

Amphibian Conservation and Wetland Management in the Upper Midwest: A Catch-22 for the Cricket Frog?

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Habitat loss is undoubtedly the largest single factor contributing to amphibian declines (Wyman 1990; Wake 1991; Vial and Salor 1993). But habitat loss alone cannot explain all amphibian losses, even in the midwestern United States. For example, in an earlier paper (Lannoo et al. 1994) my colleagues and I estimated about a three-order-of-magnitude decline in northwestern Iowa northern leopard frog (*Rana pipiens*) numbers over the past century. Over this same time period, Iowa has lost somewhere between 90 and 98 percent of its wetlands (Leja, Chpt. 36, this volume), a roughly two-order-of-magnitude drop. Therefore, a full-order-of-magnitude decline in leopard frog numbers in this region remains unexplained. These conclusions are supported by comparing Frank Blanchard's (1923) published descriptions and cataloged field notes with our more recent data. Blanchard reported that leopard frog tadpoles were the "widespread and abundant amphibian of the region" and "at least one specimen [of tiger salamander] was found in nearly every pond seined," while in the early 1990s we found leopard frogs in twenty-four of thirty-four wetlands sampled and tiger salamanders in eighteen of thirty-two wetlands sampled. Blanchard's cricket frog (*Acris crepitans blanchardi*) declines are occurring in the absence of a similar magnitude of wetland loss (and indeed in the absence of similar declines in other amphibian species) in the northern tier of midwestern states. The question that arises is whether the alteration of remaining habitats can explain amphibian declines beyond those predicted by habitat loss.

Wetlands constrain the organisms that inhabit them through hypoxia and desiccation. Animals that have

access to the water surface avoid hypoxia by breathing atmospheric oxygen, an option under summer nighttime conditions but not under the ice during northern winters (Manion and Cory 1952; Barica and Mathias 1979; Bradford 1983). Animals avoid desiccation either through aestivation or by seeking alternate habitats. Extreme hypoxia and desiccation generally occur during prolonged (two- to three-year) droughts, which develop in the upper Midwest on a roughly ten-year cycle (Bachmann and Jones 1974; Lannoo 1996a,b).

In the upper Midwest, wetland basins vary in size and depth along a continuum from small, temporary wetlands to large recreational lakes. For the purpose of this discussion, I divide these basins into three types based on oxygen and drying regimes during droughts (Fig. 34-1):

1. Basins that dry—seasonal (e.g., Type III, Stewart and Kantrud 1971; PEMC, National Wetlands Inventory [NWI] classification) and semipermanent wetlands (e.g., Type IV, Stewart and Kantrud 1971; PEMF, NWI classification)
2. Basins that retain water but become hypoxic—permanent wetlands (e.g., Type V, Stewart and Kantrud 1971; PEMH and POWH, NWI classification)
3. Basins that retain water and contain high oxygen levels—lakes (LEM and LOW, NWI classification)

In the Prairie Pothole region of northwestern Iowa (van der Valk 1989), aquatic vertebrates sort themselves out by habitat type. Six or seven native amphibian species, which have lungs as larvae and therefore can breathe atmospheric oxygen, are found in wetlands (Ta-

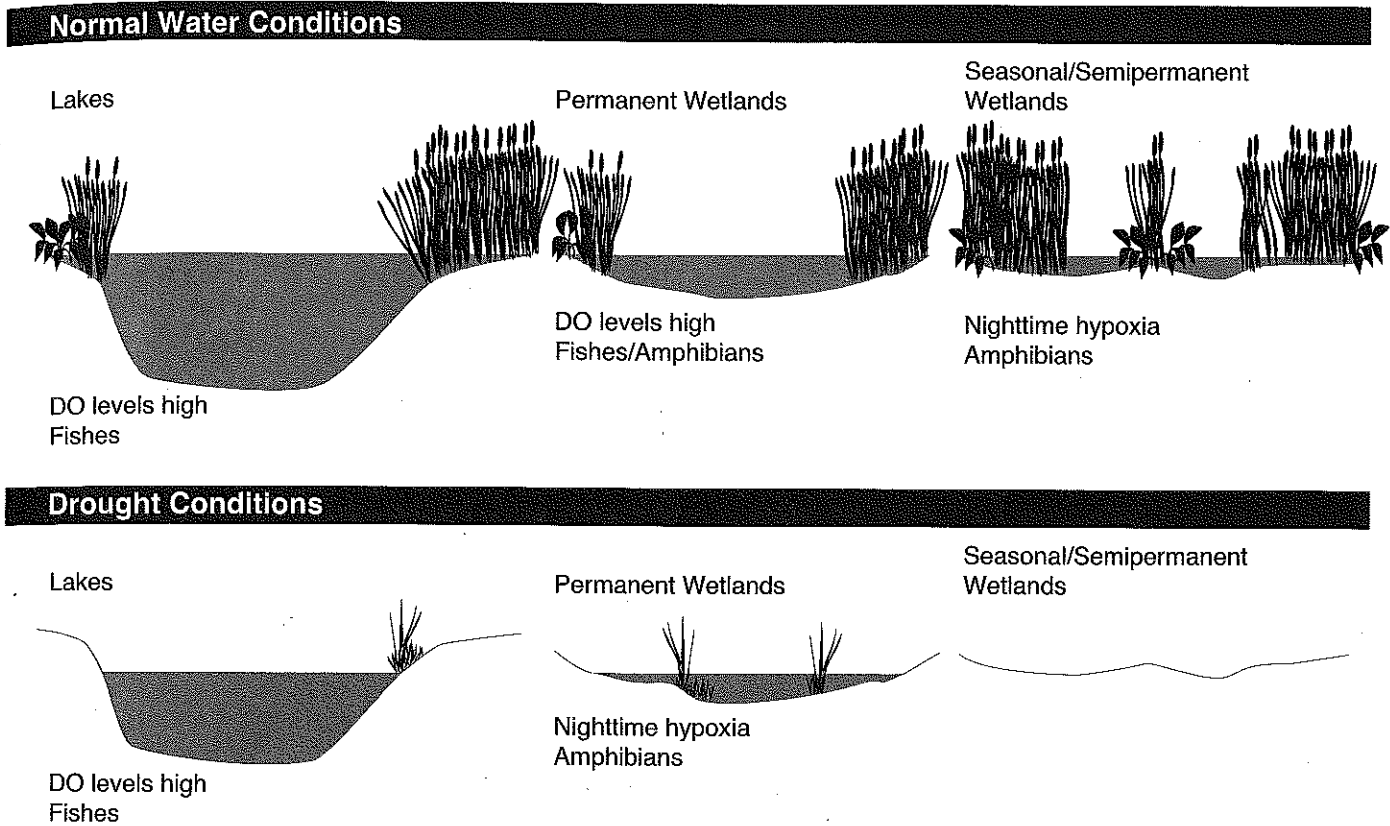


Figure 34-1. Schematic diagrams illustrating interactions between amphibians and wetland types across drought cycles. During average- to high-water years (top), amphibians will successfully reproduce in seasonal and semipermanent wetlands and in the permanent wetlands that do not contain fishes. During droughts (bottom), amphibians will tend to be restricted to breeding in permanent wetlands. These wetlands may lose their fish fauna as they acquire the daily dissolved oxygen (DO) fluctuations characteristic of semipermanent wetlands during average- to high-water years; these wetlands therefore will tend to summerkill and perhaps winterkill.

ble 34-1; Blanchard 1923; Lannoo et al. 1994), while about four dozen fish species are found naturally in lakes (Larrabee 1927a,b; Lannoo 1996a). Habitat separation (allotopy) is nearly complete between these groups; wetland hypoxia and periodic desiccation exclude fishes (Ayles et al. 1976; Barica and Mathias 1979; Peterka 1989), and established predatory fishes in lakes feed upon and eliminate most species of amphibian larvae (Burger 1950; Blair 1951; Levi and Levi 1955; Brandon and Bremer 1967; Efford and Mathias 1969; Pennak 1969; Tanner et al. 1971; McCann 1977; Sexton and Bizer 1978; Petranka 1983; Sexton and Phillips 1986; Semlitsch 1987, 1988; Semlitsch and Gibbons 1988; Figiel and Semlitsch 1990; Bradford 1991; Bristow 1991; Liss and Larson 1991; Holomuzki 1995; but see Taylor 1983; Kats et al. 1988; Lawler 1989; Werner 1991). In the Prairie Pothole region, exceptions to this allotopy include

American toad (*Bufo americanus*) tadpoles, which are occasionally found in lakes or river backwaters; Great Plains toad (*Bufo cognatus*) tadpoles, which are reported to occur in rivers (Stebbins 1985); mudpuppies (*Necturus maculosus*), which occur in larger bodies of water (Bishop 1943); and brook sticklebacks (*Culea inconstans*) and minnows in the genus *Pimephales*, which are occasionally found naturally occurring in pothole wetlands (personal observation; also Peterka 1989).

In the upper Midwest, amphibians successfully reproduce in seasonal and semipermanent wetlands under normal water conditions; they will also successfully reproduce in permanent wetlands if no predatory fishes are present (Petranka 1983; Sexton and Phillips 1986; Bradford 1989, 1991; Bradford et al. 1993; Fellers and Drost 1993; Brönmark and Edenhamn 1994). Fishes will be found in lakes and in the permanent wetlands that

Table 34-1. The native amphibians of northwestern Iowa, after Lannoo et al. (1994)

Caudata
Ambystomatidae
Eastern tiger salamander (<i>Ambystoma tigrinum tigrinum</i>)
Proteidae
Mudpuppy (<i>Necturus maculosus maculosus</i>)?
Anura
Bufonidae
American toad (<i>Bufo americanus</i>)
Great Plains toad (<i>Bufo cognatus</i>)*
Ranidae
Northern leopard frog (<i>Rana pipiens</i>)
Hylidae
Gray treefrog complex (<i>Hyla versicolor/chrysoceles</i>)
Western chorus frog (<i>Pseudacris triseriata triseriata</i>)
Blanchard's cricket frog (<i>Acris crepitans blanchardi</i>) [†]

*Appears to have naturally immigrated within the past two decades.

[†]Extirpated.

they have managed to colonize (Fig. 34-1). (For a remarkably similar view of the effects of water permanence on amphibians, with an emphasis on tadpoles, activity levels, and invertebrate predators, see Skelly 1997.) During droughts, amphibians will be excluded from breeding in seasonal and semipermanent wetlands due to dry conditions (Pechmann et al. 1989; Wissinger and Whiteman 1992; Dodd 1993, 1994; Semlitsch et al. 1996) but can breed in permanent wetlands that do not hold fish or once held fish that have since been extirpated through hypoxia (Fig. 34-1). Lakes, of course, hold fish regardless of water regime.

An Empirical Model

Under natural conditions, permanent wetlands will contain a flexible fauna, favoring fishes during high-water years and amphibians during drier years (Fig. 34-2). Permanent wetlands provide reproductive sites for amphibians during prolonged droughts, when seasonal and semipermanent wetlands are unavailable (Dodd 1994). Therefore, the effects of drought on amphibians will depend on the extent that permanent wetlands are anthropogenically impacted, for example, by aquacultural practices (see below; Lannoo 1995, 1996a).

The following specific hypotheses can be derived from the scenario proposed above.

1. Amphibian species with high breeding site fidelity (philopatry) during average- to high-water years will be unlikely to shift breeding sites during droughts from seasonal or semipermanent wetlands to permanent wetlands.

Many studies report either philopatry or small home ranges among amphibian species with a complex life history, including the species and genera represented in the upper Midwest (see Table 34-2; but see also Dodd 1993, 1994). Philopatry is not absolute, however. In several of these species, dispersal has been documented between adjacent populations (Cummings 1912; Semlitsch 1983b; Breden 1987; Caldwell 1987; Sjögren 1991; Sjögren Gulve 1994; Alfaro 1995; Sexton et al., Chpt. 35, this volume). Furthermore, dispersal into new areas occurs. In northwestern Iowa, amphibians naturally recolonize restored wetlands rapidly, in many cases during the first spring following the restoration (Lannoo et al. 1994; Lannoo 1996a,b).

2. The ability of a species to survive a drought will be directly proportional to a species' longevity and/or its tendency to shift breeding sites to permanent wetlands (Dodd 1993).

Many ambystomatid salamanders and bufonid, ranid, and hylid frogs for which there are data (Table 34-3)

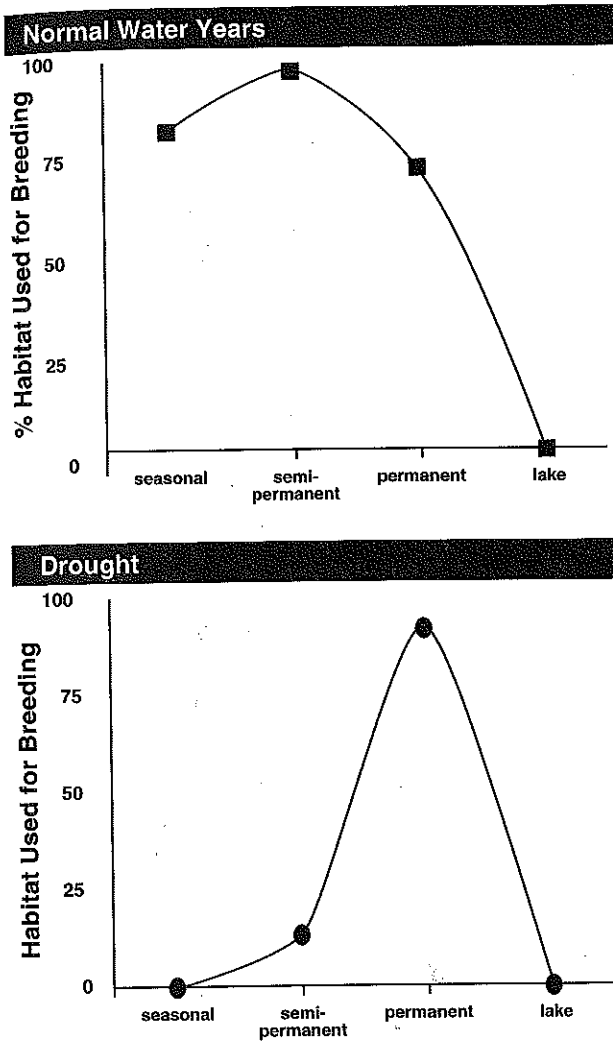


Figure 34-2. The probability that wetlands will support successful reproduction of amphibians varies with water regime. Note that during average- to high-water years, seasonal and semipermanent wetlands support high levels of amphibian breeding (top). During droughts, however, seasonal and semipermanent wetlands dry, and permanent wetlands must support the bulk of amphibian breeding. The probabilities illustrated here assume historical conditions: that virtually all seasonal and semipermanent wetlands support amphibian breeding during average- to high-water years (Blanchard 1923) and that an estimated 75 percent of permanent wetlands are fishless. Again, fishes that managed to colonize permanent wetlands during normal years will likely be extirpated during droughts due to summer and/or winter hypoxic conditions. It follows that anthropogenic alterations of permanent wetlands, which typically make them unsuitable for successful amphibian reproduction, will limit the drought tolerance of amphibian populations.

appear to live long enough to survive two- to three-year droughts. Furthermore, Pechmann et al. (1991) report that tiger salamanders, other *Ambystoma* species, and the ornate chorus frog (*Pseudacris ornata*) can delay reproduction for up to five years under drought conditions. In contrast, Burkett (1984) demonstrates that Kansas populations of Blanchard's cricket frog have a short life span. Average life expectancy is four months; only 5 percent of the population survive the winter; complete population turnover occurs every sixteen months. While cricket frogs in central Indiana do not seem to be affected by a single year of drought (S. Perrill, personal communication), cricket frogs likely cannot postpone breeding past one or two years. Delaying reproduction may prolong the life span of amphibians (Caldwell 1987), but cricket frogs would need to double or triple their life span to survive a prolonged drought. The other option available to them is to shift breeding sites to permanent wetlands (Dodd 1993, 1994; S. Perrill, personal communication).

3. Permanent wetlands will be used as alternative amphibian breeding sites during droughts in proportion to the wetlands' proximity to seasonal and semipermanent wetland breeding sites (see Brown and Dinsmore [1986] for a general discussion and Sjögren [1991] and Sjögren Gulve [1994] for the European *Rana lessonae*).

For many amphibians, wetlands are easier to locate if they are close rather than distant. If distant wetlands are somehow known, migrating to them across a fragmented landscape becomes a greater challenge. Sjögren (1991), Laan and Verboom (1990), and Mann et al. (1991) have found that, in an array of ponds, distance from a source population reduces the probability of the presence of amphibian species.

4. Amphibian species with toxic or distasteful eggs or tadpoles, such as *Bufo* (Licht 1968; Brodie et al. 1978; Kruse and Stone 1984; Brodie and Formanowitz 1987) and bullfrogs (*Rana catesbeiana*) (Kruse and Francis 1977; Formanowitz and Brodie 1982), or with highly efficient antipredator responses to fishes (Brockelman 1969; Beiswenger 1975, 1977; Petranka et al. 1987; Sih et al. 1988; Resitarits and Wilbur 1991; Skelly 1994, 1995; Holomuzki 1995) will be more likely than species without such attributes to be found in permanent wetlands during any phase of the drought cycle (see also Kruse and Francis 1977).

Amphibians that have evolved mechanisms to avoid

Table 34-2. Studies citing philopatry or small home ranges in amphibian genera represented in the upper Midwest

Family Species	Reference
Bufonidae	
American toad (<i>Bufo americanus americanus</i>)	Oldham 1966; Dole 1972
Western toad (<i>Bufo boreas</i>)	Tracy and Dole 1969
European toad (<i>Bufo bufo</i>)	Reading et al. 1991; Schlupp and Podloucky 1994
Marine toad (<i>Bufo marinus</i>)	Brattstrom 1962; Carpenter and Gillingham 1987
Fowler's toad (<i>Bufo woodhousii fowleri</i>)	Breden 1987
Hylidae	
Pacific treefrog (<i>Hyla regilla</i>)	Jameson 1957
Cope's gray treefrog (<i>Hyla chrysoscelis</i>)	Ritke et al. 1991
Ornate chorus frog (<i>Pseudacris ornata</i>)	Pechmann et al. 1991
Western chorus frog (<i>Pseudacris triseriata triseriata</i>)	Smith 1987
Ranidae	
Northern leopard frog (<i>Rana pipiens</i>)	Dole 1965
Bullfrog (<i>Rana catesbeiana</i>)	McAttee 1921; Raney 1940
Green frog (<i>Rana clamitans melanota</i>)	Shirose and Brooks 1995
Mink frog (<i>Rana septentrionalis</i>)	Shirose and Brooks 1995
Wood frog (<i>Rana sylvatica</i>)	Berven 1990
Ambystomatidae	
<i>Ambystoma</i>	Williams 1973
Jefferson salamander (<i>Ambystoma jeffersonianum</i>)	Douglas and Monroe 1981
Spotted salamander (<i>Ambystoma maculatum</i>)	Shoop 1965; Whitford and Vinegar 1966; Douglas and Monroe 1981; Stenhouse 1985; Phillips and Sexton 1989
Marbled salamander (<i>Ambystoma opacum</i>)	Shoop and Doty 1972; Douglas and Monroe 1981; Stenhouse 1985; Pechmann et al. 1991
Mole salamander (<i>Ambystoma talpoideum</i>)	Hardy and Raymond 1980; Semlitsch 1981; Semlitsch et al. 1988; Pechmann et al. 1991
Eastern tiger salamander (<i>Ambystoma tigrinum tigrinum</i>)	Semlitsch 1983a; Pechmann et al. 1991

certain predators will always be more successful when exposed to these predators than will other species. Therefore, predator-tolerant species will have a wider variety of breeding habitat options available to them.

5. Amphibians and fishes can co-occur, at least in the short term, if the fishes are nonpredatory.

In northwestern Iowa, examples of nonpredatory fishes that co-occur with amphibian larvae include the brook stickleback and bluntnose and fathead minnows (*Pimephales notatus* and *Pimephales promelas*, respectively) (personal observation; see also Peterka 1989). Interactions between amphibians and these fishes will be based on competitive, rather than predatory, factors. In my experience with *Pimephales* introductions, as the sum-

mer progresses competition will eventually favor these fish.

6. Predatory interactions between midwestern fishes and tadpoles will always favor fishes (Bradford 1991; Sjögren 1991; Alfaro 1995), because midwestern tadpoles are herbivorous. Predatory interactions between fishes and tiger salamander larvae will depend more on the size of the interacting individuals than on the fish species involved.

Aquatic vertebrates tend to be "gape-limited" (Zaret 1980). That is, they swallow their prey whole, and therefore the largest prey a predator can ingest depends upon the predator's mouth size, which within a species is typically dependent on body size. The tadpoles of the

Table 34-3. Longevity of amphibian species and genera represented in the Prairie Pothole region of the upper Midwest. Age may vary among populations, particularly along a north-south gradient, so these values should only be used as an estimate of life span in the upper Midwest.

Species	Maximum Age (yrs.)	Technique	Location	Source
American toad (<i>Bufo americanus americanus</i>)	36 years in captivity 5*	Osteology	Illinois	Dickerson 1906 Acker et al. 1986
Bullfrog (<i>Rana catesbeiana</i>)	6+	Osteology	Missouri	Schroeder and Baskett 1968
Northern leopard frog (<i>Rana pipiens</i>)	4**	Osteology	Quebec	LeClair and Castanet 1987
Asiatic frog (<i>Rana sakuraii</i>)	5*	Osteology	Japan	Kusano et al. 1995
Blanchard's cricket frog (<i>Acris crepitans blanchardi</i>)	1.5	Mark-recapture	Missouri	Burkett 1984
Western chorus frog (<i>Pseudacris triseriata triseriata</i>)	2+	Mark-recapture	Upper Mich.	Smith 1987
Southern chorus frog (<i>Pseudacris nigrita</i>)	2***	Toe clipping	S. Carolina	Caldwell 1987
Ornate chorus frog (<i>Pseudacris ornata</i>)	2***	Toe clipping	S. Carolina	Caldwell 1987
Illinois chorus frog (<i>Pseudacris streckeri illinoensis</i>)	2+	Toe clipping	Cent. Illinois	Tucker, this volume
<i>Ambystoma</i>	25 years in captivity			Duellmann and Trueb 1986
Mole salamander (<i>Ambystoma talpoideum</i>)	5 females* 7 males*	Mark-recapture	Louisiana	Raymond and Hardy 1990

*Reproductive individuals.

**Force (1933) calculates the age of first breeding at three years in populations in the lower peninsula of Michigan.

***Maximum age two years, turnover rate essentially annual.

upper Midwest (with the possible exception of the plains spadefoot toad [*Spea bombifrons*]; see Farrar and Hay, Chpt. 10, this volume) have small mouths specialized for scraping and ingesting algae and periphyton; they are not carnivorous at any stage of their life history. In turn, they are susceptible to fish predation. Salamander larvae are predatory and when large can severely impact larval fish populations (Lannoo 1996a). One form of tiger salamander has uncoupled mouth size from body size. Cannibal morph tiger salamander larvae have proportionately large heads and mouths and hypertrophied vomerine teeth (Powers 1907; Lannoo and Bachmann 1984; Whiteman and Howard, Chpt. 32, this volume) and may have a greater tendency toward piscivory than do typical morph larvae.

7. If prolonged droughts are not adversely affecting amphibian populations, the reappearance of amphibians in rehydrated seasonal and semipermanent wetlands following droughts should closely match the species composition and abundance of the predrought assemblage. Conversely, if droughts are impacting amphibians, recolonization following droughts should be gradual rather than immediate and involve adding species as well as individuals.

In my experience, droughts impact amphibian populations. Postdrought amphibian assemblages are reduced compared to predrought assemblages; over time and with good water levels, numbers increase back to predrought levels (Lannoo et al. 1994). This recruitment can come either from within the population or

from adjacent populations: If postdrought reductions do not involve the loss of species, recruitment could come solely from within each population—the offspring of surviving adults. Additional animals could immigrate from neighboring populations. If reductions involve the loss of species, individuals from these species must immigrate from neighboring populations (Corn and Fogleman 1984 for the northern leopard frog). Recolonization rates will be based on regional abundance (Laan and Verboom 1990) and the proximity of breeding adults emerging from overwintering sites to the wetland.

It has become axiomatic in conservation biology that anthropogenic habitat fragmentation poses a major threat to many populations. Fragmentation endangers populations by reducing their size, increasing their isolation, restricting gene flow, reducing habitat quality, reducing habitat area and heterogeneity, and increasing edge effects (Wilcove et al. 1986). Sjögren (1991), Wake (1991), and Wyman (1990) have suggested that habitat fragmentation has played a role in the recent declines and disappearances of amphibian populations. In fact, there are several examples of amphibians disappearing from naturally drought-susceptible habitats where the normal avenues used by recolonizing individuals have been compromised. Corn and Fogleman (1984) have suggested that the local extinctions of northern leopard frogs that they observed might be a common natural occurrence, because small populations in drought-susceptible ponds are separated by dry forests that provide few dispersal routes. Likewise, Bradford (1991) observed that mortality and extinctions in populations of *Rana mucosa* in the Sierra Nevada, California, were probably due to natural causes that occurred irregularly in time and space. The historical persistence of these populations probably depended upon recolonization from other sites following such extinctions, but the widespread introduction of fish to lakes and streams in the Sierra Nevada during this century may now preclude such dispersal. Similarly, Weygolt (1989) feared that forest destruction might prevent the recolonization of hylodine frogs that were probably eliminated by drought from the forests around Santa Theresa, Brazil.

Alternative Interpretations

Several workers have noted an apparent incongruity between the constraint of philopatry and an unpredictable breeding habitat. The usual interpretation is that selection has favored juvenile dispersal (i.e., philopatric as-

sociations are determined in juveniles, not in larvae or in metamorphosing animals). For example, Gill (1978a) concluded that, for the newt (*Notophthalmus viridescens*), small pond habitats are population sinks (see below), that homing behavior evolved as a consequence of natural selection within metapopulation centers, and that the eft stage is the mechanism of dispersal to new ponds. Breden (1987) calculated that about 49 percent of juvenile Fowler's toads (*Bufo woodhousii fowleri*) in each generation disperse to adjacent ponds in the Indiana Dunes. Caldwell (1987) suggested that selection has favored juvenile dispersal in *Pseudacris* treefrogs as an alternative to longevity and iteroparity of individual females. But are philopatric adults able to change breeding sites when they discover that their "home" wetland is not suitable for breeding? Brandon and Ballard (Chpt. 15, this volume) and Tucker (Chpt. 14, this volume) demonstrate that, when historic sites are made unsuitable for breeding because of natural fish introductions, Illinois chorus frog (*Pseudacris streckeri illinoensis*) adults migrate to a nearby suitable wetland to breed. A second alternative is for amphibians to remain near the home pond and postpone breeding (Pechmann et al. 1991). But as pointed out above, the success of this behavior is directly related to life span. Therefore, this is not an option for a species with a short life span, such as the cricket frog. Furthermore, what happens when migrating philopatric adults discover a newly established suitable breeding habitat? Some animals must breed in the new basin—restored wetlands are rapidly colonized, even during wet years when natal ponds hold water.

The Metapopulation Concept

The scenario proposed here is consistent with the concept of metapopulations, where the emphasis is placed on the interactions among local populations and the regional metapopulation is treated as the functional unit. In metapopulations, individual populations are generally divided into sources and sinks. Source populations are considered to produce an overabundance of animals, which can then disperse into sink populations. Sink populations lose more individuals than they can gain through reproduction alone (Levin 1976; Pulliam 1988; Hanski and Gilpin 1991; for *Notophthalmus*, see Gill 1978a,b). Typically, our impressions of source and sink populations are tied to habitat quality—source populations inhabit optimal habitats, sink populations occupy suboptimal or marginal habitats—and habitat quality has been assumed to be static over time. Here, I suggest

that wetland quality changes for amphibians and that each population can be either a source or a sink depending on habitat type, fish presence, and phase of the drought cycle (Table 34-4). Temporary and semipermanent wetlands should support source populations during average- to high-water years but become sink populations during droughts. Permanent wetlands that contain fish are sinks except during and immediately after droughts, when summer- and/or winterkills reduce or eliminate fishes and provide at least the potential to support source populations. Permanent wetlands that do not hold fish should always support source populations, except perhaps when exposed to heavy predation pressure from invertebrates (Caldwell et al. 1981; Travis et al. 1985).

Management

The question frequently arises: How does one manage for amphibians? The answer in the upper Midwest appears to be to provide a series of fishless wetlands of various types—from seasonal to permanent—placed within the home range of the various native species. These wetlands should be connected by upland migration corridors (or better yet, an undisturbed landscape; see Fahrig and Merriam 1985) and habitat for terrestrial life history stages. If even one of these factors is overlooked—i.e., there are no permanent wetlands, wetlands contain fish, wetlands are too far apart, or there is no adjacent terrestrial habitat—one can reasonably expect that the requirements of amphibians will not be met at some point across the drought cycle and that population sizes and perhaps the number of species will be reduced.

A Case Study: The Cricket Frog

The most intractable mystery involving amphibian declines in the upper Midwest is the disappearance of the cricket frog (Hay, Chpt. 11, this volume). This frog is now extirpated from much of this region, including northwestern Iowa. There, the exact spots where cricket frogs were collected in the early part of the twentieth century have been visited repeatedly (Blanchard 1923; Tweed 1938), and none have been found (Lannoo et al. 1994; Lannoo 1996a,b). Whereas factors such as UV-B radiation and habitat contamination due to agricultural chemicals cannot be ruled out, cricket frog declines may simply be due to a combination of three factors: the cricket frog's short adult life span, prolonged droughts, and anthropogenic alterations of permanent wetlands.

In short, the cricket frog's brief life span dictates that this animal must breed annually. If droughts dictate that frogs must breed in permanent wetland, and if permanent wetlands are being rendered unsuitable for successful cricket frog reproduction by anthropogenic factors, then we would expect to find the cricket frog declines that we are now observing. Isolation of habitats due to landscape fragmentation would preclude recolonization and further exacerbate these effects. Ralin and Rogers (1972) demonstrate that cricket frogs are unusually susceptible to drought. Further support for this hypothesis comes from the fact that cricket frogs are declining in the northern portion of their range (dominated by discrete pothole wetlands) but are doing well in the southern portion of their range (dominated by continuous riparian habitats). There may be north-south gradients in UV-B effects and agricultural impacts in the Midwest, but these have not been investigated with reference to amphibian declines. If the scenario described above is true, cricket frogs are faced with a catch-22 situation during prolonged droughts: they may either delay breeding or breed in wetlands that have been co-opted for anthropogenic uses, such as aquaculture. Neither situation will result in reproductive success.

The hypothesis proposed here is not supported by the observation that cricket frog populations inhabiting riparian wetlands are also in decline in the upper Midwest. Drought cycles should have little effect on the reproductive success of riparian populations; in fact, historically in Wisconsin, cricket frog populations were most robust along medium and large rivers, such as the Black, Rock, and Wisconsin Rivers (R. Hay, personal communication). It is true that the seasonal flooding characteristic of these riparian wetlands has been reduced by dams built during the 1930s and 1940s and that in response, populations of paddlefish (*Polyodon spathula*), northern pike (*Esox niger*), and walleye (*Stizostedion vitreum*) have declined (R. Hay, personal communication). The effect of dam building on cricket frogs remains unknown. Wetland cricket frog populations may have declined in response to anthropogenic alterations of permanent wetlands, and riverine populations may have declined in response to dams. It may also be true that wetland and riparian cricket frog populations in the upper Midwest have declined because they have been affected by some common factor as yet unidentified.

General Considerations

For the scenario proposed for cricket frog declines to

Table 34-4. Interactions between amphibians and wetland types across drought cycles (refer to Figs. 34-1 and 34-2) viewed in a metapopulation context

	Wetland Type			
	Seasonal	Semipermanent	Permanent	Lake
Water Regime				
Normal water levels	Source	Source	Source if fishless Sink if fish present	Sink Sink
Drought	Sink	Sink*	Source	Sink

*Some semipermanent wetlands may hold water long enough to support reproduction in anurans with a brief tadpole stage, such as bufonids.

be realistic, permanent wetlands currently must be undergoing anthropogenic changes on a regional scale. In fact, this may be one of the strongest components to this argument. I have discussed anthropogenic impacts on permanent wetlands elsewhere (Lannoo 1995, 1996a,b) but will briefly summarize them here: (1) drainage culverts and weirs that connect wetlands to lakes—culverts serve as corridors for fishes to migrate into wetlands; (2) aquacultural practices—the raising of game fish and bait fish has altered many, if not most, of the permanent wetlands of the upper Midwest and involve both publicly and privately owned basins; and (3) bullfrog introductions—because bullfrog tadpoles must overwinter, bullfrogs congregate in and around permanent wetlands. Bullfrogs feed heavily on amphibians (e.g., cricket frogs, Burkett 1984) and other smaller vertebrates to the point of excluding them. In northwestern Iowa, in habitats where introduced bullfrogs occur, native amphibians that were historically present are absent (while native amphibians are present in similar nearby wetlands that do not contain bullfrogs; Lannoo et al. 1994; Lannoo 1996a,b). Introduced bullfrogs spread during high-water years. Bullfrogs introduced into northwestern Iowa have spread into Minnesota (Oldfield and Moriarty 1995).

Finally, it is important to realize that the model proposed here does not address all of the factors involved in the reproductive success of Prairie Pothole amphibians. Other factors that have been shown to influence reproductive success include timing of breeding (Harris 1980; Semlitsch 1983a, 1988; Shirose and Brooks 1995), larval competition (Brockelman 1969; Wilbur 1972; Morin 1983; Alford and Wilbur 1988; Wilbur and Alford 1985),

and larval predation (Voris and Bacon 1966; Wilbur 1972; Caldwell et al. 1981; Morin 1983; Semlitsch 1983a; Stenhouse et al. 1983; Wilbur et al. 1983; Lannoo and Bachmann 1984). These factors are important and may be crucial to reproductive success, but each is contingent on animals finding a breeding site across both a naturally changing and an anthropogenically altered landscape.

Summary

While habitat destruction is often implicated as the major factor underlying modern amphibian declines, in the upper Midwest habitat alteration probably plays a larger role. Natural wetlands constrain the organisms that inhabit them through hypoxia and desiccation, conditions contingent on water level. Extreme hypoxia and desiccation generally occur during prolonged droughts, which develop on a roughly ten-year cycle in the upper Midwest. Wetland basins in this region range in size and depth along a continuum from small, temporary wetlands to large recreational lakes. Under normal conditions amphibians here successfully reproduce in seasonal and semipermanent wetlands. Amphibians will also successfully reproduce in permanent wetlands if no predatory fishes are present. During droughts, amphibians will be excluded from successfully reproducing in seasonal and semipermanent wetlands (because they hold little or no water) but can reproduce in permanent wetlands without fish or that once held fish that were extirpated through drought-induced hypoxia. I suggest that, under natural conditions, permanent wetlands contain a flexible fauna, favoring fish during high-water

years and amphibians during dry years. Therefore, permanent wetlands provide reproductive sites for amphibians during prolonged droughts, when seasonal and semipermanent wetlands are unavailable. It follows that the effect of droughts on amphibians will depend on the extent that permanent wetlands are impacted by anthropogenic factors, the most serious and widespread probably being aquacultural practices.

While all amphibian species in the upper Midwest have been affected by aquaculture, Blanchard's cricket frogs (*Acris crepitans blanchardi*) may be the hardest hit. These frogs have a life span of only sixteen months and therefore may encounter an ecological situation for which they have no behavioral or life history solution. Faced with drought, modern populations of cricket frogs appear to have two options: postpone reproduction or reproduce in anthropogenically altered permanent wetlands. Neither may ultimately result in successful reproduction; cricket frogs cannot outlive multiyear droughts, and many permanent wetlands are impacted. Cricket frog declines in the northern portion of their

range may be at least partially explained by the effects of drought on an anthropogenically altered landscape.

Management for amphibians in the Prairie Pothole region of the upper Midwest should include habitat: (1) that contains relatively closely spaced but isolated, fishless wetlands; (2) that consists of an assortment of wetland types, including temporary and permanent basins; (3) in which wetlands are connected by upland corridors; and (4) that can be used by mammals in their terrestrial life history stages.

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