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Cooper, Scott D

Dudley, Tom L

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Author(s): Scott D. Cooper and Tom L. Dudley

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Ed.

The interpretation of “controlled” vs “natural” experiments in streams

Scott D. Cooper and Tom L. Dudley, Dept of Biol. Sci., Univ. of California, Santa Barbara, CA 93106, USA

In a recent comment Miller (1986) criticized three papers (Hart 1981, McAuliffe 1983, 1984) dealing with exploitative competition among invertebrate grazers in streams. His basic argument was that the interpretation of these experiments was confounded by artifacts introduced by the experimental manipulations, and that “natural” experiments (a posteriori correlational re-analysis of the data) provided more “unequivocal” tests of hypotheses than could “controlled” experiments. In response to the first point, we contend that the experimental artifacts postulated by Miller were unlikely to be operating, or were of little consequence, in these studies. Our major disagreement, however, lies with the latter statement because natural experiments, as defined by Miller, do not provide unequivocal tests of hypotheses. In our responses to Miller’s criticisms we deal primarily with the studies by McAuliffe (1983, 1984). We do not discuss Hart (1981) because Hart (1986) has defended his conclusions in a separate rebuttal.

Validity of experimental artifacts

We certainly agree with Miller’s (1986) plea for the importance of considering potential methodological artifacts when interpreting the results of field experiments. We do not feel, however, that Miller adequately evaluated, nor provided evidence for, postulated artifacts in McAuliffe (1983, 1984), and defend McAuliffe’s conclusions because the methodologies and analyses were sound.

McAuliffe (1984) manipulated the densities of grazing caddis larvae (*Glossosoma*) on bricks by applying vaseline-coated rubber bands around treatment bricks

as barriers to *Glossosoma* colonization. After 23 d he found an inverse relationship between the abundance of *Glossosoma* and of algae and other grazers on all bricks. Barriers were then removed, allowing the examination of short-term colonization by grazers (primarily mayflies), to evaluate the relative importances of exploitative vs interference competition. Mayfly densities were higher after 24 h on the bricks with barriers removed than on control bricks.

Miller contends, however, that these results may have been due to experimental artifacts independent of the manipulation of *Glossosoma* densities. Most of Miller’s criticisms rest on the supposition that vaseline barriers (and bare zones following removal) affected movement of non-target taxa in such a way that they confounded McAuliffe’s conclusions. In fact, with the exception of glossosomatids, we and other investigators have observed little effect of vaseline barriers on stream insects, including predatory stoneflies and other stone-cased caddis larvae (*Helicopsyche*) (G. Lamberti, N. Hemphill, pers. comm., Dudley and D’Antonio, unpubl.).

To determine the effects of vaseline barriers, we examined insect behavior on clay tiles which had been conditioned for 10 d to 3 wk in Rattlesnake Creek, California (see Cooper et al. 1986). A pair of 10 × 20 × 1 cm tiles, one surrounded by a rubber band coated with vaseline, was placed into each of a number of open cages containing a layer of cleaned gravel. Cages were 35 × 25 cm plastic pans with the sides replaced by 1 mm Nitex. Known numbers of common invertebrates were then added to the cages (one taxon per cage (40–200 ind), one to four replicate cages), and the number on each tile was counted after one to three days. *Baetis* spp., the most common mayfly in our and McAuliffe’s systems, showed no preference for either tile in any of

Tab. 1. Responses of invertebrates to encounters with vaseline barriers. * = crossed barrier while falling off tile.

Taxon	No. of encounters	% crossing		% avoid
		crawl	swim	
Ephemeroptera				
<i>Baetis</i>	47	72	28	7
<i>Callibaetis</i>	37	26	74	11
<i>Heptagenia</i>	39	100	0	0
<i>Paraleptophlebia</i>	4	100	0	0
Plecoptera				
<i>Calineuria</i>	8	88	12	0
Trichoptera				
<i>Agapetus</i>	28	11*	0	89
<i>Gumaga</i>	12	100	0	0
<i>Tinodes</i>	2	100	0	0
Mollusca				
<i>Physa</i>	34	91	0	9

four replicate cages (Vaseline (V):Control (C) numbers = 14:21, 10:8, 4:8, and 3:5; $\chi^2 = 0.2$ to 1.4, P all > 0.10). The glossosomatid *Agapetus* was inhibited by the barrier (V:C = 0:14 and 0:10, $\chi^2 = 10$ to 14, $P < 0.005$ for both), but the brachycentrid *Micrasema* was not (V:C = 12:14, $\chi^2 = 0.2$). Mean numbers for three other taxa were low, but roughly equal on vaseline vs control tiles: *Callibaetis* 2.8 vs 2.0, $n = 2$; *Heptagenia* 1.3 vs 1.2, $n = 3$; *Physa* 3.1 vs 2.2, $n = 2$. In some cases, we also counted the numbers of individuals resting on the sides of vaseline vs control bricks. Where numbers were sufficient for statistical tests it was apparent that baetids did not rest on vaseline barriers; however, numbers of brachycentrids, physids, and heptageniids were similar on the sides of vaseline vs control bricks. The numbers of chironomid tubes present on the tops of vaseline vs control bricks kept in two cages for over two weeks were very similar: 35 vs 31 and 24 vs 17 ($\chi^2 = 0.2$ and 1.2, $P > 0.10$).

We also directly observed the responses of invertebrates to vaseline barriers on tiles (Tab. 1). Glossosomatid larvae were the only animals that clearly avoided them; most other taxa were impervious to barriers, readily crawling over or resting on vaseline. Reactions were very similar to encounters with a control band without vaseline. Taxa that we often observed colonizing or emigrating by drifting or swimming (e.g., *Baetis*) were particularly unaffected by vaseline barriers. Because stoneflies readily cross barriers (Tab. 1), because mayflies quickly recolonize areas (Kohler 1984), and because stoneflies apparently remain in coarse substrates during both night and day (Williams 1986), it is unlikely that nocturnally-foraging stoneflies have any effect on daytime densities of mayflies on tops of tiles, as suggested by Miller. To test this hypothesis we followed the experimental protocol outlined above but added two predatory stoneflies (*Calineuria californica*) to each of three pans: one containing *Baetis* and two containing heptageniids. Over the four days of this ex-

periment numbers of baetids on vaseline vs control tiles were not significantly different (means = 20 vs 15.5, $\chi^2 = 0.5$, $P > 0.10$). Numbers of heptageniids on tiles were too low for statistical tests, but roughly equal (V:C = 1:2.5 and 2.5:1.2). In general, vaseline barriers are effective in preventing glossosomatid colonization of tiles, but have little effect on the emigration or immigration of other taxa.

In his earlier study, McAuliffe (1983) placed two sets of bricks into his study stream: one set had been in the stream for 28 d and supported variable periphyton densities (reintroduced bricks) whereas the second set had no periphyton (newly-introduced bricks). He monitored the colonization of invertebrates to these bricks at 3, 7, and 14 d, and by using data for all bricks over the experimental period found a positive correlation between grazer and algal abundances. Miller criticizes McAuliffe's analysis because the newly-introduced bricks purportedly contained lower algal densities than would naturally be found in the field. Miller then states that the re-introduced bricks support the range of algal densities found in the field and performs correlational analyses using only data from the re-introduced bricks.

Unfortunately, McAuliffe did not measure algal density on natural substrates so it is difficult to know if algal abundance on bricks was comparable to that in the stream. However, bricks do not support the variation in algal densities that occurs naturally because artificial substrates (bricks) do not provide the habitat heterogeneity found among natural substrates (Lamberti and Resh 1985). Estimates of diatom densities on natural substrates often vary over at least an order of magnitude (e.g., DeSeve and Goldstein 1981), contrasting with a range of 70 to 265 cells cm^{-2} on McAuliffe's re-introduced bricks. Miller's assumption regarding the range of natural algal densities on bricks is probably invalid; algal densities on natural substrates were certainly more variable than those on the re-introduced bricks.

It is clear, however, that reported algal densities for both the newly-introduced and re-introduced bricks in McAuliffe's (1983) paper were much lower than those reported in the literature (e.g., Gumtow 1955, Douglas 1958, Jones 1978, Blinn et al. 1980, Peterson 1987), although the large variation reported for natural substrates indicates that algal densities as low as McAuliffe's may occasionally occur (e.g., DeSeve and Goldstein 1981) perhaps after floods that overturn or scour rocks (Gumtow 1955, Jones 1978). It is likely that McAuliffe (1983) underestimated algal densities on his bricks, a point corroborated by McAuliffe (1984) where reported algal densities were ca. two orders of magnitude higher. Whatever the reasons for McAuliffe's low estimates, however, McAuliffe's sampling protocol was consistent and showed that his manipulations succeeded in exposing grazers to algal abundances varying by 60 fold. Because McAuliffe's stated purpose was to examine grazer responses to variations in algal abundance,

we believe that his experiment achieved that aim. Miller's criticisms are only valid if one assumes that grazer responses to manipulated algal abundances will be different than their reactions to natural algal densities. Nowhere does Miller provide evidence for this assumption, which we consider to be unreasonable.

We contend, therefore, that the criticisms regarding experimental "artifacts" in McAuliffe (1983, 1984) identified by Miller (1986) are largely invalid or irrelevant. This is not to deny the importance of their consideration, but a critical evaluation of the presumed artifacts suggests that either they are unlikely to be operating, or that they would not significantly alter the patterns that McAuliffe obtained.

Statistical problems of data re-analysis

We also disagree with Miller's re-analysis of McAuliffe's (1983, 1984) data which consisted of splitting it into subsets. From the 1983 study Miller examined the correlation between grazer and resource abundances only for the reintroduced bricks, which he claims represented a natural range of food levels. Using the 1984 data he performed correlations between *Glossosoma* and algal densities, and between *Glossosoma* and "other grazer" densities; he analyzed separately the data for bricks with and without barriers. Miller found almost no significant relationships among grazers and resource levels, so concluded that these relationships were not important in the field.

It should be first stressed that McAuliffe's experiments were designed to be analyzed by comparison of means between treatments, and his major conclusions were based on these tests. The correlations in McAuliffe's paper were included primarily for illustrative purposes. Furthermore, as outlined above, we believe that the artifacts postulated by Miller are invalid, so there is little justification for splitting the data and performing within-treatment correlations. By dealing with a subset of McAuliffe's data (reducing numbers of replicates) Miller effectively limited his ability to detect statistically significant relationships between grazer and algal abundances by increasing the probability of a Type II error (Allan 1984). Also, by narrowly restricting the range of values of the independent variable (algal or glossosomatid abundance), differences can be easily overridden by the effects of secondary variables or sampling error, especially when sample sizes are reduced.

To illustrate these points we re-examined data presented in Douglas (1958: Fig. 5) which show a clear, negative relationship between natural algal densities and the densities of a glossosomatid caddis larvae (*Agapetus*). Algal densities on natural substrates varied over 60 fold (ca. 2500–160000 cells cm^{-2}), similar to the amount of variation found across all of McAuliffe's (1983) bricks, and there was a highly significant negative correlation between algae and grazer abundance when we analyzed all of the data (Spearman's $p =$

-0.66 , $P < 0.001$, $N = 22$). We then analyzed random subsets of these data where the highest algal density was approximately 2.5 to 7 times that of the lowest density, the same magnitude of variation observed on McAuliffe's (1983) re-introduced bricks and on bricks within each treatment in McAuliffe (1984). Only one of seven correlations was significant ($P < 0.05$) and absolute values of Spearman's p ranged from 0.14 to 0.67 (-0.67 to $+0.36$, $N = 7 - 11$, 5 of 7 P s > 0.10). These difficulties can be especially confounding when numbers are low. In the 1984 study, *Ephemerella doddsi* and 'other grazers' (mostly heptageniids) colonized bricks formerly with barriers at densities < 2 per brick, and were virtually absent on bricks without barriers, so it is not surprising that Miller found no correlations within each treatment. Thus, McAuliffe's manipulation of the major grazer, or of algae, may be necessary to provide sufficiently wide ranges for examining the relationships among grazers and their resources.

Problems with interpreting natural experiments/correlation studies

Miller's fundamental contention is that his "natural experiments", or within-treatment correlations, provided unequivocal tests of the relationships among grazers and their resources. In other words, correlations among non-manipulated populations of grazers and algae gave less ambiguous conclusions regarding community interactions than did McAuliffe's manipulative experiments.

A basic difficulty with Miller's correlations was that the data were based on static measures of grazer and resource abundances. Such correlations ignore the dimension of time, when in fact the history of a patch must be known in order to interpret algal or grazer dynamics within the patch. A variety of data indicates that stream grazers both track and deplete their resources (Hart 1981, 1987, McAuliffe 1983, 1984, Lamberti and Resh 1983, Kohler 1984, Lamberti et al. 1987, Hill and Knight 1987). Both processes function simultaneously, with time lags because grazers do not respond instantaneously to resources and vice-versa. When grazers track their resources, one would find a positive correlation between grazer and algal levels; however, a negative correlation would be found on the same patch once grazers had depleted the resource. Grazers leave depleted patches resulting in association of low densities of grazers and algae until the algae regrow. In a given area of stream, then, algal patches are in different stages of depletion or renewal depending on current and past exposure to varying grazer densities. Hence, it may be difficult to establish any correlation among consumers and their resources in natural systems (as in Sih 1985), despite intense and highly deterministic interactions between them.

McAuliffe (1984) maintained large differences in treatment levels (glossosomatid or algal densities) through experimental periods, so he could unambigu-

ously interpret the results of between-treatment comparisons. Miller, on the other hand, narrowly restricted the range of values of the independent variable that he examined by looking only at within-treatment correlations, and had no idea what the grazing history of his patches (bricks within a treatment) were. Because of this uncertainty in knowing grazing history, Miller's correlations tell us little about relationships among grazers and their resources.

Even if Miller did find significant correlations, and he did in one instance, it is not clear that such correlations reveal anything about the effects of grazers on their resources and, ultimately, on competitors. A positive correlation may suggest that the grazer is tracking its resource, but says nothing about whether grazers are controlling, or having little effect on, that resource. Furthermore, significant correlations may be absent if grazing pressure is intense, keeping algae at uniformly low levels. The effects of consumers on resources, and in turn on competitors, requires manipulation of that consumer or the comparison of consumption rates to renewal rates of the resource.

In traditional natural experiments, the researcher chooses two or more similar areas which differ with respect to the independent variable of interest (Diamond 1986). Differences in dependent variables, such as the abundances of animals and plants, among these sites are then attributed to this 'independent' variable. However, study sites nearly always differ in more than this single factor, so patterns cannot be unambiguously attributed to the independent variable of interest. Miller's "natural experiments" were simply a posteriori correlational analyses, without suitable natural variation in what would be mislabelled the independent variable. They suffer the same ambiguity associated with true natural experiments, that differences in other variables among bricks (e.g., current, light) potentially confound or obscure relationships among grazers and their resources. In manipulative experiments, theoretically only the factor of interest is manipulated. Other factors vary independently of treatment, so one can unambiguously conclude that differences between treatments resulted from the manipulations (Connell 1974).

In reality, all three of these analyses of association (correlations, natural and manipulative experiments) entail assumptions concerning confounding influences, but we strongly feel that well-designed manipulative experiments will involve fewer, and less important, alternate interpretations. Manipulations of the dominant consumers or resources (as in Hart 1981, McAuliffe 1983, 1984) can allow the examination of a wider range of ecological conditions, and may promote identification of more complex, dynamic, and less obvious interactions. For example, if a dominant competitor nearly eliminates another species from some areas one would not see a correlation between these species in those areas. Only by eliminating or reducing the dominant competitor might these relationships be revealed.

Although Miller (1986) draws conclusions about the importance of interactions among grazers and their resources from correlational analyses, we contend that one cannot make conclusions about processes (e.g., herbivory, competition, resource tracking) from an examination of patterns (i.e. correlations or lack thereof). Correlations are useful for identifying such patterns, but inferences of mechanisms are not tenable due to the logical circularities inherent in this approach. In essence, patterns cannot be used to test hypotheses regarding the processes resulting in those same patterns. A number of processes can result in the same pattern, and other variables can obscure or confound the relationships. One must examine the processes themselves. Independent manipulations of the factors of interest, in concert with intuition and a thorough knowledge of the natural history of a system, can provide clearer evidence of the processes resulting in observed patterns.

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Interpreting seed survivorship curves

W. M. Lonsdale, CSIRO Div. of Entomology, Tropical Ecosystems Research Centre, PMB 44 Winnellie, NT 5789, Australia

Summary. Survivorship curves for seeds in the soil are widely regarded as being generally log-linear (Deevey Type II). What we know of population structures of seeds, however, would suggest that such curves ought to be the exception for soil seed banks rather than the rule. They therefore remain a problem to be explained. Five possible explanations are proposed for the apparently uniform Type II survival patterns shown by seed populations. It is argued that the phenotypic control of seed longevity would lead to generally convex (Type I) curves, and this, together with fine-scale temporal and spatial changes in seed demography, would mean that, for seed populations, the non-parametric methods used for comparing the demography of seedling cohorts may be more appropriate than comparisons of half-lives.

In many growing plants the type of survivorship curve has been shown to vary between cohorts and with environmental conditions (e.g., Mack and Pyke 1983, Tremlett et al. 1984), and attempts to characterize species or groups of species as displaying a characteristic curve may be inappropriate (Solbrig and Solbrig 1979). Indeed, variability is likely to be the rule rather than the exception.

In contrast, survivorship of long-lived (i.e. lasting more than one year) seeds in the soil is almost always regarded as following a log-linear or Deevey Type II decline (e.g., Harper 1977:104, Cook 1980, Fenner 1985:65, Begon and Mortimer 1986:17, Watkinson 1986). Sometimes log-linear decay is simply assumed at the outset (e.g., Chancellor 1986), and sometimes it is inferred from scanty data sets (e.g., Froud-Williams et

al. 1983). The implication is that seeds living in the soil suffer a constant probability of death (Roberts 1972b). Nevertheless, the evidence for this crucial demographic assumption is in fact limited (Cook 1980), largely deriving from the experiments of H. A. Roberts (Roberts 1970, Roberts and Feast 1973).

A Type II decay curve means that the frequency distribution of seed age at death will be log-normal (Fig. 1a, b). It appears that most mortality of seeds in the soil is due to the breakdown of dormancy mechanisms and subsequent germination while buried in the soil (Roberts 1972b), although loss due to pathogens cannot be ruled out (Cook 1980). It would surely be inconceivable that all species should have log-normal frequency distributions of longevity if this were under phenotypic control. Seed weight, for example, can affect dormancy

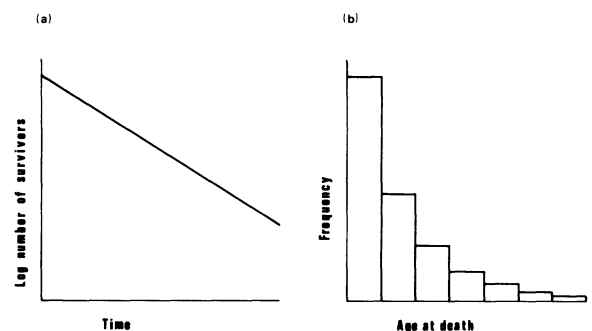


Fig. 1. Typical log-linear survivorship curve of seeds in the soil (a) and the corresponding frequency distribution of age at death (b).