million frogs were exported annually from Asia, and in 1990 India was still exporting 70 million frogs each year, resulting in serious population declines. It also is known that biological supply houses in the United States shipped 9 million frogs (mostly *Rana*) per year in the early 1970s (Gibbs et al. 1971). Any removal is especially important for species that normally maintain small breeding population sizes and take several years to reach reproductive maturity (*Ambystoma tigrinum,* Semlitsch 1983; *Rana capito,* Semlitsch et al. 1995). Second, the reintroduction of wild-collected or captive-reared amphibians (intentional or accidental) into natural populations may expose native animals to diseases or pathogens not present in the region (e.g., fish fungus, Blaustein et al. 1994*a*). Last, reintroductions from other regions may disturb the local or regional genetic structure of populations and, hence, their ability to adapt to local environmental conditions.

CRITICAL POPULATION AND LANDSCAPE PROCESSES

Field and experimental studies indicate that both local population dynamics and ecological connectivity of amphibian populations at the landscape level must be considered in any effective management plans. There are 3 critical factors that must be considered in all management plans (1) local population dynamics—the number or density of individuals dispersing from individual wetlands, (2) diversity of wetlands—the availability of breeding habitat primarily regarding wetland hydroperiod, and (3) metapopulation dynamics—the probability of dispersal among adjacent wetlands or the rescue and recolonization of local populations. I discuss the biological mechanisms that underly each of these 3 factors along with their interactions, and their importance to maintaining local or regional diversity. Last, I make suggestions concerning critical elements in management plans that include both the maintenance and restoration of natural processes that benefit amphibians.

Local Population Dynamics

The majority of amphibian species use aquatic habitats for some portion of their life cycle. Species with a complex life cycle (i.e., having both larval and adult stages) use aquatic habitats, such as bogs, vernal pools, temporary ponds, and even streams for mating, oviposition, and larval growth. It is important to understand that such aquatic habitats are dynamic, often filling and drying on an annual basis, and that amphibians are specifically adapted to such processes.

Most pond-breeding amphibians live in the surrounding terrestrial habitat (usually within 200 m; Madison 1997, Semlitsch 1998) during the non-breeding season. Breeding adults typically migrate to the aquatic habitat during favorable weather conditions for mating and oviposition, and adults, subsequently return to terrestrial habitats (Semlitsch and Ryan 1999). Breeding adults of some species remain in the pond for only 1–2 days (e.g., spadefoot toads, *Scaphiopus holbrooki*; wood frog, *Rana sylvatica*; spotted salamander, *Ambystoma maculatum,* personal obersvation) whereas others may spend several weeks or months (e.g., gray tree frog, *Hyla versicolor*; green frog, *R. clamitans*; tiger salamander, *Ambystoma tigrinum,* personal observation). Aquatic larvae feed, grow, and develop in the pond until metamorphosis, after which they emigrate as juveniles to terrestrial habitats. Larval periods vary among species and with environmental conditions (e.g., food and temperature) but can range from just 21 days for spadefoot toads (*Scaphiopus* sp.) to 1–2 years for bullfrogs, (*Rana catesbeiana*; personal observation).

Because of high species diversity (e.g., ponds in the southern United States may have >20 species; Wiest 1982, Dodd 1992, Semlitsch et al. 1996, Scott and Bufalino 1997) and high larval densities in many ponds, species interactions and density-dependence are likely to be important for regulation of natural populations and communities (Wilbur 1980, Pechmann 1994). Several excellent field studies have demonstrated a strong regulatory effect of density on growth and survival of larvae and on maturation after metamorphosis (Smith 1983; Petranka and Sih 1986; Petranka 1989; Scott 1990, 1994; Van Buskirk and Smith 1991). These studies indicate that as larval density increases, larvae grow more slowly, larval period increases, and fewer individuals reach metamorphosis. Because of the strong influence of larval density and because less than 5% of larvae normally metamorphose (Herreid and Kinney 1966, Licht 1974, Semlitsch 1987), it is theorized that population regulation occurs primarily in the larval stage (Istock 1967, Wilbur 1980). A recent study, however, suggests that some density-dependent regulation might also occur in the terrestrial juvenile or adult stage of some species (Pechmann 1994).

Growth and development of amphibian larvae are the basic processes that culminate in metamorphosis. Growth and developmental rates of amphibian larvae vary greatly and are strongly affected by environmental factors such as food, temperature, initial density, disease, and chemical contamination (Wilbur and Collins 1973, Alford and Harris 1988, Carey et al. 1999). In turn, phenotypic variation can influence larval success through the timing of metamorphosis and body size at metamorphosis. High growth rates enable tadpoles to metamorphose quickly to escape death in drying ephemeral ponds (Smith 1983; Semlitsch 1987; Newman 1988*a*,*b*), to escape aquatic predators (Smith 1983; Woodward 1983; Travis et al. 1985*a*,*b*), or to maximize size at metamorphosis in more permanent ponds (Wilbur and Collins 1973). Large size at metamorphosis can also result in better physiological and locomotor performance in the terrestrial environment (Pough and Kamel 1984, Goater et al. 1993), higher juvenile survival, earlier first reproduction, and larger size at first breeding (Berven and Gill 1983, Smith 1987, Berven 1990, Semlitsch et al.

1988). Successful larval development of many species to metamorphosis in natural aquatic habitats is affected by the interaction of physical factors related to pond hydroperiod, intra- and interspecific competition for food, and predation by fish or aquatic insects. Metamorphosis from the aquatic larval habitat to the terrestrial environment is the critical step by which individuals are recruited into the breeding population. Because breeding adults have a strong preference to return to natal ponds (Oldham 1966, Breden 1987, Berven and Grudzien 1990), metamorphosing juveniles are the primary dispersal stage (Gill 1978). Thus, high success rates of metamorphosis help maintain local populations, and likely supplies dispersers to found new populations or for reestablishment of extirpated populations.

Long-term studies have shown that variation in the amount and timing of rainfall among years affects pond hydroperiods, thereby affecting species ability to produce metamorphs (Pechmann et al. 1991, Semlitsch et al. 1996). Long pond hydroperiods favor species with long larval periods, whereas short hydroperiods favor those with short larval periods. Consequently, population regulation at any 1 pond changes dramatically year to year, and thereby affects the relative abundance of amphibian species. Species persist because each is periodically favored and exhibits boom years where large numbers of metamorphs are produced (Gill 1978, Semlitsch 1983, Berven 1990, Pechmann et al. 1989) rather than constant low-level reproductive success each year. Multiple years of reproductive failure due to unfavorable conditions such as rapid pond drying or fish predation result in decline and eventual extinction of local species populations (e.g., dwarf salamander, *Eurycea quadridigitata,* Semlitsch et al. 1996). It is apparent that most amphibian populations, even in pristine and relatively undisturbed areas, also are vulnerable to extinction. Those populations in highly disturbed or chemically contaminated habitats are even more vulnerable. Management plans that include actions to ensure natural hydroperiods and a high probability of larval survival to metamorphosis, such as preventing wetland drainage, invasion of fish predators, or eliminating chemical contamination via runoff, will help maintain local species populations and provide dispersers for recolonization.

Community Dynamics in Relation to Pond Hydroperiod

The maintenance of amphibian communities is strongly influenced by the hydroperiod of wetland habitats (Pechmann et al. 1989, Semlitsch et al. 1996). Species characteristics such as physiological tolerances and life-history requirements determine the immediate use of ponds, whereas the genetic ability of a population to adapt to pond conditions determines long-term use. A critical factor like pond drying that varies annually within and among ponds may be viewed as a disturbance for larval amphibians, as larvae may be killed if the site dries before metamorphosis can occur. Likewise, increased water permanence also negatively affects larval amphibians by allowing many predators, especially fish, to persist. Heyer et al. (1975) and Wilbur (1980, 1984) suggested that extremely temporary ponds (<30 days) or permanent ponds (>1 yr) are used by fewer species of amphibians than ponds with intermediate hydroperiods (among all semipermanent or seasonal Palustrine wetlands; e.g., Types 1, 2, 3, 6, 7, and 8; Cowardin et al. 1979). If rapid drying and pond permanence are considered as 2 ends of a disturbance continuum, then amphibian species diversity is maximized at intermediate levels of disturbance (Levin and Paine 1974, Gibbons 1976, Connell 1978, Odum et al. 1979). Thus, once a pond is colonized by adults, success depends on synchrony between the annual availability of water (i.e., time of filling, hydroperiod length) and the timing of reproduction. Following successful reproduction, species' characteristics such as larval requirements for food, temperature tolerance, predator avoidance, and minimum length of the larval period all interact to determine larval success along the gradient of pond hydroperiod. Overall, a species' success at the population level is determined primarily by the number and quality of metamorphosing larvae leaving a pond, and thus, the number recruited into the terrestrial adult population.

Predation and competition interact within pond hydroperiod in communities of pond-breeding amphibians (Morin 1981, 1983; Smith 1983; Wilbur 1987; Werner and McPeek 1994; Skelly 1995; Semlitsch et al. 1996; Wellborn et al. 1996). Because all salamanders (larval and adult) are carnivorous and frequently occur at high densities, they can exert strong predation pressure on amphibian communities (Morin 1981), especially small, herbivorous anuran tadpoles. Salamanders can maintain populations only in ponds with long hydroperiods. Predatory fish generally occupy permanent ponds (deepwater and permanently flooded Lacustrine wetlands; e.g., types 4 and 5; Cowardin et al. 1979) and occasionally they colonize seasonal wetlands where they remain until the next drying cycle. Predatory fish can reduce or completely eliminate small vulnerable salamanders and anuran larvae, and other amphibians without effective skin secretions or behaviors that deter predators (Heyer et al. 1975, Caldwell et al. 1980, Woodward 1983, Morin 1986, Kats et al. 1988, Lawler 1989, Hews 1995, Kats and Dill 1998, Tyler et al. 1998). Thus, local and regional distribution of amphibians can be strongly influenced by the presence of predatory fish (Petranka 1983, Moler and Franz 1987, Bradford 1989, Bradford and Graber 1993, Bronmark and Edenhamm 1994, Skelly 1996, Aker 1998, Azevedo-Ramos et al. 1999).

In ponds with short hydroperiods that lack predatory fish or salamanders, some anuran species breed in 1 or 2 nights and produce large numbers of fast-developing larvae that compete for limited food through exploitative and interference competition, sometimes even switching from herbivory to carnivory or cannibalism (Collins and Cheek 1983, Newman 1989, Pfennig 1990). Interspecific competition for food reduces growth and developmental rates, increases length of the larval period, and hence, vulnerability to desiccation or exposure to predators in more permanent ponds (Wilbur 1987, Wilbur and Fauth 1990). Reduced growth and developmental rates also reduce body size at metamorphosis, which in turn, may increase age at first reproduction and decrease size at first reproduction, survival to first reproduction, and fecundity (Berven and Gill 1983; Smith 1987; Berven 1988, 1990; Semlitsch et al. 1988; Scott 1994).

Complex interactions between predation and competition have been experimentally demonstrated in artificial ponds. For example, Morin (1981) showed that, in the absence of salamander predators, some anuran species whose larvae forage efficiently can outcompete other species and dominate in numbers of metamorphs. In the presence of predators, however, competitively superior species may be preferentially eaten, allowing other competitively inferior species to increase in relative abundance. Wilbur (1987) also demonstrated that predation can ameliorate the effects of competition at high densities by removing larvae from the community and lowering effective density, thereby allowing survivors to grow more rapidly and metamorphose before ponds dry. Thus, regulation of community structure within an amphibian pond occurs through the predictable interaction of hydroperiod, competition, and predation (Wellborn et al. 1996).

Spatial and temporal variation in the physiochemical and hydrological characteristics of ponds due to climatic conditions, habitat succession, and anthropogenic disturbance usually produce a mosaic of habitats available to amphibians (Semlitsch et al. 1996, Werner and Glennemeier 1999, Skelly et al. 1999). Pond hydroperiods vary tremendously, even in undisturbed regions (Schalles et al. 1989). Different species do well in different years, depending on pond hydroperiod. The eastern tiger salamander (*Ambystoma tigrinum*) with a long larval period can only produce metamorphs in years when a pond fills during the breeding season and does not dry for 3–4 months (Semlitsch 1983). Also, it is known that some anuran species (spadefoot toad, narrow-mouthed toad, *Gastrophryne carolinensis*; pine woods tree frog, *Hyla femoralis*) can only produce large numbers of metamorphs after a pond dries completely and refills later in the season, thereby eliminating all competitors and predators (Pechmann et al. 1989, Semlitsch et al. 1996).

It is important to note, however, that maintaining ponds with hydroperiods that are too long also is not conducive to successful metamorphosis in most species. Ponds with hydroperiods of >2 years (e.g., farm ponds) accumulate a diverse array of aquatic insect predators, aquatic salamanders, and are available for colonization and maintenance of fish populations. In fact, some ponds may be close to rivers, streams, canals, and drainage ditches that flood seasonally, thereby allowing fish to colonize ponds each year. Some amphibian species can coexist with fish because they possess antipredator behaviors and skin toxins (cricket frog, *Acris gryllus*; green tree frog, *Hyla cinerea*; bullfrog, green frog). However, the majority of amphibians are eliminated by predatory fish (Heyer et al. 1975, Bradford 1989, Hecnar and M'Closkey 1997). Thus, pond drying is a natural process that eliminates or reduces predation on larval amphibians and can be used as an effective management technique. An effective management plan must maintain or restore an array of natural ponds that vary in hydroperiod from perhaps 30 days to 1–2 years to insure that all local species have sites where the probability of reproductive success is high, even in extremely dry or wet years. In addition, protecting natural hydroperiods from the effects of drainage and increased evapotranspiration due to tree establishment during later stages of succession will help preserve a diversity of amphibian species.

Metapopulation Dynamics

It is important to maintain a natural array of isolated wetlands connected by appropriate terrestrial habitats so that amphibian metapopulations can prosper. A metapopulation is a set of local populations (number or density may vary with landscape or region), among which processes of gene flow, extinction, and colonization may occur. There are 2 primary factors governing amphibian metapopulation dynamics: the number or density of individuals dispersing among ponds, and the dispersal distances and probability of successfully reaching ponds (Hanski and Gilpin 1991, Sjogren 1991, Gibbs 1993).

Alteration and loss of wetlands reduces the total number or density of ponds where amphibians can reproduce and successfully recruit juveniles into the breeding population. Ultimately, a reduction in the number of wetlands reduces the total number of individual amphibians available to found new populations or colonize habitats where populations have become extinct. Because small seasonal pools and temporary ponds (<4.0 ha) are the most numerous type of wetlands in many natural landscapes (Gibbs 1993, Semlitsch and Bodie 1998), their loss especially reduces the number of source populations. Such small, temporary wetlands are often used by more species and produce more metamorphs for recruitment than either ephemeral pools or permanent ponds (Pechmann et al. 1989, Semlitsch et al. 1996). Thus, any failure to protect small wetlands can result in loss of the best breeding ponds from the landscape. Even in the best breeding ponds that are undisturbed by agriculture or development, reproductive failure occurs in many years due to other factors such as low rainfall, increasing the probability of population extinction (estimated annual reproductive failure rates of 42–56% for 13 species over 16 years in South Carolina; Semlitsch et al. 1996). Dodd (1993, 1995) also noted frequent reproductive failure in local amphibian populations due to drought. Consequently, the probability of local extinction is naturally high, and terrestrial juveniles are only periodically available to disperse and rescue populations. Human disturbance that adds to the probability of reproductive failure (e.g., ditching ponds, fish introductions) and disrupts this process will ultimately increase the probability of local declines and extinctions.

Even if recruitment failures are less frequent in more stable geographic regions, reductions in pond density and changes in spatial configuration are still critical to dispersal processes. Reduced pond density increases the distance between neighboring ponds, thereby affecting critical source-sink processes (Brown and Kodric-Brown 1977, Gill 1978, Pulliam 1988, Gibbs 1993, Semlitsch and Bodie 1998). Wetland loss causes an exponential increase in inter-pond distance or isolation (Gibbs 1993, Semlitsch and Bodie 1998). Inter-pond distances directly affect the probability of recolonization, and consequently, the chance of rescuing amphibian populations from extinction (Sjogren 1991, Skelly et al. 1999). This is critical because most individual amphibians cannot migrate long distances due to physiological limitations, and adults return to home ponds, usually after migrating no more than 200–300 m (Semlitsch 1998). An estimate of genetic-neighborhood size for wood frog populations averages only 1,126 m, suggesting that migration and gene flow are near zero at these distances (Berven and Grudzien 1990). This latter dispersal estimate is extremely short considering that it includes whole populations and takes place over an evolutionary time scale that includes multiple generations. Semlitsch and Bodie (1998) demonstrated that the loss of all natural wetlands <4.0 ha in size (current wetland protection threshold for Permit 404) in South Carolina would increase the nearest-wetland distance from 471 to 1,633 m. This distance is likely many times greater than can be traversed by most species even in several generations. Thus, the loss or alteration of small wetlands could severely impede source-sink processes and place remaining wetlands at increased probabilities of population extinctions (Gibbs 1993, Travis 1994).

Finally, because the maintenance of terres-

Table 2. Critical elements of effective and biologically based management plans for amphibians that consider both population and landscape processes.

Critical elements
Maintenance or restoration of temporary wetlands with a diverse array of hydroperiods.
Protection of terrestrial buffer zones of natural vegetation and associated habitats to protect core breeding sites (wetlands and streams).
Protection of amphibian communities from invasion by fish predators (both native and exotic).
Protection of the integrity of ecological connectivity (i.e., stepping stone ponds with corridors of natural vegetation) among wetlands in the landscape.
Restriction of chemical use (salt, oil, fire retardants, vegetation growth retardants, herbicides, pesticides) on site, but especially near ditches, streams, or wetlands.
Prohibition of release of any captive-raised or maintained amphibians, whether native or exotic.
Identify and resolve conflict between current management practices and those necessary for amphibians.

trial habitat between ponds may be critical for successful survival and dispersal (an issue of much debate; Saunders and Hobbs 1991), it is likely necessary to provide migration corridors or buffer zones of natural vegetation between adjacent ponds (Semlitsch 1998). Although few data are available on the dispersal of amphibians through terrestrial habitats, a recent study in a forested landscape of the northeastern United States clearly indicates that open, clearcut areas are avoided by dispersing juveniles of some species (deMaynadier and Hunter 1999). Thus, management plans that maintain continuous natural habitat (forested or grasslands depending on the region) adjacent to ponds or between neighboring ponds would help maintain source-sink dynamics of amphibians.

MANAGEMENT IMPLICATIONS

If our goal is to maintain or enhance present levels of amphibian diversity, then resource managers must incorporate several critical elements into current management plans (Table 2). Semi-aquatic organisms such as amphibians (also some birds, snakes, turtles, and insects) depend on the management of both terrestrial and aquatic ecosystems along with natural processes. Thus, the quality and quantity of aquatic and terrestrial habitat are important for the maintenance of viable populations and communities of amphibians.

Maintaining natural terrestrial habitats peripheral to wetlands is critical to carry out all life-history functions. Depending on the current state of those habitats in a particular area or reserve system, plans should first consider maintaining that habitat along with any important natural processes (e.g., periodic drying). Secondly, if the habitat is degraded or natural processes have been lost or averted, then restoration is conducive to amphibian success. Plans should minimize practices that directly degrade terrestrial habitat near breeding sites through intensive timber harvest, agriculture (including the periodic planting of food plots for game species or mowing), construction of buildings, and indirectly through site preparation (e.g., herbicide use). Such practices will likely disrupt local population processes by impacting the adult breeding population in the terrestrial environment surrounding a pond or along streams. If commercial activities such as timber harvest or recreational activities are necessary, buffer zones should be maintained around wetlands or along streams to prevent sedimentation and soil compaction, and removal of coarse woody debris should be minimized (deMaynadier and Hunter 1995). Also, minimizing roads or motorized vehicle traffic near breeding sites will reduce the number of road-kills of breeding adults (Fahrig et al. 1995, Lamoureux and Madison 1999) and potentially reduce loss of metamorphosing juveniles during the dispersal period. Redirecting new roads away from wetlands and the use of culverts or tunnels under existing roads to direct amphibian movements at known concentration points near breeding ponds is currently done in Europe and should be seriously considered more in the United States (van Leeuwen 1982, Langton 1989).

Likewise, practices to aquatic habitats should minimize effects (direct or indirect) on growth and metamorphosis of larvae. Obvious practices include the restriction of chemical use; for example, herbicide use along roads for weed control, salt on roads to eliminate ice, fire retardants, growth retardants on vegetation along roads or under powerlines, and pesticide use to control insects, especially near pools, ditches, streams, and ponds where runoff would find its way into wetlands. Sedimentation in aquatic habitats from permanent roads or temporary logging roads should be minimzed to prevent harmful effects on eggs, embryos, and gilled larvae. Less obvious, wetland management practices that drawdown marshes (also lowering the watertable for ephemeral pools) at appropriate times to enhance waterfowl production may decrease the probablity of metamorphosis of amphibian species, especially species with long larval periods. Likewise, flooding marshes (also raising the watertable) for waterfowl may facilitate the colonization of ephemeral pools by fish. Although no data are available on the effects of traditional management practices for game species such as drawdowns, burning, and mowing on nongame species like amphibians, managers should be aware of potential conflicts.

Further, managers also should consider responses to natural processes such as floods, fires, or succession. Any of these processes can be beneficial or harmful depending on the species, the region, and how the natural disturbance regime interacts with anthropogenic changes to the landscape. Periodic fires in the southeastern United States, for example, can increase productivity by releasing nutrients into ponds, thereby, increasing productivity and the number of metamorphosing juveniles. Fire also can reverse vegetation succession, especially the establishment of trees in wetland basins that increase transpiration of water and reduce light for primary production by closing the canopy. Vegetation succession can have a strong effect on species composition of amphibian communities (Skelly et al. 1999) and increases the probability of extinction of early successional species (Denton et al. 1997). If fires occur too frequently or during periods of terrestrial breeding migration, negative impacts may result. Awareness of positive, negative, and synergistic effects can help managers deal with processes of disturbance on a case-by-case basis to maintain natural regimes. However, 1 of the most difficult questions to answer concerning management of natural disturbance regimes is what was the natural frequency and extent of the disturbance factor historically, and is that regime now compatible with other land use practices.

Management plans also should eliminate avenues of colonization by fish such as drainage ditches that connect fish-inhabited areas (streams or rivers) with amphibian breeding ponds. Restoration of temporary wetlands will insure natural drying processes can work effectively to eliminate fish if they do invade. Elimination of other invasive species such as exotic fish or bullfrog larvae where they are not native by manipulated drying also would serve to promote successful metamorphosis of native species.

Plans that maintain natural vegetation buffer zone around ponds (recommended 164 m from the edge of wetlands; Semlitsch 1998) and along streams (recommended width 30–100 m but adjusted for stream width, slope, and site use; Rudolph and Dickson 1990, McComb et al. 1993, deMaynadier and Hunter 1995) will increase the probability of species persistence. It is critical to maintain an adequate area as well as a diversity of terrestrial habitats to maximize survival of juvenile and adult populations. Recent studies show that most amphibians must have access to a diversity of feeding and overwintering habitats in terrestrial environments, often some distance from breeding sites (Madison 1997, Lamoureux and Madison 1999). Although the value of natural vegetation corridors among wetlands is controversial for many species (Saunders and Hobbs 1991), with little known about their use by amphibians, most biologists advocate their consideration in management plans (Gibbs 1998). Even in the absence of vegetation corridors, the restoration of small wetlands to serve as stepping stones may increase the probability of rescue and species persistence because of the important effect distance has on dispersal success (Skelly et al. 1999).

Finally, it is also important to consider how a plan for amphibian management may conflict with plans for other wildlife species; that is, the possible tradeoff in management efforts and outcomes. As management plans become more inclusive of nongame species, the complexity of efforts will increase, and pose new problems to solve. One of the best and most pressing examples may be management for game fish such as trout, *Salmo* spp.; bass, *Micropterus* spp.; and bluegill (*Lepomis macrochirus*). A plan that restricts fish stockings to only the largest permanent ponds (i.e., deepwater lacustrine habitats, less desirable for amphibians) and those that are most easily accessed by fisherman (i.e., near roads) could leave an adequate number of other sites strictly for amphibians, and thereby, preserve both the sport fishery and the native faunal diversity.

What is apparent from the summary of current information is that both local population dynamics as well as metapopulation, source-sink dynamics are important to understanding any amphibian declines, regardless of the cause. If most or all of the 7 elements of the prescription for amphibian management can be enacted (Table 2), then it is likely that amphibian communities will persist and local declines may be reversed. Consider that some human impacts are temporary (e.g., short-lived chemical contamination); therefore, given favorable habitat conditions in adjacent areas, amphibians can often recolonize and undergo rapid population growth. Without the opportunity to recolonize restored habitats, populations would go extinct and eventually could lead to collapses of regional amphibian fauna (Drost and Fellers 1996). Although some data are available on individual effects of disease and chemical contamination on amphibians or on amphibian population response to single factors like competition or fish predation, investigations at multiple levels and scales such as individual, population, community, and landscapes have been limited. I strongly encourage more studies that link effects at multiple levels and especially tests of models of long-term population viability that include metapopulation dynamics and human disturbance factors at relevant spatial and temporal scales (Halley et al. 1996). My comments, suggestions, and summary of information are intended to provide a framework for future research on management issues pertaining to amphibians.

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GENETIC VARIABILITY AMONG POPULATIONS OF THE FLORIDA GRASSHOPPER SPARROW

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Abstract: Genetic variability within and among the 6 known populations of the endangered Florida grasshopper sparrow (*Ammodramus savannarum floridanus*) was examined using randomly amplified polymorphic DNA (RAPDs) and microsatellites. Information from DNA profiling may provide insight into sparrow movements and a basis for recovery efforts. Blood samples were collected from 118 individuals in southcentral Florida. Distances separating populations varied from 4.0 to 33.3 km. Measures of allele frequencies indicated reduced heterozygosity (mean $F_{IS} = 0.134$). Both the RAPD and microsatellite markers indicated little genetic differentiation among populations, except that the 2 smallest populations showed some genetic differentiation from the other populations based upon the RAPD markers. Small geographic distances and intervening unsuitable habitat do not appear to inhibit movements between populations. Genetic similarities also may indicate populations that are only recently isolated due to habitat fragmentation.

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The Florida grasshopper sparrow is 1 of 12 recognized subspecies (Vickery 1996) based upon its isolated breeding range and phenotypic characteristics (American Ornithologist's Union 1957). The sparrow was classified as endangered in 1986 because of its restricted distribution, loss of habitat, and decline in numbers (U.S. Fish and Wildlife Service 1988). Breeding aggregations are known from only 6 locations and <1,000 birds may exist Delany et al. (1999).

The objective of this study was to determine the genetic diversity within and among the 6 known populations of Florida grasshopper sparrows. Detailed genetic databases are important in the management of endangered species (Avise and Nelson 1989, Hall et al. 1992, Moritz 1994). The level of genetic variation may influence a population's growth rate and ability to adapt to changing environmental conditions (Leberg 1993). Severe reduction in numbers can cause reduced genetic variability with implications for long-term viability (Primack 1993). Populations of grassland birds often vary in abundance in response to an inherently unstable habitat (Cody 1985:197). The Florida grasshopper sparrow is at the edge of the species' geographic range and may thereby exhibit relatively low abundance and greater variability (Curnutt et al. 1996). Information from DNA profiling may provide insight into movements among Florida grasshopper sparrow populations and provide a basis for habitat management plans and possible translocation (U.S. Fish and Wildlife Service 1988).

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