Small, Clustered Wetlands Promote Amphibian Persistence

A diversity of wetlands—small and large, permanent and ephemeral—are important for the biodiversity of amphibians.

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The perennial argument about whether several large or many small wetlands are best for mitigation and conservation is still debated among practitioners in many disciplines. Although we believe many of the arguments for larger wetlands are a function of narrow historical momentum favoring deep, open-water wetlands and the economics that building a single large wetland is cheaper, the arguments against large wetlands are substantial and can be supported on biological grounds (e.g. Semlitsch and Bodie 1998; Snodgrass et al. 2000). In this paper, we will present our perspective on why amphibians appear to do best in smaller, seasonal wetlands and why wetland spatial arrangement on the landscape in clusters is beneficial. Although we acknowledge that amphibians represent just one group of organisms using wetlands, we believe they are important for ecosystem function and they may represent other taxa with similar life histories.

The essential argument against large wetlands for amphibians centers on their permanence and accumulation of predators. Although we know that there are exceptions, wetlands that are large in area and deep are generally more permanent than small, shallow wetlands. This is a basic function of the sheer volume or depth of water they hold and the lack of drying on a biologically relevant time scale. We acknowledge that all wetlands may dry under extreme circumstances over the long term, but large wetlands certainly do not dry annually or even every few years. It is more likely for them to dry only after droughts and at time scales of 10-20 years. For many organisms, like amphibians, life cycles and generation times are usually annual or just a few years. This permanence of large wetlands selects for organisms that both require and tolerate static aquatic conditions, and in many cases, these conditions select for largebodied predatory species, especially fish (Wellborn et al. 1996). The opposite end of the hydroperiod spectrum selects for species that require and tolerate ephemeral conditions associated with rapid, seasonal drying of wetlands, especially small, fast-growing prey species (Wellborn et al. 1996). Because the larval aquatic stage of nearly all frogs and toads is small, fast-growing, and herbivorous, they easily fall into the vulnerable prey category. Most require predator-free aquatic habitats that are primarily seasonal wetlands. Some species, of course, are fairly large and possess strong anti-predator mechanisms to survive in predator-rich wetlands, such as bullfrogs or green frogs that have skin toxins. However, these species represent a small

fraction of the other 90+ species of North American anurans, and in many cases, bullfrogs and green frogs are common or invasive. In large wetlands, these latter two species can dominate and limit the native diversity of amphibian species. The other portion of amphibian biota are aquatic salamander larvae that are carnivorous but still relatively small and highly susceptible to predation by larger predator species like fish. Thus, large, permanent wetlands exclude a significant portion of amphibian biodiversity. Small wetlands, on the other hand, dry seasonally and, most importantly, prevent the accumulation of both invertebrate and fish predators. Therefore, as argued previously (Semlitsch and Bodie 1998), these smaller seasonal wetlands usually contain higher species richness and higher abundance than larger permanent wetlands. Results from a recent study of constructed ponds in Missouri shows that species richness is highest at relatively small sizes centered on just ~400 m² (Figure 1).

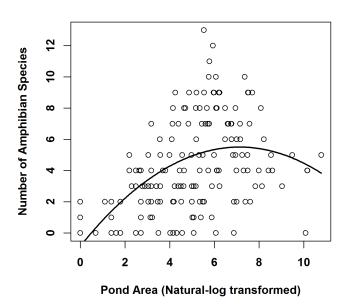


Figure 1. Relationship between amphibian species richness and pond surface area (m2) from N = 169 constructed ponds in Missouri (unpublished data).

Our second perspective is that wetlands arranged close together in clusters promotes amphibian abundance and persistence. We argue this with two relevant facts: the first of which is that landscapes of natural wetlands are dominated by large numbers of small wetlands. For example, on the South Carolina coastal plain, 46% of natural depressional wetlands are 1.2 hectares or less, and 87% are 4.0 hectares or less in size (Figure 2; Semlitsch and Bodie 1998). The high number of small wetlands results in a high density on the landscape and shorter inter-wetland distances than a few large wetlands on the landscape. Wetlands in the northeastern United States such as vernal pools are even smaller and denser (Colburn 2004). The spatial distribution of wetlands becomes critical for two reasons: (1) it insures multiple breeding options for amphibians in close proximity; and (2) it ensures that local population extinctions can be easily reversed by recolonization if distances between adjacent wetland are close enough for dispersal. Average dispersal distance of amphibians is roughly 1.0-1.5 kilometers, and inter-wetland distances beyond this reduce the probability of rescue through recolonization and increases the chance of regional species extinctions (Semlitsch 2008). Studies have shown that as small wetlands are lost or not replaced, the remaining large wetlands become more dispersed and the interwetland distance increases significantly (Gibbs 1993; Semlitsch and Bodie 1998). If this distance exceeds the dispersal distance of amphibians, rescue is not possible. Again, not all species respond the same, and large species such as bullfrogs can likely disperse longer distances than small chorus frogs or most salamanders that possess limited movement capacity. Further, the clustering of wetlands also promotes increased larval abundance of common anuran species (Shulse et al. 2010) and for salamanders (Peterman et al. 2013). Although we do not know the mechanism of how the presence of nearby wetlands actually promotes larval abundance, we suggest nearby wetlands may act as a reservoir of breeding adults, provide a

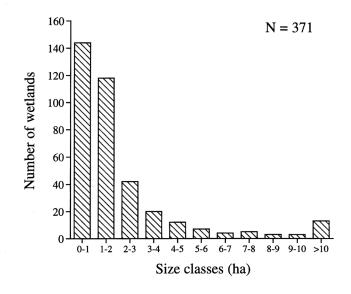


Figure 2. Size distribution of N = 371 natural depressional wetlands on the coastal plain of South Carolina (figure from Semlitsch and Bodie 1998).



A constructed wildlife pond at the Daniel Boone Conservation Area, Warren County, Missouri. Inset of an adult ringed salamander, Ambystoma annulatum, that breeds predominantly in small forested ponds as shown here.

broader selection of alternative breeding sites, or somehow promote mate choice, oviposition, or larval survival.

The last point we would like to make is that we do not advocate only small wetlands, and that a "cookie-cutter" approach does not work. In fact, we advocate a diversity of wetlands sizes, large and small, permanent and ephemeral. We believe a diversity of wetland sizes benefits a range of species adapted to different portions of the hydroperiod gradient due to different times to drying. A diversity of sizes also better matches a range of climatic conditions experienced over time, including the buffering of reproductive success during wet and dry cycles that may become increasing apparent with global climate change. Large more permanent wetlands may be the only sites that are available for breeding during droughts. Small, ephemeral wetlands may be the only breeding sites that are fish-free during wet years or floods. It is also important to consider elevational diversity with respect to wetland placement. Wetlands within the 100-year floodplain, no matter how small, will be subjected to fish colonization more frequently than those in the 500year, or even those placed outside the floodplain in upland habitat. However, we also advocate that the landscape needs to have a large proportion of small wetlands to promote amphibian production locally but remain in close proximity to promote rescue and recolonization across the landscape. Thus, matching the natural historical distribution of wetlands in many respects often matches the greatest diversity of wetlands, clustering on the landscape, and promotes amphibian persistence.

References continued on page 25

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servation Program, they could receive some regulatory agreement such as a Safe Harbour Agreement, or technical and practical support. Such programs give the landowner freedom from binding remuneration and so with it, the privacy and discretion over their own property that they desire. With a careful balance of smaller payments and smaller intrusion, some great conservation actions have been achieved on the ground, fostered by artful coordination and support of nonprofit organizations. This type of landowner conservation, free from binding remuneration, accordingly requires very little oversight and at best can result in a conservation easement recorded on the land. Landowners appreciate such an approach because it involves less agency oversight and in many cases can allow them to use their land with minor adjustment to their practices. These features-leniency and independence-are valuable elements to attract a wide range of landowners across many states. This kind of wide, landscape-level reach is required when conserving listed and candidate species in a meaningful way, and the Services are rightfully focused on this aspect of conservation: broadening landowner support. The

standards applied in these programs should reflect this overall goal, and include the flexibility required. This leaves space to create clear standards to address another sort of program and tool: compensatory mitigation to address unavoidable negative impacts from development projects.

TOOL TWO: COMPENSATORY MITIGATION

This form of conservation, implemented via the U.S. Fish and Wildlife Service's (FWS') 2003 Conservation Banking Guidelines, is focused on supplying conservation to address the unavoidable negative impacts of development projects. As a result, this tool requires much higher standards of those landowners participating so as to ensure conservation occurs in perpetuity and with appropriate agency oversight. Actions must go over and above simply providing a positive impact at the site of conservation. By involving measurability and a negative impact, compensatory mitigation is necessarily distinct from other landowner incentive approaches.

These requirements bring with it far less discretion and flexibility of the landowner program described above because the purpose of participating in a compensatory mitigation program is to provide a measureable offset for a measurable impact. Conservation needs to be delivered transparently and perpetually, and if unifying standards were applied, this would go some way to ensure that these were delivered, regardless how compensatory mitigation is applied.

Without the important distinction between tools and the standards required for each, there is a risk of bringing potentially varying outcomes into the compensatory mitigation realm. This poses significant risk to the overall positive conservation of endangered species, like those sought after from places such as California. FWS' desire should be the best conservation via mitigation outcome and have the right tools with the right standards to make that assured. Potentially applying un-unified and competing standards across all forms of private land conservation will result in poorer conservation outcomes. At worst, it could even undermine and eliminate the proven tool for mitigation, and with it the significant infusion of investment dollars into conservation that high-quality conservation banking brings.

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