Research Notes

Are Small, Isolated Wetlands Expendable?

RAYMOND D. SEMLITSCH AND J. RUSSELL BODIE

Division of Biological Sciences, University of Missouri, Columbia, MO 65211-7400, U.S.A.,
email rays@biosci.mbp.missouri.edu

Abstract: *What is most evident in the recent debate concerning new wetland regulations drafted by the U.S. Army Corps of Engineers is that small, isolated wetlands will likely continue to be lost. The critical biological question is whether small wetlands are expendable, and the fundamental issue is the lack of biologically relevant data on the value of wetlands, especially so-called "isolated" wetlands of small size. We used data from a geographic information system for natural-depression wetlands on the southeastern Atlantic coastal plain (U.S.A.) to examine the frequency distribution of wetland sizes and their nearest-wetland distances. Our results indicate that the majority of natural wetlands are small and that these small wetlands are rich in amphibian species and serve as an important source of juvenile recruits. Analyses simulating the loss of small wetlands indicate a large increase in the nearest-wetland distance that could impede "rescue" effects at the metapopulation level. We argue that small wetlands are extremely valuable for maintaining biodiversity, that the loss of small wetlands will cause a direct reduction in the connectance among remaining species populations, and that both existing and recently proposed legislation are inadequate for maintaining the biodiversity of wetland flora and fauna. Small wetlands are not expendable if our goal is to maintain present levels of species biodiversity. At the very least, based on these data, regulations should protect wetlands as small as 0.2 ha until additional data are available to compare diversity directly across a range of wetland sizes. Furthermore, we strongly advocate that wetland legislation focus not only on size but also on local and regional wetland distribution in order to protect ecological connectance and the source-sink dynamics of species populations.*

Son los Humedales Pequeños Prescindibles?

Resumen: *Algo muy evidente en el reciente debate sobre las nuevas regulaciones de humedales elaboradas por el cuerpo de ingenieros de la armada de los Estados Unidos es que los humedales aislados pequeños seguramente se continuarán perdiendo. La pregunta biológica crítica es si los humedales pequeños son prescindibles y e asunto fundamental es la falta de datos biológicos relevantes sobre el valor de los humedales, especialmente los llamados humedales "aislados" de tamaño pequeño. Utilizamos datos de GIS para humedales de depresiones naturales en la planicie del sureste de la costa Atlántica (U.S.A.) para examinar la distribución de frecuencias de los tamaños de humedales y las distancias a los humedales mas cercanos. Nuestros resultados indican que la mayoría de los humedales naturales son pequeños y que estos humedales pequeños son ricos en especies de anfibios y sirven como una fuente importante de reclutas juveniles. Análisis simulando la pérdida de humedales pequeños indican un gran incremento en la distancia al humedal mas cercano lo cual impediría efectos de "rescate" a nivel de metapoblación. Argumentamos que los humedales pequeños son extremadamente valiosos para el mantenimiento de la biodiversidad, que la pérdida de humedales pequeños causará una reducción directa en la conexión entre poblaciones de especies remanentes y que tanto la legislación propuesta como la existente son inadecuadas para mantener la biodiversidad de la flora y fauna de los humedales. Si nuestra meta es mantener los niveles actuales de biodiversidad de especies, los humedales pequeños no son prescindibles. En base en estos datos, las regulaciones deberían por lo menos proteger humedales tan pequeños como 0.2 ha hasta que se tengan a la mano datos adicionales para com-*

Paper submitted April 1, 1998; revised manuscript accepted June 24, 1998.

parar directamente la diversidad a lo largo de un rango de humedales de diferentes tamaños. Mas aún, abogamos fuertemente por que la regulación de los pantanos se enfoque no solo en el tamaño, sino también en la distribución local y regional de los humedales para poder proteger la conexión ecológica y las dinámicas fuente y sumidero de poblaciones de especies.

Wetlands Debate

New regulations drafted by the U.S. Army Corps of Engineers that reduce protection for "headwater" or "isolated" wetlands have sparked a controversy among environmentalists, academic scientists, other federal agencies, and the Army Corps itself (Kaiser 1998). What is most evident in this debate is that small, isolated wetlands will likely continue to be lost no matter what the outcome. Why is there a bias against protecting small, isolated wetlands? The critical biological question is whether small wetlands are expendable, and the fundamental issue is the lack of biologically relevant data on the value of wetlands, especially so-called "isolated" wetlands of small size. Although the recently proposed legislation (U.S. Army Corps of Engineers, draft proposal) actually reduces the threshold size for developing wetlands from 4.0 ha to 1.2 ha (via Nationwide Permit 26), we believe that both the current and proposed legislation are inadequate for maintaining the biodiversity of wetland flora and fauna. We argue that small wetlands are extremely valuable for maintaining biodiversity in a number of plant, invertebrate, and vertebrate taxa (e.g., amphibians) and that the disappearance of small wetlands will cause a dire reduction in the ecological connectance among remaining species populations.

Frequency and Distribution of Small Wetlands

Determining the frequency distribution of wetland sizes more appropriately addresses the biological importance of individual wetlands than approaches concerned only with how the total area would be affected by the loss of large versus small wetlands. Simple calculations show that a greater reduction in total wetland area obviously results from the loss of large wetlands. These calculations are often used to illustrate the importance of large wetlands, despite the absence of relevant biological data, and contribute to the bias against the value of small wetlands. Area is not the only important factor. We argue that the number of individual wetlands is more important because it addresses the abundance and distribution of individual wetland populations, which is the most basic unit of community dynamics responsible for maintaining species diversity (Ricklefs & Schluter 1993) and the most basic unit of population dynamics responsible for maintaining genetic diversity (Futuyma 1998). Therefore, the abundance of wetlands is directly related to critical processes of ecological change, such as connectance and source-sink dynamics, and of evolutionary change, such as genetic structure and local adaptation.

To examine the question of natural wetland abundance, we used as an example isolated depression wetlands distributed on the southeastern Atlantic coastal plain (U.S.A.). Existing geographic information system data from the 780-km^2 Savannah River Site (SRS) in South Carolina (Schalles et al. 1989; Kirkman et al. 1996) were used to describe the size frequency and spatial distribution of all detectable depression wetlands known as Carolina bays at this site. Carolina bays are natural elliptical depressions found in the southeastern United States that vary in size and geological age (Sharitz & Gibbons 1982). The 371 wetlands ranged in size from 0.22 (lower detection limit) to 78.2 ha, occurring at a density of 0.476/km^2. The frequency distribution was highly skewed, with many more small than large bays (Fig. 1). In fact, 46.4% of the bays were 1.2 ha or less, and 87.3% were 4.0 ha or less. What is more, data for the frequency of small wetlands are conservative because bays smaller than 0.2 ha were not represented due to detection limits and may be common and quite important for some amphibian species.

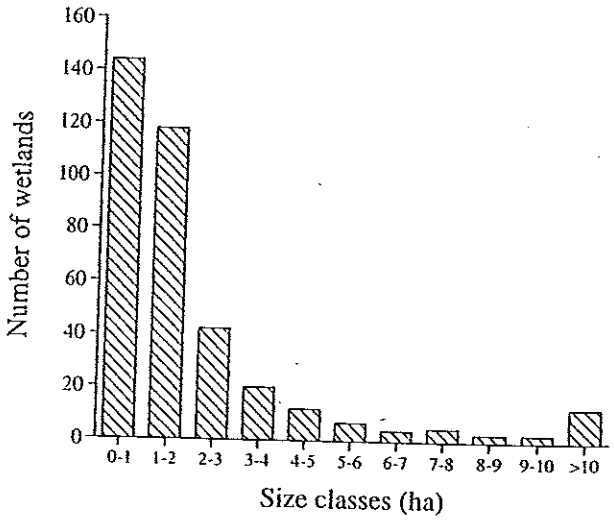

Figure 1. Distribution of natural depression wetland sizes (n = 371) from the Savannah River Site on the upper coastal plain of South Carolina. The lower limit of detection from geographic information system data was 0.2 ha.

Of course, we should also question whether this data set is representative of other regions of the country. We have no reason to believe that the data are not representative of the entire southeastern United States, especially other undisturbed areas that have not already suffered a great loss of natural wetlands. Our results may also be comparable to regions other than the southeastern United States; for example, an analysis of wetlands in Maine revealed a slightly higher density (0.59/km^2) but a similar high proportion of small wetlands (62% smaller than 4.05 ha; Gibbs 1993). Data from other regions, however, are needed to corroborate this general pattern that a majority of natural wetlands are small.

Biodiversity of Small Wetlands

From an ecological perspective, small wetlands are crucial for maintaining regional biodiversity. For example, in a long-term study at a 0.5-ha Carolina bay on the SRS (Semlitsch et al. 1996), we observed one of the highest species diversities known for amphibians. We used amphibians as our model because they may constitute the greatest biomass among vertebrates in some ecosystems (Burton & Likens 1975) and are of global concern due to reported declines (Wake & Morowitz 1991; Blaustein et al. 1994) and extinctions (Pounds & Crump 1994). Furthermore, there is a wealth of information concerning community regulation and metapopulation dynamics for wetland amphibians (e.g., Gill 1978; Morin 1983; Smith 1983; Wilbur 1987; Berven & Grudzien 1990).

A 16-year monitoring study at a small wetland (0.5 ha) known as Rainbow Bay has documented 27 species of anurans and caudates (Semlitsch et al. 1996). In addition, the study also recorded the breeding activity of 41,776 females and the production of 216,251 metamorphosing juveniles during the 16-year period (Table 1 in Semlitsch et al. 1996). Monitoring studies of other small wetlands for shorter periods of time on the SRS have yielded similar numbers of amphibian species: Sun Bay (0.5 ha), 22 species (Gibbons & Semlitsch 1981); Karen's Pond (0.08 ha), 19 species; Risher Pond (1.1 ha), 18 species (Gibbons & Bennett 1974); Ginger's Bay (1.0 ha), 20 species; Squirrel Bay (0.5 ha), 21 species (D. Scott, personal communication). These data suggest that the levels of species richness found at Rainbow Bay are not uncommon and are representative of the region. Furthermore, studies of small, temporary wetlands in Florida (16 species of anurans and caudates at a 0.16-ha pond; Dodd 1992; Dodd & Cade 1998), Tennessee (19 species of anurans and caudates over 9 years at two small ponds each smaller than 0.2 ha; Scott & Bufalino 1997), and Texas (15 species of anurans alone; Wiest 1982) have yielded comparable numbers of species. Although we currently know of no study that statistically compares amphibian diversity in small and large isolated wetlands—a particularly important comparison—some available data from Florida suggest that large wetlands may be less diverse (Moler & Franz 1987). Large wetlands tend to be more permanent and thus contain predatory fish and perhaps a greater variety or abundance of invertebrate predators that can exclude amphibian larvae (Morin 1983; Wilbur 1987; Semlitsch et al. 1996).

Our example demonstrates that small wetlands may be of significant biological importance, especially in producing large numbers of metamorphosing juvenile amphibians and potentially in maintaining the diversity of the regional amphibian fauna. We further suggest that such wetlands also are of general importance because they harbor large numbers of species of other taxa that are perhaps less mobile than birds or mammals and are therefore more strongly affected by the loss of small wetlands: wetland plants such as sundews (*Drosera* spp.) and pitcher plants (*Sarracenia flava*, *S. purpurea*; Sharitz & Gibbons 1982), microcrustaceans (Mahoney et al. 1989), and aquatic insects (Kondratieff & Pyott 1987; Sharitz & Gibbons 1982; Gaddy 1994).

Consequences for Metapopulation Dynamics

The less obvious consequence of losing small, isolated wetlands lies in potential changes to the metapopulation dynamics of the remaining wetlands. There are two primary effects to consider (Gibbs 1993): (1) a reduction in the number or density of individuals dispersing and (2) an increase in dispersal distances among wetlands. The loss or alteration of any wetland, large or small, reduces the total number of sites at which pond-breeding amphibians can reproduce and successfully recruit juveniles into the breeding population. For amphibians the loss of small wetlands especially may reduce the number of source populations because juvenile recruitment is related to an optimal wetland size and intermediate hydroperiod that favor the periodic drying characteristic of small wetlands (Pechmann et al. 1989). Even at the best sites, however, reproductive failure in many years for nearly all species increases the probability of extinction (estimated annual reproductive failure rates are 42–56% for 13 species over 16 years in South Carolina; Semlitsch et al. 1996). Thus, the loss of small wetlands could be detrimental to rescue effects via a reduction in the population density and number of dispersing juveniles (contra Gibbs 1993). Even if recruitment failures proved to be less severe in other geographic regions, the change in wetland density over a local area would still become critical for other metapopulation processes. The effects of reduced wetland density also are manifested by an increase in the distance between neighboring wetlands and are critical to source-sink processes. In particular, a reduction in wetland density can decrease the probablity that a population can be "rescued" from extinction by a neighboring source popu-

lation because of lower numbers of available recruits and greater distances between wetlands (Brown & Kodric-Brown 1977; Gill 1978; Pulliam 1988; Gibbs 1993).

To illustrate this point, we again use the example from the 371 Carolina bays on the SRS in South Carolina. We examined how the loss of individual wetlands affects the straight-line distance to the nearest wetland. The average distance to the nearest wetland directly affects the probability of migration and recolonization and, consequently, the chance of population rescue from extinction. It is also important to note that many pond-breeding salamanders, and possibly many anurans, are philopatric to natal ponds and do not emigrate long distances (most less than 200 m; Semlitsch 1998). In fact, an estimate of genetic-neighborhood size for wood frogs averages only 1126 m, suggesting that migration and gene flow are near zero at these distances (Berven & Grudzien 1990). From our example, we can see that the loss of small wetlands would dramatically increase the nearest-wetland distance from the initial 471 m (including all 371 wetlands) to 666 m with the loss of all wetlands smaller than 1.2 ha (proposed protection threshold) to 1633 m with the loss of all wetlands smaller than 4.0 ha (current protection threshold) (Fig. 2). What is most pertinent to current and proposed wetland-size legislation is that there would be a 41.3% increase (+195 m) in distance between nearest bays with the loss of all wetlands smaller than 1.2 ha and a 136.1% increase (+641 m) in distance with the loss of all wetlands smaller than 4.0 ha. We conclude from our analysis that the loss of a majority of small wetlands could severely impede source-sink processes and place remaining wetlands at increased probabilities of population extinctions (also see Gibbs 1993; Travis 1994).

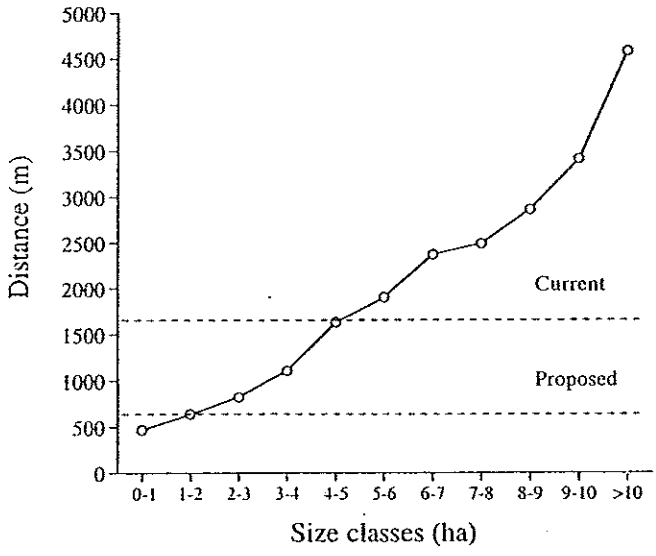

Figure 2. Mean distances between nearest wetlands (n = 371) on the Savannah River Site on the upper coastal plain of South Carolina. The mean nearest-neighbor distance was recalculated sequentially with all previous wetland size classes removed. Dashed lines indicate current and proposed U.S. Army Corps of Engineers wetland size legislation thresholds.

Implications for Management and Legislation

Small, isolated wetlands are not expendable if our goal is to maintain present levels of species biodiversity. We have shown that current and proposed legislation is inadequate for maintaining regional wetland biodiversity in at least one important group of vertebrates, amphibians. This is especially disheartening in light of the many reports of declining amphibian populations worldwide, and in particular because of habitat loss in the southeastern United States (Dodd 1997). We further suggest that such legislation is inadequate for other taxa, such as plants, microcrustaceans, and insects, that use small wetlands. At the very least, based on these data, regulations should protect wetlands as small as 0.2 ha until additional data are available to compare diversity directly across a range of wetland sizes. Furthermore, in order to protect the ecological connectance and source-sink dynamics of species populations, we strongly advocate that wetland legislation focus not only on size but also on local and regional wetland distribution. For instance, a 1.0-ha wetland isolated by 1000 m may have more rather than less biological value than a 1.0-ha wetland with neighboring wetlands 100–200 m away.

Only through analyses similar to those we have presented can a realistic view of the biological consequences of wetland legislation be understood. We hope our comments stimulate new efforts into research that includes analyses of how biodiversity relates to wetland size and spatial distribution and how metapopulation processes are affected by the loss of wetlands, both large and small.

Acknowledgments

We thank M. Boone, K. Dodd, R. Franz, J. Krenz, A. Welch, and one anonymous reviewer for comments on the manuscript. The geographic information system (GIS) layer of Carolina bays was provided courtesy of G. Wein and the Savannah River Ecology Laboratory's Remote Sensing and GIS Laboratory. Data collection was supported by Financial Assistance Award Number DE-FC09-96SR18546 from the U.S. Department of Energy to the University of Georgia Research Foundation.

Literature Cited

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

Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. Conservation Biology 8:60–71.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449.

Burton, T. M., and G. E. Likens. 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia 1975:541–546.

Dodd, C. K., Jr. 1992. Biological diversity of a temporary pond herpetofauna in north Florida sandhills. Biodiversity and Conservation 1:125–142.

Dodd, C. K., Jr. 1997. Imperiled amphibians: a historical perspective. Pages 165–200 in G. W. Benz and D. E. Collins, editors. Aquatic fauna in peril: the southeastern perspective. Special publication 1. Southeast Aquatic Research Institute, Lenz Design and Communications, Decatur, Georgia.

Dodd, C. K., Jr., and B. S. Cade. 1998. Movement patterns and the conservation of breeding amphibians in small, temporary wetlands. Conservation Biology 12:331–339.

Futuyma, D. J. 1998. Evolutionary biology. 3rd edition. Sinauer Associates, Sunderland, Massachusetts.

Gaddy, L. L. 1994. The ecology of seven rare wetland species in Carolina bays and bay-like depressions in the western Coastal Plain of South Carolina. Report. U.S. Forest Service, Savannah River Forest Station, Aiken, South Carolina.

Gibbons, J. W., and D. H. Bennett. 1974. Determination of anuran terrestrial activity patterns by a drift fence method. Copeia 1974:236–243.

Gibbons, J. W., and R. D. Semlitsch. 1981. Terrestrial drift fences with pitfall traps: an effective technique for quantitative sampling of animal populations. Brimleyana 7:1–16.

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

Gill, D. E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecological Monograph 48:145–166.

Kaiser, J. 1998. New wetlands proposal draws flak. Science 279:980.

Kirkman, L. K., R. F. Lide, G. Wein, and R. R. Sharitz. 1996. Vegetation changes and land-use legacies of depression wetlands of the western coastal plain of South Carolina: 1951–1992. Wetlands 16:564–576.

Kondratieff, B. C., and C. J. Pyott. 1987. The anisoptera of the Savannah River Plant South Carolina U.S.A. thirty years later. Odonatologica 16:9–24.

Mahoney, D. L., D. A. Mort, and B. E. Taylor. 1989. Species richness of calanoid copepods, cladocerans, and other branchiopods in Carolina bay temporary ponds. American Midland Naturalist 123:244–258.

Moler, P. E., and R. Franz. 1987. Wildlife values of small, isolated wetlands in the southeastern coastal plain. Pages 234–241 in R. R. Odum, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the third southeastern nongame and endangered wildlife symposium. Georgia Department of Natural Resources, Atlanta.

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

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

Pounds, J. A., and M. L. Crump. 1994. Amphiban declines and climate disturbance: the case of the golden toad and harlequin frog. Conservation Biology 8:72–85.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Ricklefs, R. E., and D. Schluter. 1993. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, IL.

Schalles, J. F., R. R. Sharitz, J. W. Gibbons, G. J. Leversee, and J. N. Knox. 1989. Carolina bays of the Savannah River Plant. Savannah River Plant National Environmental Research Park Program, Aiken, South Carolina.

Scott, A. F., and A. Bufalino. 1997. Dynamics of the amphibian communities at two small ponds in Land Between the Lakes over the past decade. Page 117 in A. F. Scott, S. W. Hamliton, E. W. Chester, and D. S. White, editors. Proceedings of the seventh symposium on the natural history of Lower Tennessee and Cumberland River valleys. Austin Peay State University, Clarksville, Tennessee.

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

Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. Pages 217–248 in M. L. Cody and J. A. Smallwood, editors. Long-term studies of vertebrate communities. Academic Press, San Diego, California.

Sharitz, R. R., and J. W. Gibbons. 1982. The ecology of southeastern shrub bogs (pocosins) and Carolina bays: a community profile. FWS/OBS-82/04. U.S. Fish and Wildlife Service, Washington, D. C.

Smith, D. C. 1983. Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. Ecology 64:501–510.

Travis, J. 1994. Calibrating our expectations in studying amphibian declines. Herpetologica 50:104–108.

Wake, D. B., and H. J. Morowitz. 1991. Declining amphibian populations: a global phenomenon? Alytes 9:33–42.

Wiest, J. A., Jr. 1982. Anuran succession at temporary ponds in a post oak-savanna region of Texas. Pages 39–47 in N. J. Scott, Jr., editor. Herpetological communities. U.S. Fish and Wildlife Service, Washington, D.C.

Wilbur, H. M. 1987. Regulation of structure in complex systems: experimental temporary pond communities. Ecology 68:1437–1452.