

Comments

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EXPERIMENTAL VENUE AND ESTIMATION OF INTERACTION STRENGTH: COMMENT

David R. Chalcraft,^{1,3} Christopher A. Binckley,² and William J. Reseterits, Jr.²

While experiments are vital for understanding how ecological systems operate, different philosophies exist concerning how experiments should be conducted (e.g., Petranka 1989, Dunham and Beaupre 1998, Reseterits and Fauth 1998, Skelly and Kiesecker 2001; also see the special features in *Herpetologica* [1989; 45:111–128] and *Ecology* [1996; 77:663–705, see Dahler and Strong 1996]). Recently, Skelly (2002) asked how experimental venue (i.e., cattle tanks set up as mesocosms in a field setting vs. screened enclosures placed into natural ponds) influences competitive interactions between two species of larval anurans (*Pseudacris crucifer* and *Rana sylvatica*) and how results from the two venues match a standard of realism. He observed that density affected competitive interactions among larval anurans in mesocosms but not in enclosures and concluded that enclosures were more realistic because the observed size of tadpoles measured in the field was more similar to the size of tadpoles predicted by the enclosure experiment than by the mesocosm experiment. Although an empirical examination of venue is valid, we believe that this study has serious flaws and claims differences between venues that erroneously devalue the use of mesocosms. Our goal is to reinterpret the results from Skelly (2002) in light of its design, point out methodological/statistical issues associated with his study, and argue that both venues can make meaningful contributions to the field of ecology if they are designed correctly with regard to the questions being asked and the specific population of interest.

Fisher's commandment "Thou shalt not confound"

In any well-designed experiment, either all attempts are made to control for factors other than those ma-

nipulated by the experimenter (venue and density in this case), or uncontrolled factors are distributed among experimental units by a strict process of randomization or can reasonably be assumed to be randomly distributed across experimental units and hence treatments (Fisher 1956, Hurlbert 1984). Any factor that varies systematically with a particular manipulation presents a potential explanation for differences in outcome. This defines "confounding," a potentially fatal flaw to any experiment.

Confounding enters into the experimental design of Skelly (2002: 2001) because different "methods typical of those developed by practitioners" were needlessly employed to establish his enclosures and mesocosms (Table 1). The "typical" methodologies for enclosure and mesocosm experiments are designed to address different types of questions. The enclosures used in Skelly (2002) were designed to mimic conditions in a specific set of ponds in order to predict what happens in those particular sites (i.e., his standard for "realism") while his mesocosms were established using "typical" methodologies created to address general, less site-specific, ecological questions. Mesocosm methodology, however, is not immutable and can vary in many ways not considered by Skelly (2002) (see Table 1). These modified methodologies would have easily allowed a mesocosm design that more adequately mimicked conditions in the specific set of ponds where enclosures were placed. Consequently, the comparison of mesocosms and enclosures did not test the effect of venue but tests whether two experiments set up in different ways for different purposes give different results. Another treatise on experimental venue (Carpenter 1996) that claimed microcosm/mesocosm experiments are "irrelevant and diversionary" also suffered from confounding (see Drenner and Mazumder 1999).

Lack of independence

The underlying conceptual framework for both mesocosms and enclosures is the same; experimental units represent independent entities to which specific treatments are applied. Independence is lost when processes occurring in one experimental unit affect others. Since independence is assumed in most statistical analyses, lack of independence can invalidate ecological experiments (Hurlbert 1984, Underwood 1997). Given the importance of chemical cues in the ecology of aquatic organisms (see Chivers and Smith [1998] and Kats and Dill [1998] for reviews), including larval anurans (e.g., Petranka et al. 1987, Kats et al. 1988, Anholt et al. 2000, Eklov 2000, Laurila 2000, Relyea 2000, Peacor and Werner 2001), mesh-enclosure experiments conducted within natural ponds must address the potential

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¹ Department of Biology, East Carolina University, Greenville, North Carolina 27858 USA.

² Program in Ecology, Evolution and Integrative Biology, Old Dominion University, Norfolk, Virginia 23529 USA.

³ E-mail: chalcraftd@mail.ecu.edu

TABLE 1. An incomplete list of factors that could have caused the experimental venues examined by Skelly (2002) to produce different results.

Factors	Affects larval anuran performance? [†]	Enclosures	Mesocosms	Matching possible between venues (enclosures and mesocosms)?
Venue	???	mesh enclosures	cattle tanks	no [‡]
Water source/chemistry	yes ^{1, 2, 3}	synoptic pond	well	yes; use real pond water in mesocosms ^{4, 5, 6} or manipulate water chemistry in mesocosms to simulate particular characteristics of natural ponds (e.g., pH ³)
Litter composition	yes ¹⁹	synoptic pond	forest hardwood and rabbit chow	yes; use real pond litter in mesocosms ^{1, 2, 7, 8, 9}
Litter quantity	???	30 L	600 g	yes
Chemical cues exchanged	yes ^{10, 11, 12, 13, 14}	yes	no	yes; use nonpermeable enclosures or physically exchange water among mesocosms
Canopy cover	yes ¹⁵	semi-closed with screen lids	open (50% shade-cloth lids)	yes; although mesocosm arrays are typically placed in open fields ^{4, 5, 6, 7, 8, 9} , this is not sacrosanct; both venues were covered with screen lids, but a semi-closed pond experiences less ambient light than an open field.
Pond age	yes ^{8, 16, 17, 18}	fill date: prior to fill date of mesocosms	fill date: 1 and 2 April 2001	yes; match dates of filling and drying as pond hydroperiod has a significant effect on larval anurans ^{8, 16, 17, 18} . Differences in date of filling could affect how much nutrients were released from organic matter via decomposition, the presence of different dominant species of algae and zooplankton, etc.
		end date: 7 and 8 June 2001	end date: 7 and 8 June 2001	

Note: Sample references are provided illustrating the specific points. Key to superscripts: 1, Warner et al. (1991); 2, Warner et al. (1993); 3, Sadinski and Dunson (1992); 4, Chalcraft and Resetarits (2003a); 5, Chalcraft and Resetarits (2003b); 6, Chalcraft and Resetarits (2004); 7, Morin (1983); 8, Wilbur (1987); 9, Fauth and Resetarits (1991); 10, Skelly (1992); 11, Van Buskirk and Yurewicz (1998); 12, Peacor (2003); 13, Relyea (2004); 14, Resetarits et al. (2004); 15, Skelly et al. (2002); 16, Tejedo and Reques (1994); 17, Skelly (1995); 18, Wilbur and Alford (1985); 19, Rubbo and Kiesecker (2004).

[†] The “???” indicates that it is unknown how a particular factor affects the performance of larval anurans. This does not indicate that such factors are not important, but rather that they have not been fully investigated.

[‡] Only one of these differences is immutable between enclosures and mesocosms: venue.

lack of independence as chemical cues easily pass through mesh enclosures (e.g., Relyea 2000, Peacor and Werner 2001, Relyea 2004, Resetarits et al. 2004). Although it is unclear how far chemical cues from different organisms disperse, studies suggest that the distance can be very large (Chivers and Smith 1998), and that cues may persist for extended periods (Kats and Dill 1998). For example, a single 1-g snail (*Pomacea paludosa*) can produce enough chemical cue to produce an active space (i.e., volume of water that contains sufficient cue to elicit a response) of 250 000 L (Chivers and Smith 1998). Given that Skelly's enclosures were placed in water that is 0.5 m deep, the chemical cues from this single snail would have an active area of 500 m²! Such a large active space is not unique to this particular species (reviewed by Chivers and Smith [1998]). Thus, if any of the possible inhabitants have a potentially large active space, and cues are persistent, then screened enclosures within a single body of water

need to account for the possibility that experimental units are interdependent.

Although Skelly (2002) placed replicate sets of enclosures in different ponds (blocks), interdependence among experimental units is still a concern as different treatments were applied (i.e., competitor density) to multiple experimental units within individual ponds. Consequently, the lack of detectable differences among treatments within his enclosure experiment could have resulted from all experimental units within a pond responding to conditions generated by one or more treatments (or to the general conditions prevalent in the pond—see *Understanding the environmental context*, below). His mesocosms, however, did not suffer from this problem.

Enclosures can be established to increase the likelihood of independence by placing only a single enclosure in any given pond. This raises obvious logistical problems and would increase unexplained varia-

tion if sites vary in unmeasured parameters (e.g., size, dissolved O_2 , pH, species composition, etc.) that nonetheless affect response variables. However, the scope of inference and thus generality of the observations would also be increased. A simple alternative would be to place multiple, nonpermeable enclosures (cattle tanks?) into a pond. Viewing enclosures in the broader context of these limitations and the methods needed to correct them makes it difficult to argue that enclosures should inherently be more realistic than mesocosms.

Understanding the environmental context

In addition to the potential problem of exchanging chemical cues between experimental units, the exchange of chemicals and resources between enclosures and the external aquatic environment could homogenize environmental conditions among enclosures within ponds (blocks) and thus potentially mask true treatment effects. This condition is not correctable by extracting block effects. Skelly (2002) did not report what other organisms occurred in the ponds where his enclosures were placed (with the exception that other larval *Rana sylvatica* occurred and larval *Pseudacris crucifer* were absent) but it is likely that many species occurred in this common matrix. These species (including *R. sylvatica*) could alter resources or emit chemical cues that change the behavior/physiology of individuals within the enclosures. As indicated by Skelly (2002), *R. sylvatica* density did alter growth of conspecifics in mesocosms but not in enclosures. He assumed, however, that larval *R. sylvatica* outside of enclosures had no effect on the observed competitive interactions. This would be surprising because larval anurans can significantly reduce the amount of algae available to diffuse or grow through enclosures (see Alford [1999] for review), and species of larval anurans can produce chemical cues and growth inhibitors that affect both hetero- and conspecific individuals (e.g., Steinwascher 1978). Although it is possible that larval anurans did not substantially reduce resources in the ponds studied by Skelly (2002), this suggests that his study applies only to the subset of ponds where resource depletion is minimal. Similarly, a number of studies (e.g., Van Buskirk and Yurewicz 1998, Relyea 2004, Resetarits et al. 2004) have demonstrated that chemical cues from predators (fish or larval dragonflies) can alter or eliminate the effects of conspecific density on the growth of larval anurans. Consequently, the presence of predators or competitors in the surrounding matrix provide at least two biologically meaningful explanations for the absence of density effects in enclosures and the convergence of results between venues at the highest larval *R. sylvatica* densities (see Skelly 2002: Figs. 1 and 2).

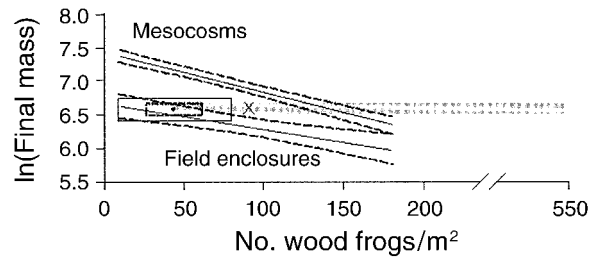


FIG. 1. A modification of Skelly's (2002:2009) Fig. 2 "Relationship between the natural logarithm of *Rana sylvatica* mass . . . and density." The solid regression lines and their 95% confidence intervals (dashed lines) represent the relationship between initial experimental density of *R. sylvatica* and final size of *R. sylvatica* in mesocosm and enclosure experiments. The solid black dot represents the mean mass of *R. sylvatica* in natural ponds at termination of the experiment and mean density of *R. sylvatica* in natural ponds measured at unspecified point(s) in time. The hollow dotted rectangular box defines 1 SE (i.e., their 68% CI) for these measurements as reported by Skelly (2002), the larger hollow rectangular box represents the 95% confidence intervals for these same measurements to make them more comparable to the regression estimates.

Berven's (1990) study of *R. sylvatica* in natural ponds suggests that survival from egg to metamorph ranges from 0.07 to 8%. Thus, the solid gray box outlines the possible range of initial densities for *R. sylvatica* in the natural ponds shortly after eggs hatched (i.e., the time at which the experiment started and experimental densities were established). Its left-most edge (the mean density plotted by Skelly, ~44 individuals/m²) corresponds to zero mortality of *R. sylvatica* in the natural pond over the duration of the experiment (~40 days), while the right-most point (~550 individuals/m²) corresponds to Berven's most optimistic value for *R. sylvatica* survival (8.0%); plotting Berven's lowest value would expand the potential range of initial densities by two orders of magnitude.

The two venues are equally good predictors of the size of wild individuals if the initial density of wild populations was X (~91 individuals/m²) because the mass of the wild individuals is equidistant to the two regression lines at this density.

Arguing that a common aquatic matrix provides a greater natural context for enclosure experiments holds only if chemical cues and resources are exchanged between enclosures and the common matrix, but not among enclosures themselves, and is only useful if one is attempting to model nonindependent systems (e.g., sites within a pond vs. separate and independent ponds). With no detailed understanding of the natural context in which enclosures are placed, however, we are no closer to understanding which "elements matter to species" (Skelly 2002:2100). Skelly's (2002) study can be contrasted with Park's (1954), which also demonstrated context-dependent competitive interactions between species. Although Park's (1954) work would be deemed unrealistic by some since it was not conducted in the field, his controlled manipulation of the environmental context allowed him to determine why

competition was context dependent. Given the design of Skelly's (2002) experiment, no explanation for context-dependent interactions can be provided. Although enclosure (or mesocosm) experiments can be designed to examine how environmental context affects species interactions (e.g., Chalcraft and Andrews 1999), neither the enclosure results nor the contrast between enclosures and mesocosms (Skelly 2002) provide insight into the processes affecting larval anuran performance. Controlled manipulation of environmental context, as is often done in mesocosm experiments (e.g., Wilbur 1987, Warner et al. 1993, Rubbo and Kiesecker 2004), can provide such insight into the natural scenarios in which particular mechanisms may or may not be important.

A trade-off between realism and precision.—Although not discussed by Skelly (2002), his study reinforces the well established view that mesocosm experiments allow for more precise estimates of treatment effects because they are inherently less variable (Morin 1998). This is reflected in the fact that *Pseudacris crucifer* survival was more variable in enclosures than in mesocosms (see Skelly 2002: Fig. 1c) and the 95% confidence interval associated with the effect of initial *Rana sylvatica* density was at least twice as large in enclosures than in mesocosms (see Skelly 2002: Fig. 2). Although it had been previously suggested that enclosure and mesocosm studies produce equally variable results (Skelly and Kiesecker 2001), these analyses confounded experimental venue with other factors that render multiple interpretations. For example, species identity was confounded with venue as only 6 of the 31 species of larval anurans considered for the meta-analysis occurred in both mesocosm and enclosure studies, and more species appeared in mesocosm (23) than in enclosure experiments (14). If one accepts the idea that Skelly's (2002) enclosures were more realistic than his mesocosms, one must accept the expense of lost precision. Such a trade-off has long been recognized by ecologists and provides a rationale for conducting experiments in different venues to take full advantage of their different strengths (Morin 1998). Resisting the notion that such trade-offs exist or promoting the value of one aspect of the trade-off (e.g., realism, precision, or generality) only stifles creativity when exploring ecological processes.

Are enclosures more realistic?—Skelly (2002) suggests that his enclosure experiments are more realistic than his mesocosm experiments. We challenge this claim on (at least) four fronts. First, realism was based on the output of larval *Rana sylvatica* from the specific ponds in which the enclosures were placed, causing observations in the enclosures and ponds to be interdependent. Consequently, there is no independent standard of realism against which performance in the two

different venues can be judged. Thus, one reason why mesocosms failed the test of realism is because the design of the test failed to give them the opportunity to pass. Assuming an unconfounded design, a better standard of realism would have involved sampling other ponds and comparing the observed responses in mesocosms and enclosures to the mean (and range of) responses from that independent collection of ponds.

Second, the target species, *Pseudacris crucifer*, did not naturally occur in the vernal ponds during the year of the experiment, and only occurs in these ponds sporadically across years (D. K. Skelly, personal communication). Previously, Skelly (1995) demonstrated lowered performance of *P. crucifer* when placed in vernal ponds that are either "temporary" (i.e., dry annually) or "intermediate" (i.e., dry some years but not others), so it is not surprising that *P. crucifer* performed poorly at all experimental densities when placed in enclosures located in similar vernal ponds. Consequently, the different outcomes reported by Skelly (2002) do not reflect differences in realism between venues, but simply reflect differences in suitability from the perspective of the focal organism, *P. crucifer*. The generic mesocosms constituted a more favorable habitat than ponds where *P. crucifer* fails to consistently establish.

Third, Skelly (2002) claimed that the final mass of *R. sylvatica* collected from the ponds in which the enclosures were placed fell within the range predicted by the enclosure experiment. Even if we ignore the interdependence between the ponds and enclosures and accept this measurement as a reasonable standard by which to judge realism, the graphical presentation in Skelly's (2002) Fig. 2 (reproduced in our Fig. 1) is inaccurate because the regressions of *R. sylvatica* size on *R. sylvatica* density reflect initial stocking densities in mesocosms and enclosures, while the density point plotted as the standard for realism reflects final densities after substantial mortality has occurred in the natural ponds. Consequently, the location of the "wild" populations in Skelly (2002: Fig. 2) should be shifted to the right along the x -axis. Such a shift significantly downplays the claim concerning final mass as the confidence intervals (CI) associated with the two experimental venues are closer, the CI for the enclosure experiment larger and, the mean final mass in mesocosms and enclosures more similar at high than at low densities.

If we ignore the issue of the lack of independence between the wild standard and the enclosure results and simply ask what initial density of *R. sylvatica* in the wild would make the two venues equally good predictors of the size of the wild individuals, we merely look for the initial density that would produce an observed final mass equidistant between the two regres-

sion lines. This occurs at a density of ~ 91 tadpoles (the "X" in Fig. 1), which translates into a survival rate of 48%. Consequently, if natural survivorship is $>48\%$ the wild population lies closer to the enclosures, if $<48\%$ it lies closer to the mesocosms. Given Berven's (1990) estimate of survival (0.07 to 8%) in natural ponds, survival on the order of 48% or greater is unlikely. Skelly's overall survival estimate for *R. sylvatica* in both his enclosure and mesocosm experiments (81%), which are free of predators, is unlikely to be a good estimate of premetamorphic survival in natural ponds where predators are present. Unfortunately, we do not know the actual value, since it is unclear when Skelly's reported density estimates were made. Even if pipe sample estimates were made within a few days after egg hatching, this provides only a *minimum* estimate of density because the person performing the sampling can disturb tadpoles and cause them to evade capture (Shaffer et al. 1994). Consequently, pipe sampling is a good way to derive relative but not absolute estimates of density. Absolute estimates taken at the same time tadpoles were introduced into enclosures and mesocosms would be needed to make the wild data even roughly comparable to the experimental data.

Fourth, Skelly (2002) plotted the standard errors (i.e., 68% CI) for density and mass of *R. sylvatica* collected in natural ponds rather than their 95% CI as he did for his enclosure and mesocosm experiments. Because 95% CI are equivalent to 1.96 standard errors, the 95% CI for the density of the "wild" population would include nearly a third of the range of density values presented in Skelly's (2002) Fig. 2. Had the 95% CI for both mass and density been shown and a more accurate estimate of the initial *R. sylvatica* density in natural ponds been provided, they may well have overlapped the 95% CI for the mesocosm experiment (Fig. 1). Furthermore, the wide CI from the enclosures do not lend credence to the notion that enclosure experiments produce realistic estimates, but rather reinforce the notion that enclosure experiments provide less statistical power to reject null hypotheses, including that of realism. Had more unexplained variation (resulting in wider CI) been associated with mesocosm experiments, they could also be argued to be "realistic" for completely invalid reasons. Taken together, all of these facts preclude any claims of greater "realism" in the enclosures.

A balanced and fair appraisal of experimental venue.—We are consistently surprised to read papers challenging the value of mesocosm/microcosm experiments in comparison to the purportedly greater value of field enclosure or whole-system manipulations. Although appraisal of various experimental venues is healthy for the development of comprehensive and synthetic theory (Wilbur 1987), much of that appraisal has come in

the form of criticism of mesocosm/microcosm experiments because they are thought to be unrealistic and diversionary, rather than in the form of truly objective assessments or definitive experimental designs. Different venues have unique advantages and disadvantages (Morin 1998) and the contributions of any given approach depend largely on the skill and creativity of its practitioners. Certainly, many of our comments on Skelly (2002) can also be applied to mesocosm studies suffering from similar design and statistical flaws. We hope readers recognize that each type of experimental venue can be useful when experiments are properly designed (e.g., no interdependent experimental units or confounding), that methodologies can be employed to temper the disadvantages of various venues while preserving their advantages, and that future appraisals of experimental venue must be balanced and fair.

Skelly (2002:2001) suggests that ecologists should focus on experimental venue to better understand ecological processes because it will "force the decomposition of venue into the elements that matter to species." There seems little need to force the idea of decomposing systems into the "elements that matter to species" as ecology has a long history of experiments (using a wide variety of experimental venues) specifically designed to decompose the natural environment into its critical elements. Without such experiments it is not possible to tease apart causal relationships from meaningless but significant correlations; that is the very impetus for the use of experiments in ecology (Hairston 1989, Paine 1994, Underwood 1997, Resetarits and Bernardo 1998). Although focusing on venues could provide insight into ecological processes if the experiments are designed correctly, it is considerably more efficient (i.e., time, effort, and money) to design an enclosure or mesocosm experiment that directly examines the specific elements thought to matter.

In summary, there is no evidence provided in Skelly (2002) that anything inherent in the differences between enclosures and mesocosms causes them to differ in their ability to predict the outcome of real-world interactions, or gives one approach hegemony in the world of experimental ecology. Similarly, there is no real evidence from the natural world that mesocosm experiments or other experiments using model ecosystems are somehow more contrived than their counterparts in enclosures, whole ponds, etc., or that they have misled us in our quest to understand how the real world works (Resetarits and Fauth 1998, Jessup et al. 2004). In fact, experiments and field studies in natural ponds suggest that many processes identified as important in mesocosms are indeed important in natural ponds (e.g., Smith 1983, Berven 1990, Scott 1990, Resetarits and Fauth 1998, Loman 2004). A synthetic and general understanding of ecological processes is a primary re-

quirement of a predictive ecology. Although mesocosms/microcosms only provide a caricature of nature, they do contain real species, undergo real ecological processes (Cadotte et al. 2005) and provide an essential level of generality with respect to those processes (Morin 1998, Resetarits and Fauth 1998). Though they may not tell us what “does happen” at a particular site at a particular time, they may allow us to ask the right questions when we get there (Lawton 1998).

Unintentional, unrecognized confounding, interdependent experimental units, and inappropriate controls are among the most common and costly forms of experimental contrivance, preventing truly objective tests and causing strong conclusions to be drawn where no chain of causation exists. The clearest result from Skelly (2002) is that if two experiments are designed in different ways to answer different questions, you will likely get different answers; this holds true regardless of venue. While clearly of interest, “What does happen in nature” at any particular place and time is a very small subset of what does or could happen in nature. As Heraclitus (flourished ca. 513 B.C.) recognized millennia ago, “You cannot step twice into the same river” (Plato 1998:33); “What does happen in nature” is necessarily idiosyncratic. Recognition of both the tremendous variety of extant ecological systems and the potential impacts of global climate change, species loss, and a wide variety of other phenomena suggest it is vitally important to determine “What can happen in nature” as well. In our quest for a truly predictive ecology, all of the tools of the ecologists trade have their place (Lawton 1998, Werner 1998).

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