
From Cattle Tanks to Carolina Bays

The Utility of Model Systems for Understanding Natural Communities

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Experimental observations are only experience carefully planned in advance.

—Sir Ronald A. Fisher, 1935

You cannot step twice into the same river.

—Heraclitus, fl. 513 B.C.

A primary goal of ecological research is to identify generalities that can simplify the natural world from a jumbled collection of special cases to an ordered array of classifiable sets. This goal is shared by all ecologists and stems from the belief that complex ecological systems operate on a finite set of principles. Once these are understood, ecologists expect some level of predictive ability with regard to ecological phenomena. It has long been recognized that perhaps the most serious constraint in ecological research is the sheer number of factors affecting natural systems, coupled with the large number of unique natural communities we hope to understand. A parallel consideration is that sufficient resources will never be available to study every system on the planet. Thus, the search for generality and predictive power is not simply an abstract theoretical pursuit but an absolutely essential component of the ecological research paradigm. Ecologists use observation, experimentation, and deduction to generate predictive models that simplify the natural world and permit general statements about how it works. Only by obtaining a fundamental and general comprehension of the processes that shape natural systems can we hope to understand not only those systems that are intensively studied but also those innumerable systems that will never be studied. And only then can our basic understanding give rise to the informed and broadly applicable conservation decisions necessary to keep the world working.

As ecologists develop theories and models about how the world works, they also look for ways to rigorously test them. Experimentation is often referred to as a means of testing observed phenomena; often the “observed phenomena” are generated from theory rather than from observation or they are derived directly from previous experiments (Peckarsky, this volume). Fair tests of observed phenomena/theory require that

null hypotheses can be rejected; this demands both adequate replication to obtain statistical power and sufficient control over experimental conditions to detect a signal (effect) against a background of noise (random variation). Achieving both these prerequisites is often difficult or impossible to achieve in nature (Lawton, this volume; Morin, this volume); we may be able to detect very strong signals in natural systems, but our ability to detect subtle yet potentially important effects in complex and noisy systems (Peckarsky, this volume) is often severely constrained by limits on replication and control. An alternative approach to manipulating natural communities is to re-create communities in artificial mesocosms that are under more complete control of the investigator. Model experimental systems, including mesocosms, allow a level of rigor and control either unobtainable or prohibitively expensive in natural systems; and because artificial mesocosms/microcosms are relatively inexpensive, they can be used to study a broad array of natural phenomena (Lawton, this volume; Morin, this volume).

While such model systems have proven their utility in testing ecological theory and exploring general ecological processes, their utility for understanding the "real world" of specific ecological systems has been questioned (e.g., Jaeger and Walls 1989, Petranksa 1989, Carpenter 1996). The basic conundrum is that experiments that allow complete control of experimental conditions are inherently unnatural, while those conducted in nature vary in ways beyond the control of the experimenter (Diamond 1986; Hairston 1989a). The mesocosm approach combines rigorous control of experimental conditions with quasi-natural situations by using artificial environments (container communities) of intermediate size in which initial community composition and experimental conditions are controlled by the investigator but also may be exposed to natural photoperiods, temperatures, precipitation, and other factors. This approach is here exemplified by experiments in pond mesocosms designed to mimic natural temporary ponds (e.g., Morin 1981, 1983a; Wilbur 1984, 1987; Fauth and Resetarits 1991) and has been applied to a wide variety of systems (e.g., see literature cited in Hairston 1989a, Gurvitch et al. 1992, Lamberti and Steinman 1993, Rowe and Dunson 1995).

Temporary ponds themselves provide an ideal system for the study of ecological communities. Each time a pond refills, a new episode in community ecology begins: species colonize, a food web develops, trophic interactions become modified as predators and prey grow, and the community develops until the pond dries. This cycle can be repeated several times a year or just once in many years, depending on the morphology and hydrology of the pond and the vagaries of precipitation. Combined with the high productivity and diversity of ephemeral ponds, this temporal repetition provides a unique opportunity to explore the rules of community assembly, particularly for taxa amenable to experimentation, such as amphibians, microcrustaceans, and odonates.

Over the past 15 years, experiments in mesocosms have demonstrated the potential role of competition (e.g., Morin 1983b, Van Buskirk 1989, Fauth et al. 1990), predation (e.g., Morin 1983b, 1987; Morin et al. 1983; Wilbur et al. 1983; Semlitsch 1987; Semlitsch and Gibbons 1988; Van Buskirk 1988; Fauth 1990), and environmental stochasticity (in the form of pond drying, acting either alone or in concert with biotic interactions; e.g., Wilbur 1984 and references therein; Travis et al. 1985; Morin 1986; Semlitsch 1987; Wilbur 1987, 1988 and references therein; Wilbur and Fauth 1990) in the population dynamics and community structure of larval amphibians and insects that inhabit temporary ponds. Other experiments have illustrated the potential role of spatial

scale (Pearman 1993), historical effects (in the form of breeding phenology: Alford and Wilbur 1985, Wilbur and Alford 1985, Morin 1987, Alford 1989, Morin et al. 1990), oviposition site choice (Resetarits and Wilbur 1989, 1991), and keystone predation (Morin 1981, 1983b; Fauth and Resetarits 1991; Kurzava and Morin 1994) in determining community structure in larval anuran assemblages. While these experiments were initiated to identify the processes that structure natural communities and to test theories related to that broad question, the experiments were carefully grounded in field data that remain largely unpublished (but see Harris et al. 1988). The experiments were thus designed so that their specific results would be applicable to the natural ponds they mimicked.

This assumption was challenged in the late 1980s by Petranksa and others (e.g., Jaeger and Walls 1989, Petranksa 1989 and references therein; also see Hairston 1989b, Morin 1989, and Wilbur 1989 for responses), who questioned the realism of experiments in both field enclosures and artificial ponds. They argued that experimental conditions, particularly high initial and final densities of larval anurans, favored biotic interactions over abiotic limiting factors that might be more important in nature. Subsequent work conducted in divided natural ponds (Petranksa 1989) and large-scale field enclosures (Scott 1990) showed striking parallels to the results of the mesocosm experiments. Nonetheless, skeptics continue to question the utility of the artificial mesocosm/microcosm approach (e.g., Carpenter 1996).

Our research on the interactions between two salamanders, the lesser siren, *Siren intermedia*, and the broken-striped newt, *Notophthalmus viridescens dorsalis*, and their role in temporary ponds was largely conducted in such artificial communities (Fauth et al. 1990, Fauth and Resetarits 1991, Resetarits and Fauth unpublished ms., Fauth and Resetarits unpublished ms.). We were aware of criticisms leveled at mesocosm experiments and grew increasingly interested in whether the primary factors controlling community structure in natural communities were the same as in their artificial counterparts. One of us (WJR) used insights gleaned from the 20 years of mesocosm experiments that focused on temporary ponds in the southeastern United States (see following discussion) to develop a simple graphical model of the maintenance of anuran species richness in Carolina bays and other temporary ponds. In this paper we describe the model and test its qualitative predictions using field data collected independently as part of a baseline survey of Carolina bay amphibians (Fauth 1993). The model was developed before Fauth's data were collated and analyzed, thus obviating tautologized predictions.

Natural History of Carolina Bays and Their Diverse Faunas

Much of the biotic diversity within the Coastal Plain and nearby portions of the Sandhills Region of the southeastern United States is concentrated in and around temporary ponds. The principal type of natural temporary ponds in this region is the Carolina bays, shallow elliptical depressions of unknown geological origin that occur in a broad band on the Atlantic Coastal Plain from the Delmarva Peninsula to northern Florida and are most numerous in the Carolinas (Savage 1982, Sharitz and Gibbons 1982, Richardson and Gibbons 1993). Carolina bays range in size from <0.5 ha to thousands of hectares and in permanence from very ephemeral ponds that seldom allow

metamorphosis of amphibians to large, permanent bay lakes such as Lake Waccamaw, which supports endemic molluscs and darters. Before European settlement Carolina bays numbered in the hundreds of thousands (Savage 1982), but today few remain unaltered by human impacts.

One of the most striking features of the ephemeral Carolina bays is their anuran diversity. Individual bays support up to 16 species of anurans out of a potential regional fauna of ~ 25 species (Morin 1983b, Wilbur and Travis 1984, Fauth 1993). Even greater numbers of anuran species may chorus from an individual pond on a single night (J. Fauth, personal observation; H. M. Wilbur, personal communication). Many tropical systems harbor greater regional diversity, but the anuran diversity supported by individual Carolina bays may be unsurpassed by that of any small body of water anywhere in the world. Smaller natural depressions and man-made temporary ponds (e.g., "borrow pits") support fewer species, but their faunas still are exceptionally diverse (Wilbur and Travis 1984). This anuran diversity provides a challenge (and a unique opportunity) to ecologists to explain its origin and maintenance.

A Model of Anuran Diversity in Carolina Bays and Other Temporary Ponds

In a series of papers (Fauth et al. 1990, Fauth and Resetarits 1991, Resetarits and Fauth unpublished ms., Fauth and Resetarits unpublished ms.), we explored the interactions between specific size classes of two competing predators, the broken-striped newt (*N. v. dorsalis*) and the lesser siren (*Siren intermedia intermedia*), and their effects on temporary pond communities. *N. v. dorsalis* and *S. intermedia* circumvent the predator avoidance strategy of many temporary pond species by persisting in the dry pond basin, which allows them to prey on the eggs and larvae of even the earliest colonists, including many species that are extremely vulnerable to predation. Both salamanders can influence species composition and community structure in temporary ponds. Because *N. v. dorsalis* and *S. intermedia* each have strong effects on prey populations, the dynamics of these two species and their interactions may be critical to the community ecology of Carolina bays and other temporary ponds.

These two species have markedly different impacts on anuran assemblages (Fig. 7-1). *N. v. dorsalis* is a keystone predator (Paine 1966) in assemblages that are characterized by strong competitive asymmetry (Morin 1983b, Fauth and Resetarits 1991), which is a common feature of anuran assemblages in temporary ponds (Morin 1981, 1983b; Wilbur and Alford 1985; Wilbur 1987; Morin and Johnson 1988; Van Buskirk 1988; Alford 1989; Fauth and Resetarits 1991). The keystone effect of *N. v. dorsalis* has been demonstrated repeatedly in artificial mesocosm experiments using anuran assemblages of varying species composition and density (Morin 1981, 1983b; Wilbur 1987; Fauth and Resetarits 1991) and is robust to the presence of a second predator, *S. intermedia* (Fauth and Resetarits 1991). The strength of the keystone effect can vary with newt density (Morin 1983b) and variation in body size among subspecies of *N. viridescens* (Morin 1986, 1987; Kurzava 1994). *N. v. dorsalis* has strong effects on the relative and absolute abundance of anurans in temporary ponds because newts prey selectively on the competitively superior species, allowing weaker competitors to persist (Morin 1981, 1983b; Fauth and Resetarits 1991). In our model, however, predation by

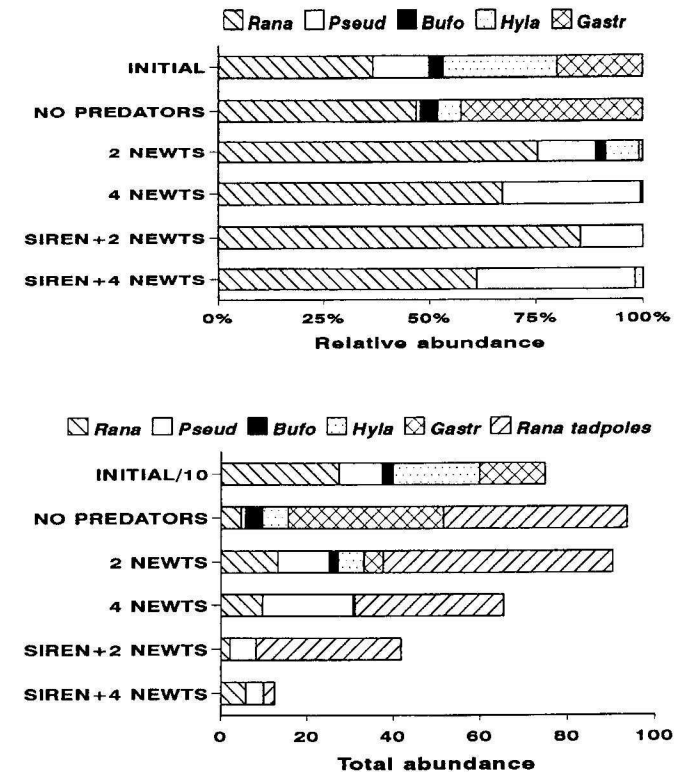


Figure 7-1. Differential effects of *Notophthalmus* and *Siren* on ensembles of larval anurans in artificial ponds. The anuran species are *Rana utricularia*, *Pseudacris crucifer*, *Bufo americanus*, *Hyla chrysoscelis*, and *Gastrophryne carolinensis*. The upper graph illustrates the effect of competitive asymmetries on species diversity in emerging anuran metamorphs and the highly significant effect of *Notophthalmus* on the relative abundance of species. The keystone effect of *Notophthalmus* is robust to the addition of *Siren*, but *Siren* has no effect on relative abundance. The lower graph illustrates the significant effect of *Siren* on the total abundance of larval anurans; *Notophthalmus* has no effect on total abundance. Modified from Fauth and Resetarits (1991).

Notophthalmus increases anuran species richness only across a relatively narrow range of potential anuran and newt densities (Fig. 7-2A). At low relative densities of *N. v. dorsalis* the keystone effect is overwhelmed (via predator satiation) and the species composition of metamorphs is largely determined by asymmetrical competitive interactions, resulting in lower species richness. At very high relative densities of *N. v. dorsalis*, anuran species richness decreases because newts eliminate some or all species (Fig. 7-2A; e.g., as in Morin 1983b).

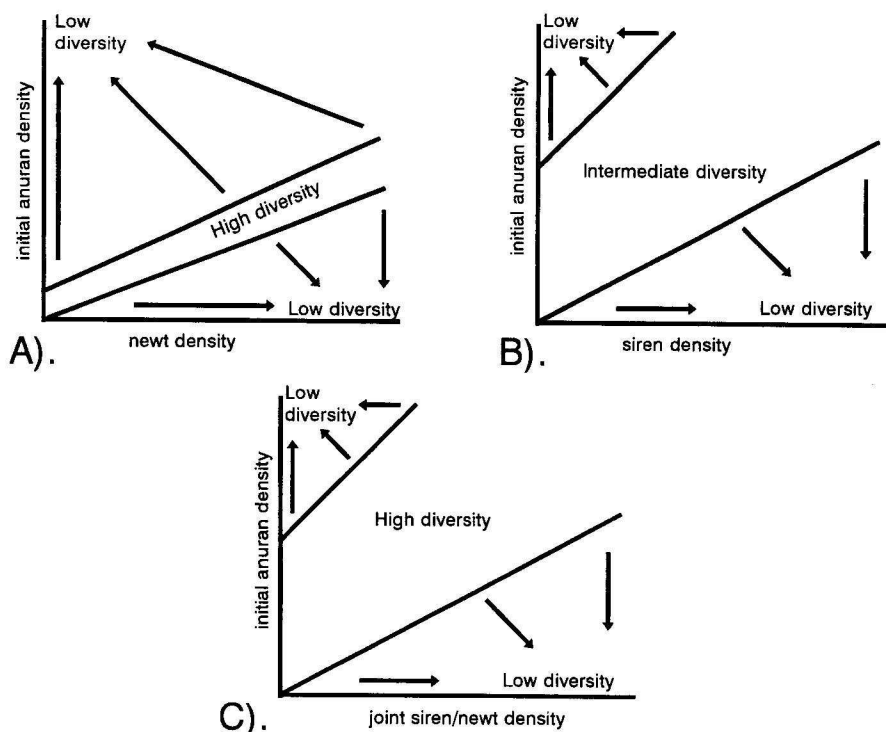


Figure 7-2. Graphical model of anuran diversity in Carolina bays and other ephemeral ponds. A, newt; B, siren; C, joint siren/newt density. Diversity is measured at the metamorph stage. The assumptions are: (1) Initial anuran species diversity (input diversity) is constant across the range of anuran densities. Increases in overall anuran densities result from increases (not necessarily equal) in the densities of component species. (2) The joint density of sirens and newts is at least 75% of their summed densities. This is a reasonable assumption based on the interactions between these two species (Fauth et al. 1990, Fauth and Resetarits 1991, Resetarits and Fauth unpublished manuscript).

S. intermedia is not a keystone predator but strongly affects the absolute numbers of larval and metamorphic anurans (Fauth and Resetarits 1991). *S. intermedia* preys on each species in direct proportion to its relative abundance (Fig. 7-1). Thus, the effects of *S. intermedia* on anuran assemblages are strikingly different from those of *N. v. dorsalis*. However, over much of the potential range of anuran and siren densities, species richness is determined by asymmetrical competitive interactions within the anuran assemblage rather than any direct impact of predation (Fig. 7-2C). Anuran diversity declines at high relative densities of *S. intermedia* because of the chance elimination of rare species and predation on weaker competitors whose populations are strongly impacted by interspecific competition. At high densities of both larval anurans and *S. intermedia*, diversity increases because predation reduces the overall density of larval anurans, thereby ameliorating the effects of interspecific competition. This is the classic

case of predation being good for the survivors because it reduces the overall intensity of competition (Wilbur 1987, 1988). However, the potential gains in diversity achieved via the nonselective predation of sirens is necessarily smaller than that achieved via the keystone predation of newts. Anuran diversity is more severely reduced at high relative densities of *S. intermedia* than at high relative densities of *N. v. dorsalis* because *S. intermedia* has a much wider gape and is therefore an effective predator for a greater portion of most anuran larval periods.

The predicted joint effects of *S. intermedia* and *N. v. dorsalis* are additive and can be visualized by overlaying the two graphs (Fig. 7-2C); note especially that the region in which the keystone predator effect is expressed corresponds to a region in which *S. intermedia* has little impact on anuran diversity. By unselectively depressing prey abundance *S. intermedia* effectively extends the range of anuran densities over which *N. v. dorsalis* functions as a keystone predator. The two predators thus promote greater anuran diversity than is possible in ponds with either predator alone or in ponds lacking both predators. As illustrated in Figure 7-3, the mechanism underlying this joint effect depends on a relatively simple combination of characteristics of the anuran prey and the two predators. The characteristics of the prey assemblage are certainly not unique to this system, nor are the critical characteristics of the predators. Thus, we expect that these same or similar functional roles may be filled by different predators in other systems, and with different sets of prey.

The graphical model generates four testable predictions:

1. At low levels of predation, increasing density of larval anurans will be negatively correlated with species richness. Larvae of most anurans are generalist feeders (Altig and Johnston 1989, Duellman and Trueb 1990), so each additional larva raises the intensity of intra- and interspecific competition. Strong competitive asymmetries quickly lead to competitive exclusion and therefore to lower within-pond diversity (Morin 1981, 1983b; Wilbur and Alford 1985; Wilbur 1987; Morin and Johnson 1988; Van Buskirk 1988; Alford 1989; Fauth and Resetarits 1991).
2. Ponds with the keystone predator *N. v. dorsalis* will have a richer anuran fauna only over a very restricted range of relative densities. At low relative densities of newts, predator satiation overwhelms the keystone effect. At high relative densities of newts, species are directly eliminated by predation, thus negating the keystone effect (Morin 1983b).
3. On average, ponds with *S. intermedia* will have a richer anuran fauna than ponds lacking *S. intermedia*. Nonselective predation by *S. intermedia* over a broader range of larval anuran body sizes reduces the overall intensity of competition by reducing larval densities (Fauth and Resetarits 1991); this is the classic case of competitive release (Wilbur 1987, 1988).
4. Ponds with both *S. intermedia* and *N. v. dorsalis* will have, on average, the richest anuran fauna. Nonselective predation by *S. intermedia* extends the range of initial anuran densities over which the keystone effect of *N. v. dorsalis* can operate, thus allowing expression of the keystone effect over a greater number of ponds. Field data suggest that natural anuran densities typically fall within the range where the presence of *S. intermedia* is required to elicit the keystone effect of *N. v. dorsalis*.

We suggest that the anuran diversity that is such a striking feature of temporary ponds in the Sandhills and Coastal Plain of the Carolinas may be a direct result of the

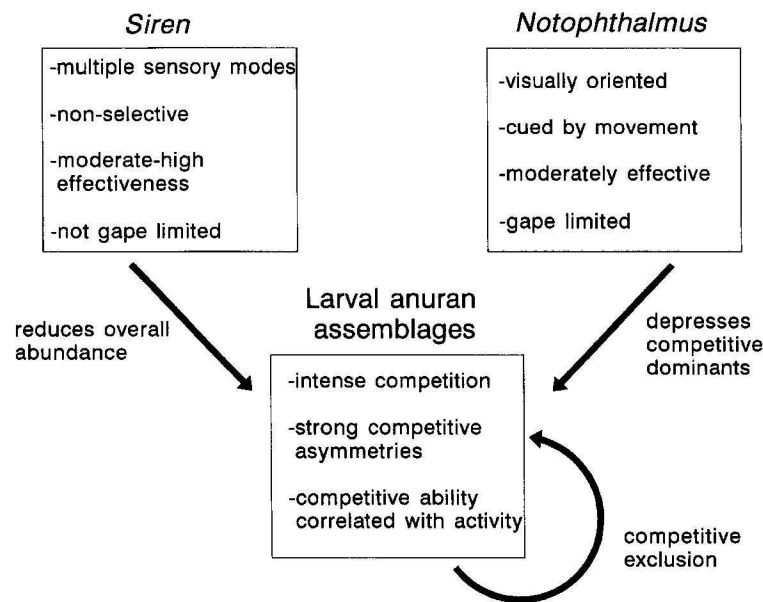


Figure 7-3. Diagram illustrating the critical features of the system. In the absence of predation, intense competition and strong competitive asymmetries reduce species diversity by means of competitive exclusion. The keystone predator effect is a simple consequence of the positive correlation between competitive ability and activity levels in larval anurans, combined with newts' reliance on prey movement as their primary mode of prey detection. Gape limitation enhances the effect on diversity by preventing complete elimination of competitive dominants. As a result, however, the keystone effect can be overwhelmed by predator satiation at high anuran densities. Sirens are consummate nonselective predators on larval anurans, using chemosensory, tactile, and visual cues to locate prey; being far less gape-limited also enhances their non-selective, generalist prey habits. In this system, *Siren* facilitates expression of the keystone effect simply by reducing overall abundances of larval anurans (continuing the architectural analogy, *Siren* is a voussior [a stone in the arch that supports the keystone] to *Notophthalmus*'s keystone).

dominance of these two predators. If they were not abundant, habitat diversity alone would be insufficient to maintain existing levels of anuran species richness. The intense competition and strong competitive asymmetries that are such reliable features of anuran assemblages (e.g., Morin 1983b, Wilbur 1987, Morin and Johnson 1988, Van Buskirk 1988, Alford 1989, Fauth and Resetarits 1991) would play themselves out, and many species would be eliminated from the region or at least restricted to the very few sites at which they held the competitive advantage. In a region dominated by ephemeral aquatic habitats that fill synchronously, the temporal axis along which species in more permanent aquatic habitats segregate is not available, and species are forced into greater overlap in both breeding sites and times. The potential for competition is greatly in-

creased because water is itself a highly seasonal resource. Thus, mechanisms that offset competitive exclusion are essential in maintaining high species diversity.

Though the keystone predator effect is probably the critical biotic mechanism promoting increased anuran diversity, its predicted dependence on *Siren* predation for its expression over much of the typical range of anuran densities greatly elevates the importance of *Siren* in the system. If (in nature) initial species diversity scales with initial anuran density, then it is at the highest potential diversity levels that competition is also the most intense. Consequently, the expected final diversity of metamorphs is the lowest based on the effects of competition alone, and the keystone predator effect has the greatest capacity to affect diversity but the least potential to be evidenced. By having a strong suppressant effect on anuran densities *Siren* can prevent the keystone effect from being overwhelmed. Thus, both predators play a critical role in anuran species diversity in temporary ponds.

A Field Test of the Graphical Model of Anuran Diversity

We tested the qualitative predictions of the graphical model (Fig. 7-2) using observational field data from JEF's intensive faunal survey of seven Carolina bays in southern North Carolina (Fauth 1993). The data were analyzed by multiple regression of four factors, hydroperiod, anuran density, siren density, and newt density, on the response variable of anuran species diversity. Previous work had identified hydroperiod as a critical factor affecting community structure in temporary ponds, especially in interaction with competition and predation (e.g., Wilbur 1984, 1987; Werner and McPeck 1994; Rowe and Dunson 1995; Semlitsch et al. 1996). Thus, we expanded on the graphical model (Fig. 7-2) to include the effects of hydroperiod in the analysis of the field data.

The field survey began when the bays, which were spread across a 600-plus km² area, were synchronously refilled by torrential rains that ended a 2-year drought. The data consisted of minnow trap samples on 5–15 dates per bay, depending on the number of sampling trips on which each bay held water during one hydrologic cycle, from September 1988 through January 1990. On each sampling date 15 plastic minnow traps (opening 2.5 cm in diameter, maximum mesh gap 0.7 cm) were set in each bay and left overnight. Traps were set in two perpendicular lines, one with seven traps parallel to the shore in 12-cm-deep water and the other with eight traps extending from the pond's edge to the deepest water available. The shallow traps rested on the bottom, while the deepwater traps were suspended so their tops just breached the surface, allowing animals with lungs to breathe.

Hydroperiod was approximated by the number of sampling dates on which a pond held water. The maximum number of *S. intermedia*, *N. v. dorsalis*, and larval anurans caught on a single trap-night comprised the estimates of density. Anuran species richness was determined from minnow trap and dip net samples and from nighttime censuses of breeding frogs over the study period. The estimates of anuran species richness for each bay agreed with previous estimates made independently by personnel of the North Carolina Wildlife Resources Commission and the North Carolina State Museum of Natural History (A. Braswell, personal communication).

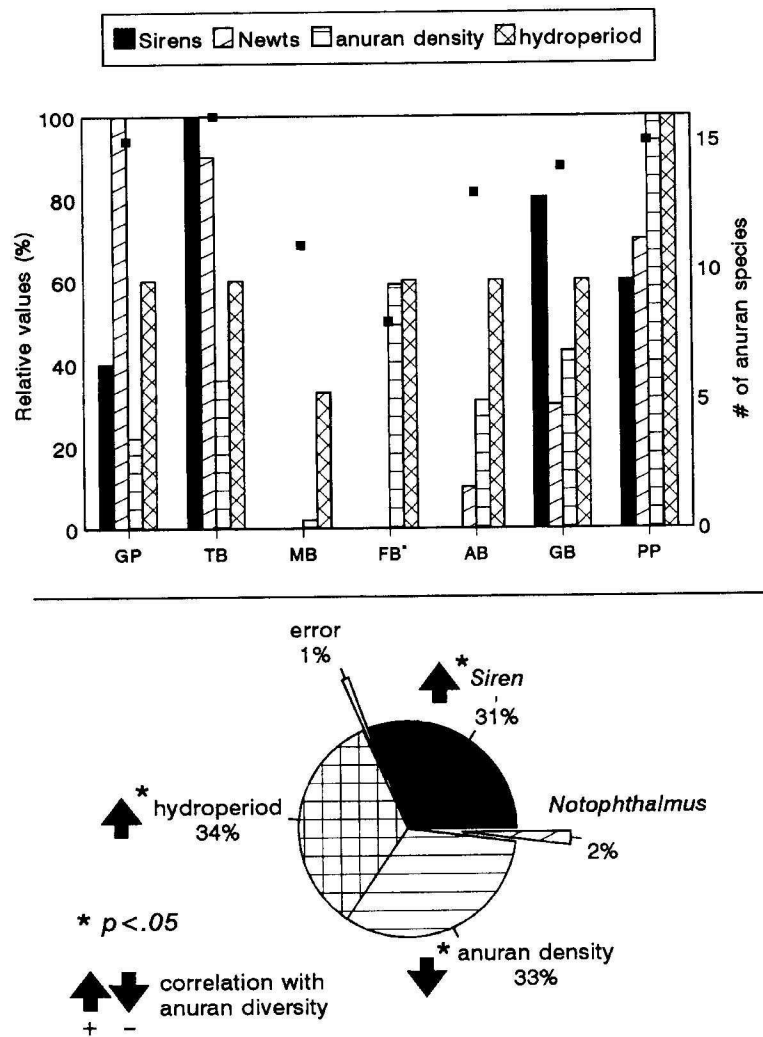


Figure 7-4. Anuran species richness in seven Carolina bays. (Top) Relative values (percentage of maximum observed value for each variable) of the four factors used in the multiple regression (*Siren*, *Notophthalmus*, and anuran densities, plus bay hydroperiod) measured in association with anuran diversity; solid squares = number of anuran species. Historically, *Notophthalmus* is recorded from all the bays but was not trapped in MB or FB during the study period; *S. intermedia* is not recorded from either of these bays. (Bottom) Results of the four-factor regression of anuran diversity, including partitioning of the variation and the direction of the effect. Regression equation: no. of anuran species = $1.06 + 1.99(\text{hydroperiod}) + 0.77(\text{no. of sirens}) - 0.02(\text{no. of newts}) - 0.20(\text{no. of tadpoles})$. Total regression model $R^2 = .997$, $F_{4,2} = 70.27$, $P = .014$.

Our four-factor multiple regression explained >99% of the variation in anuran species richness in the seven Carolina bays ($F_{4,2} = 70.27$, $R^2 = .997$, $P < .014$; Fig. 7-4). The effects of hydroperiod, larval anuran density, and *S. intermedia* density were all significant, and each explained roughly 33% of the variation in anuran species richness. As predicted by the graphical model, *S. intermedia* had a strong positive effect, while the effect of increasing density of larval anurans was strongly negative. Hydroperiod also had a strong positive effect: temporary bays that held water longer permitted more anuran species to breed. Semlitsch et al. reported similar effects of hydroperiod on amphibian diversity in 15 years of data on a natural Carolina bay in South Carolina (Semlitsch et al. 1996).

Interestingly, however, the keystone predator *N. v. dorsalis* (Morin 1981, 1983b; Fauth and Resetarits 1991) had no significant effect on anuran species richness. We offer four testable (though not mutually exclusive) explanations for this last result:

1. Contrary to previous results (Morin 1981, 1983b; Fauth and Resetarits 1991), newts may not be keystone predators in natural ponds. This hypothesis seems improbable, given the repeated demonstrations of the keystone predator effect in mesocosm experiments that differed substantially in anuran species composition, initial density, and habitat heterogeneity (Morin 1981, 1983b, Wilbur 1987; Wilbur and Fauth 1990; Fauth and Resetarits 1991).
2. Although they may not have been present during the sampling period, newts have been recorded from all of the ponds studied. Contemporary estimates of their densities may not reveal their prior effects on anuran assemblage structure. Instead, the newt effect may simply be reflected as a higher (or lower) mean number of species being recorded across all sites (the y-intercept in the regression analysis). Detecting this "ghost of predation past" will require further experiments.
3. The model may be correct; the keystone predator effect of newts may be entirely dependent on sirens reducing overall anuran densities, at least across the range of densities found in the Carolina bays sampled.
4. The newt effect could be nonlinear; the field data support the notion (incorporated in the graphical model but not in the statistical analysis) that at high densities newts no longer function as keystone predators but instead eliminate species from the anuran assemblage. The anurans that typically metamorphose from ponds that have high densities of *N. v. dorsalis* scatter their eggs on the pond bottom or float them in small surface packets. Amphibians that lay their eggs in large clumps (e.g., the tiger salamander, *Ambystoma tigrinum*, and the southern leopard frog, *Rana utricularia*) often suffer complete prehatching mortality in GP and TB, the two Carolina bays with the highest newt densities (Fig. 7-4; see also Morin 1983a).

Alternative Models of Species Richness

If there is one rule in community ecology, it is to not blindly accept the first explanation for any hypothesis (see, for example, the exchange between proponents and detractors of species co-occurrence models in Strong et al. 1984). To test the effects of bay area, spatial heterogeneity, and other environmental influences on anuran species richness, JEF measured an additional 12 environmental variables: bay area, elevation, pH, tree density, distance to the nearest and second- and third-nearest bodies of water, minimum sandrim width, distance to the nearest road and building, and the

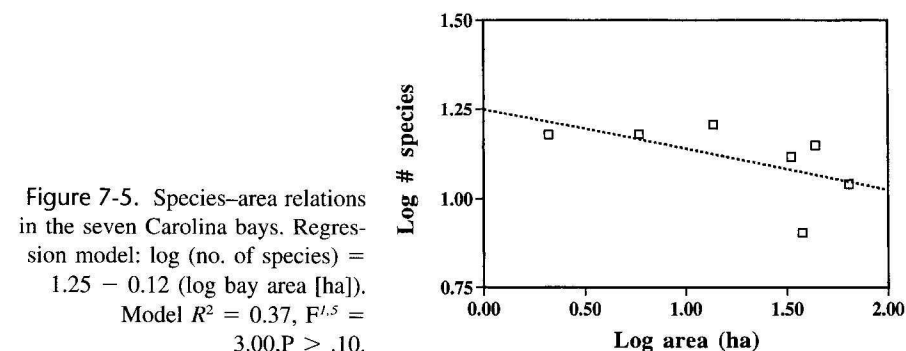
number of buildings and percentage of forested cover within a 1-km radius. Species richness was regressed versus each variable, plus their first three principal components scores, with $\alpha = 0.05$. This procedure inflates the experimentwise Type I error but reduces the risk of Type II error and therefore provides a reasonable alternative to our anuran diversity model. Species richness and pond area were also regressed on a log by log plot to test the species-area relationship that predicts more species will be found in larger bays (MacArthur and Wilson 1967). JEF also constructed and compared UPGMA (unweighted pair-group method, arithmetic average; using PAUP) phenograms of the bays' anuran species composition and environmental/limnological characteristics to investigate possible concordance between these two data sets. Species were coded as binary data (present/absent), and environmental variables were coded according to a posteriori criteria established for each variable (e.g., acid versus neutral pH).

The alternative models tested failed to explain the observed pattern of anuran species richness in the Carolina bays. Bay area was not significantly correlated with species richness ($F_{1,5} = 3.00$, $R^2 = .37$, $P = .14$) and, in any case, was in a direction opposite the predictions of species-area relations (Fig. 7-5). There was no correlation between any of 13 standard environmental variables or their principal components scores and species richness (all $P >> .10$; Fauth 1993). In addition, there was little concordance between UPGMA phenograms of the bays' environmental/limnological characteristics and anuran species composition. The only major congruence between the phenograms was identifying GP as a pond distinct from most or all of the others (Fig. 7-6). This was expected because GP lies in a different physiographic province (Sandhills Region) than the other six bays (Atlantic Coastal Plain) and thus has unique physiognomic and biotic features.

Testing these alternative explanations lends credence to our model of species diversity; our model not only explains most of the variation in species diversity but also does so far better than other, equally plausible, models based on potentially important environmental variables.

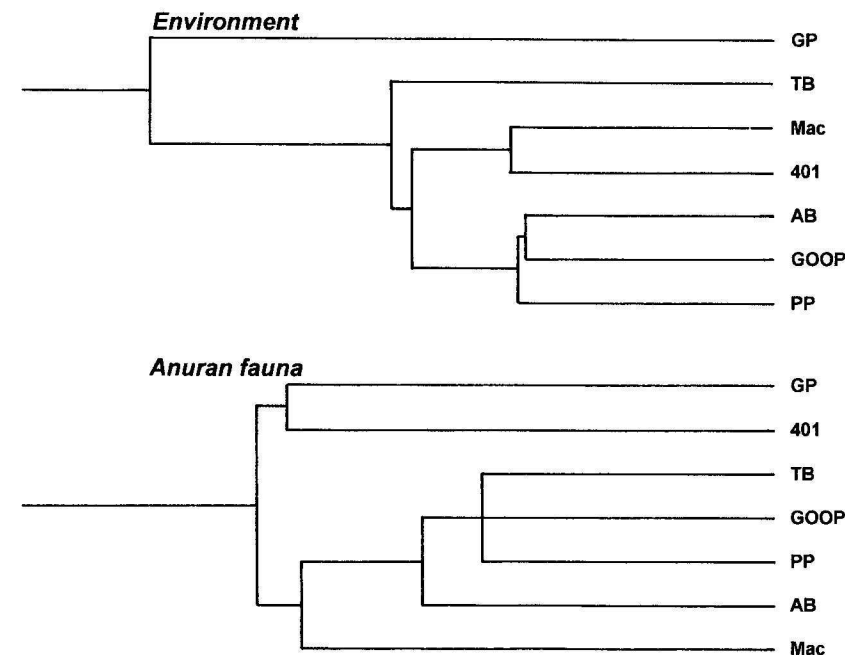
The Contribution of Mesocosms to Understanding Anuran Diversity in Carolina Bays

The field data strongly support the synthetic model developed from the larger body of mesocosm experiments, even while certain specific predictions from individual experiments are not upheld. As discussed previously, the lack of detectable effects of newts on species diversity is surprising based on the results of individual experiments but is entirely consistent with the synthetic model, which incorporates aspects not present in individual experiments. Thus, the simple graphical model has strong predictive power for species richness in Carolina bays, and that predictive power can be seen to derive not from a one-to-one match between the mesocosms and their natural analogue or from the identity of a particular experiment with the conditions seen in these specific bays, but from the detailed, emergent understanding of the processes potentially at work in temporary ponds. This understanding was achieved through thoughtful, detailed,



rigorous experiments which required the control and statistical power afforded by a model system.

The field data strongly support the predicted roles of hydroperiod, anuran density, and *S. intermedia* density in determining anuran species diversity in Carolina bays. Hydroperiod has long been suggested as an important factor influencing anuran diversity in temporary ponds (Wilbur 1987), as has the role of interspecific competition and predation (e.g., Morin 1981, 1983b; Wilbur et al. 1983; Wilbur 1987; Alford 1989; Fauth and Resetarits 1991). *N. v. dorsalis* has long been suspected to play an important



role in temporary ponds; however, little was previously known regarding *S. intermedia*. The field data support the view that the keystone effect of *N. v. dorsalis* may largely depend on the complementary effects of *S. intermedia*. Because of its overland dispersal capabilities (and the lack of such capabilities in *S. intermedia*), *N. v. dorsalis* alone may be most important in smaller, less "historically long-lived" temporary ponds, man-made borrow pits, and similar habitats that lack *S. intermedia*. These habitats are common, especially in the Sandhills, and contain *N. v. dorsalis* almost without exception (often at very high densities; e.g., Morin 1983a) but individually do not support the level of diversity seen in the Carolina bays.

Our field test of the model of anuran diversity suggests that the remarkably high and apparently stable anuran diversity of Carolina bays and other ephemeral ponds is a product of internal biotic forces (intraspecific competition and predation) coupled with the environmental stochasticity imposed by pond drying. Biotic factors accounted for two-thirds of the variation in anuran diversity, with hydroperiod accounting for the remainder. The fragile nature of diversity in temporary aquatic habitats should not be underestimated. Simply preserving the physical features of these and other similar habitats is not sufficient to protect the diversity they contain; the balance between predation, competition, and hydroperiod that specifically maintain it must be preserved. One conservation lesson that arises from our research is that diversity is not a characteristic of place but a characteristic of process. Places with high species diversity can be identified, but unless the processes that maintain that diversity are understood and preserved, their unique characteristics cannot be protected.

The Dual Role of Mesocosm Experiments

Community ecologists began using experiments relatively early in the history of the discipline to reveal the mechanisms that affect community structure (e.g., Gause 1934). The experimental approach varied according to the interests and training of the observer and the limitations imposed by particular systems, but it soon became apparent that a fundamental trade-off existed between complete control of environmental conditions and realism (*sensu* Diamond 1986; see Morin, this volume). Artificial mesocosms were introduced as a hybrid approach that retained much of the interesting variation of nature while allowing the replication and rigorous control of initial conditions required for sophisticated experimental designs; this approach has been adapted to a wide variety of aquatic systems (e.g., Maguire et al. 1968, Vandermeer 1969, Hall et al. 1970, Addicott 1974, Neill 1975, Morin 1981, Hay 1986, Resetarits 1991, Bernardo 1994). Proponents of this approach have long argued that their experiments shed light on fundamental ecological principles, but little empirical evidence has been brought to bear on the question of predictive power in natural systems.

Our field test of a model derived from the results of artificial mesocosm experiments accomplishes precisely what critics rightly argued was lacking (e.g., Petranks 1989 and references therein, Jaeger and Walls 1989): it makes predictions about nature based on the lessons learned from mesocosm experiments and determines the accuracy and utility of those predictions in a natural system. In this case, we explicitly tested a model generated from the results of mesocosm experiments in the natural system that inspired them. Our results suggest that mesocosm experiments designed primarily to test general

ecological theories could, because they also were properly grounded in natural history, simultaneously describe in detail and make specific predictions about the structure and dynamics of natural communities. Mesocosm-based experiments have been recognized for their valuable contributions to our understanding of general ecological processes. This heightened understanding undoubtedly contributes to our understanding of natural systems, even if only indirectly. Here we suggest that our reluctance to accept a more tangible, direct contribution to understanding specific natural systems or types of natural systems bears reconsideration.

We do not suggest that the level of agreement between our model and the field data will be common (in fact, we suspect we will never, ever, explain > 99% of the variation in anything again!). Much will depend on the care taken in designing the model system in the image of its natural counterpart and on the specific system being studied. Nevertheless, we are equally convinced that mesocosms can reveal much about the processes at work in natural systems. Both of us have used mesocosms to address a variety of questions in a relatively broad range of systems and organisms (e.g., Resetarits and Wilbur 1989; Fauth 1990, this volume; Fauth and Resetarits 1991; Resetarits 1991, 1995). In each case, mesocosms allowed us to look at the responses of organisms to predators or competitors (or both) at a level of detail that would be virtually impossible in field studies or field experiments on highly mobile organisms. In each case, we gained insight into both ecological theory and the dynamics of the system our mesocosms mimicked. And in each case, we were surprised by unexpected results or cryptic processes that were only revealed by the detailed responses we could assay in controlled mesocosm experiments. Although individual experiments may not reveal precisely what occurs in natural systems, we can use the cumulative knowledge from multiple experiments to "build" an emergent understanding of processes, just as we have done for the Carolina bays. Though the cost might seem rather high in terms of the number of person-years and experiments devoted to the temporary pond work, one must keep in mind the original goals of the research. Had the intent been specifically to understand the determinants of species diversity in temporary ponds or, in particular, Carolina bays, we could have done specific experiments to answer that question more directly. The critical lesson for ecology is that the trade-offs so often cited between rigor and "realism" may be more an artifact of how we think about natural systems and our own lack of creativity than a characteristic of the relationship between model systems and natural systems.

From the point of view of this article and this volume, our most important message is that we have forged a link between the results obtained in "experimental abstractions" and the dynamics of natural systems. Considering the amount of work that has been done in mesocosms and the growing use of model systems of all sorts, this result is a positive prescription for understanding ecological systems on a broad scale. The criticism that experiments in model systems cannot tell us what happens in natural systems is a hypothesis to be tested, just as any other scientific hypothesis is evaluated against the weight of evidence. We have already begun an experimental test of that hypothesis (and our model of anuran diversity) in natural temporary ponds. Here we have taken an important first step in demonstrating that mesocosm-based research, even that specifically designed to test general ecological principles, can, when properly grounded in the ecology of a specific natural system, provide a both rigorous and

economical tool for understanding that system. Clearly, the greatest gains in generality and specificity can be made when rigorous experiments in model systems are combined with solid fieldwork and strong theoretical underpinnings (Werner, this volume), as has been the case with the temporary pond work. In such cases, the potential contributions of model system-based research to understanding natural communities may not be so limited as critics would have us believe (e.g., Carpenter 1996). At the very least, well-reasoned, well-conducted experiments in model systems should enable us to ask the right questions in natural systems (Lawton, this volume); at their very best, these experiments may indeed provide the answers to those questions.

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Literature Cited

- Addicott, J. F. 1974. Predation and prey community structure: an experimental study of the effect of mosquito larvae on the protozoan community of pitcher plants. *Ecology* 55:475-492.
- Alford, R. A. 1989. Variation in predator phenology affects predator performance and prey community composition. *Ecology* 70:206-219.
- Alford, R. A., and H. M. Wilbur. 1985. Priority effects in experimental communities: competition between *Bufo* and *Rana*. *Ecology* 66:1097-1105.
- Altig, R. A., and G. F. Johnston. 1989. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetological Monographs* 3:81-109.
- Bernardo, J. 1994. Experimental analysis of allocation in two divergent, natural salamander populations. *American Naturalist* 143:14-38.
- Carpenter, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* 77:677-680.
- Diamond, J. M. 1986. Overview: laboratory experiments, field experiments, and natural experiments. Pages 3-22 in J. Diamond and T. J. Case (eds.), *Community Ecology*. Harper and Row, New York.
- Duellman, W. E., and L. Trueb. 1990. *Biology of Amphibians*. Harper and Row, New York.
- Fauth, J. E. 1990. Interactive effects of predators and early larval dynamics of the treefrog *Hyla chrysoscelis*. *Ecology* 71:1609-1616.
- . 1993. Factors Affecting the Abundance and Distribution of Amphibians in Carolina Bays. Final report to the North Carolina Nature Conservancy and the North Carolina Nongame Wildlife Commission, Raleigh, North Carolina.
- Fauth, J. E., and W. J. Resetarits Jr. 1991. Interactions between the salamander *Siren intermedia* and the keystone predator *Notophthalmus viridescens*. *Ecology* 72:827-838.
- . Unpublished ms. Detecting higher order interactions in biological systems: identifying appropriate ecological and statistical models.
- Fauth, J. E., W. J. Resetarits Jr., and H. M. Wilbur. 1990. Interactions between larval salamanders: a case of competitive equality. *Oikos* 58:91-99.
- Gause, G. F. 1934. *The Struggle for Existence*. Williams and Wilkins, Baltimore, Maryland.
- Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. *American Naturalist* 140:539-572.
- Hairton, N. G., Sr. 1989a. *Ecological Experiments: Purpose, Design, and Execution*. Cambridge University Press, Cambridge.
- . 1989b. Hard choices in ecological experimentation. *Herpetologica* 45:119-122.
- Hall, D. J., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnology and Oceanography* 15:839-928.
- Harris, R. N., R. A. Alford, and H. M. Wilbur. 1988. Density and phenology of *Notophthalmus viridescens dorsalis* in a natural pond. *Herpetologica* 44:234-242.
- Hay, M. E. 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. *American Naturalist* 128:617-641.
- Jaeger, R. G., and S. C. Walls. 1989. On salamander guilds and ecological methodology. *Herpetologica* 45:111-119.
- Kurzava, L. M. 1994. The structure of prey communities: effects of predator identity and geographic variation in predators. Ph.D. dissertation, Rutgers University, New Brunswick, New Jersey.
- Kurzava, L. M., and P. J. Morin. 1994. Consequences and causes of geographic variation in the body size of a keystone predator, *Notophthalmus viridescens*. *Oecologia* 99:271-280.
- Lamberti, G. L., and A. D. Steinman (eds.). 1993. Research in artificial streams: applications, uses, and abuses. *Journal of the North American Benthological Society* 12:313-384.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- Maguire, B., Jr., D. Belk, and G. Wells. 1968. Control of community structure by mosquito larvae. *Ecology* 49:207-210.
- Morin, P. J. 1981. Predatory salamanders reverse the outcome of competition among three species of anuran tadpoles. *Science* 212:1284-1286.
- . 1983a. Competitive and predatory interactions in natural and experimental populations of *Notophthalmus viridescens dorsalis* and *Ambystoma tigrinum*. *Copeia* 1983:628-639.
- . 1983b. Predation, competition and the composition of larval anuran guilds. *Ecological Monographs* 53:119-138.
- . 1986. Interactions between intraspecific competition and predation in an amphibian predator-prey system. *Ecology* 67:713-720.
- . 1987. Predation, breeding asynchrony, and the outcome of competition among treefrog tadpoles. *Ecology* 68:675-683.
- . 1989. New directions in amphibian community ecology. *Herpetologica* 45:124-128.

- Morin, P. J., and E. A. Johnson. 1988. Experimental studies of asymmetric competition among anurans. *Oikos* 53:398–407.
- Morin, P. J., H. M. Wilbur, and R. N. Harris. 1983. Salamander predation and the structure of experimental communities: responses of *Notophthalmus* and microcrustacea. *Ecology* 64:1430–1436.
- Morin, P. J., S. P. Lawler, and E. A. Johnson. 1990. Ecology and breeding phenology of larval *Hyla andersonii*: the disadvantages of breeding late. *Ecology* 71:1590–1598.
- Neill, W. E. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. *Ecology* 56:809–826.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Pearman, P. B. 1993. Effects of habitat size on tadpole populations. *Ecology* 74:1982–1991.
- Petranka, J. W. 1989. Density-dependent growth and survival of larval *Ambystoma*: evidence from whole-pond manipulations. *Ecology* 70:1752–1767.
- Resetarits, W. J., Jr. 1991. Ecological interactions among predators in experimental stream communities. *Ecology* 72:1782–1793.
- . 1995. Limiting similarity and the intensity of competitive effects on the mottled sculpin, *Cottus bairdi*, in experimental stream communities. *Oecologia* 104:31–38.
- Resetarits, W. J., Jr., and J. E. Fauth. Unpublished ms. Competition between juvenile sirens and adult newts: interspecific competition from hatching to maturity in a pair of generalist predators.
- Resetarits, W. J., Jr., and H. M. Wilbur. 1989. Oviposition site choice in *Hyla chrysoscelis*: role of predators and competitors. *Ecology* 70:220–228.
- . 1991. Calling site choice by *Hyla chrysoscelis*: effect of predators, competitors, and oviposition sites. *Ecology* 72:778–786.
- Richardson, C. J., and J. W. Gibbons. 1993. Pocosins, Carolina bays and mountain bogs. Pages 257–310 in W. H. Martin, S. G. Boyce, and A. C. Echternacht (eds.), *Biodiversity of the Southeastern United States: Lowland Terrestrial Communities*. Wiley, New York.
- Rowe, C. L., and W. A. Dunson. 1995. Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of central Pennsylvania, USA. *Oecologia* 102:397–403.
- Savage, H. 1982. *The Mysterious Carolina Bays*. University of South Carolina Press, Columbia.
- Scott, D. E. 1990. Effects of larval density in *Ambystoma opacum*: an experiment in large-scale field enclosures. *Ecology* 71:296–306.
- Semlitsch, R. D. 1987. Pedomorphosis in *Ambystoma talpoideum*: effects of density, food, and pond drying. *Ecology* 68:994–1002.
- Semlitsch, R. D., and J. W. Gibbons. 1988. Fish predation in size-structured populations of treefrog tadpoles. *Oecologia* 75:321–326.
- Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1996. Structure and dynamics of an amphibian community. Pages 217–248 in M. L. Cody and J. R. Smallwood (eds.), *Long-Term Studies of Vertebrate Communities*. Academic Press, New York.
- Sharitz, R. R., and J. W. Gibbons. 1982. *The Ecology of Southeastern Shrub Bogs (Pocosins) and Carolina Bays: A Community Profile*. U.S. Fish and Wildlife Service FWS/OBS-82/04, Washington, D.C.
- Strong, D. R., Jr., D. Simberloff, L. G. Abele, and A. B. Thistle (eds.). 1984. *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton, New Jersey.
- Travis, J. T., W. H. Keen, and J. Julianna. 1985. The effects of multiple factors on viability selection in *Hyla gratiosa* tadpoles. *Evolution* 39:1087–1099.
- Van Buskirk, J. 1988. Interactive effects of dragonfly predation in experimental pond communities. *Ecology* 69:857–867.
- . 1989. Density-dependent cannibalism in larval dragonflies. *Ecology* 70:1442–1449.
- Vandermeer, J. H. 1969. The competitive structure of communities: an experimental approach with protozoa. *Ecology* 50:362–372.
- Werner, E. E., and M. A. McPeck. 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. *Ecology* 75:197–213.
- Wilbur, H. M. 1984. Complex life cycles and community organization in amphibians. Pages 195–224 in P. W. Price, C. N. Slobodchikoff, and W. S. Gaud (eds.), *A New Ecology: Novel Approaches to Interactive Systems*. Wiley, New York.
- . 1987. Regulation of structure in complex systems: experimental temporary pond communities. *Ecology* 68:1437–1452.
- . 1988. Interactions between growing predators and growing prey. Pages 157–172 in B. Ebenman and L. Persson (eds.), *Size-structured Populations: Ecology and Evolution*. Springer-Verlag, Berlin.
- . 1989. In defense of tanks. *Herpetologica* 45:122–123.
- Wilbur, H. M., and R. A. Alford. 1985. Priority effects in experimental pond communities: responses of *Hyla* to *Bufo* and *Rana*. *Ecology* 66:1106–1114.
- Wilbur, H. M., and J. E. Fauth. 1990. Experimental aquatic food webs: interactions between two predators and two prey. *American Naturalist* 135:176–204.
- Wilbur, H. M., and J. T. Travis. 1984. An experimental approach to understanding pattern in natural communities. Pages 113–122 in D. R. Strong Jr., D. Simberloff, L. G. Abele, and A. B. Thistle (eds.), *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton, New Jersey.
- Wilbur, H. M., P. J. Morin, and R. N. Harris. 1983. Salamander predation and the structure of experimental communities: anuran responses. *Ecology* 64:1423–1429.