



**Prey Depletion by Odonate Larvae: Combining Evidence from Multiple Field Experiments**

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*Ecology*, Vol. 68, No. 5. (Oct., 1987), pp. 1459-1465.

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## PREY DEPLETION BY ODONATE LARVAE: COMBINING EVIDENCE FROM MULTIPLE FIELD EXPERIMENTS<sup>1</sup>

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*Abstract.* In this paper we re-analyze previously published data regarding the response of several prey populations to manipulation of predaceous larval dragonfly (Insecta: Odonata) densities in four separate field enclosure experiments. Using a computer-intensive “rerandomization” approach to testing hypotheses, we show that the individual experiments were not sufficiently powerful to consistently reject false null hypotheses. Combining the data from three comparable experiments, we can enhance the power associated with such tests.

Three prey categories (Trichoptera, Oligochaeta, and large Cladocera), constituting less than one-third of the typical odonate diet, were found to be consistently depleted in enclosures with odonate larvae; but the extent of their depletion was not increased at high (ambient) compared with low (half-ambient) odonate densities. These results support our previously published conclusions that exploitation competition was not an important phenomenon for odonate larvae in these experiments.

*Key words:* combining evidence; competition; field enclosure experiment; Odonata; power analysis; predation; prey depletion; rerandomization.

### INTRODUCTION

Experimental manipulation of populations in the field, often through the use of enclosures and/or exclosures, has become a preferred method for studying competition and predation in natural communities (Connell 1983, Schoener 1983, Sih et al. 1985). This has prompted thoughtful critiques of the designs and analyses employed (e.g., Toft and Shea 1983, Allan 1984, Bender et al. 1984, Hurlbert 1984, Walde and

Davies 1984) that set high standards for the conduct of future experiments. Having conducted a series of manipulative field experiments that meet most of these critics' criteria for good experimental design, we use them to illustrate an approach to improving statistical power that has not been mentioned in this context: combining evidence from independent experiments.

We recently completed four similar field enclosure experiments that address competition among dragonfly larvae (Insecta: Odonata) and the influence of these larvae on densities of their prey (Johnson et al. 1984, Johnson et al. 1985, Pierce et al. 1985). These experiments involved pairwise manipulation of several odonate species, and all were conducted at the same field site. Thus, we accumulated a considerable body of data

<sup>1</sup> Manuscript received 7 October 1985; revised 20 December 1986; accepted 14 January 1987.

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TABLE 1. A summary of four field enclosure experiments with larval Odonata in littoral zone (allochthonous detritus) habitats of Bays Mountain Lake. There were three treatments: NO (control, no odonates added), HD (high density, approximately ambient odonate density), and LD (low density, half-ambient odonate density).

Experiment	Dates	Enclosure size		No. replicates			Odonate species	Odonate biomass density* (mg/m <sup>2</sup> )		
		Area (cm <sup>2</sup> )	Depth (m)	HD	LD	NO		HD	LD	NO
A†	5 Sep–8 Oct 1981	1464	0.5	9	6	3	<i>Tetragoneuria cynosura</i> , <i>Celithemis elisa</i>	750 ±115	492 ±131	80 ±170
B†	22 Mar–30 Apr 1982	1464	0.2	9	6	3	<i>Tetragoneuria cynosura</i> , <i>Celithemis elisa</i>	630 ±227	570 ±216	43 ±12
C‡	24 Mar–1 May 1982	324	0.2	9	6	3	<i>Enallagma triviatum</i> , <i>Enallagma divagans</i>	1219 ±535	543 ±111	121 ±149
D§	24 Oct–21 Nov 1981	324	0.5	12	8	4	<i>Enallagma triviatum</i> , <i>Enallagma aspersum</i>	617 ±236	664 ±294	772 ±277

\* Dry mass of all odonates recovered from enclosures at the end of the experiments ( $\bar{X} \pm SD$ ).

† Johnson et al. 1985.

‡ Johnson et al. 1984.

§ Pierce et al. 1985.

bearing on the general question, “Do larval odonates deplete their prey?”

Analyses of data from our individual experiments found little statistical evidence of prey depletion, but looking at the results of these experiments together revealed consistent trends: some prey categories seemed to be consistently reduced by odonates over all the experiments, even though those reductions were not always statistically significant. Since such failures to reject null hypotheses have been part of the evidence used to suggest that exploitation competition was not important among odonate larvae in our experiments, we are particularly sensitive to the criticism (cf. Toft and Shea 1983, Allan 1984) that the power of such tests is rarely reported. In this paper we will correct that omission from our previous papers and show that by combining the evidence of several similar experiments we can improve the power of such tests, providing a clearer answer to the question posed above.

## METHODS

### Field enclosure experiments

Our four field enclosure experiments were similar in methods and designs. Each was conducted for 1 mo in littoral habitats of Bays Mountain Lake (Sullivan County, Tennessee). Crowley et al. (1983) describe the enclosures and show that prey assemblages and densities established within them were similar to those in unenclosed areas. The densities of two odonate species were manipulated in each experiment, with both high- and low-density treatment levels for each species, and a high-density treatment level including both species. But since the diets of odonate species in these experiments were quite similar (see the original papers and Merrill and Johnson 1984), we will ignore the species differences here and focus on the effects of odonate larvae on their prey. Three experiments (Table 1; Experiments A, B, and C) included control treatment levels

with no odonates added (NO), high-density odonate treatment levels (HD) at approximately ambient odonate biomass density and low-density odonate treatment levels (LD) at half-ambient density. The fourth experiment (Table 1; Experiment D) had similar treatment levels for damselfly larvae (Zygoptera) but included the ambient density of dragonfly larvae (Anisoptera) in all enclosures, including controls. Although the manipulation of damselfly larvae established large differences in numerical abundance of odonates among treatment levels in Experiment D, total odonate biomass was kept essentially constant over all treatment levels by the much larger size of the dragonfly larvae (Table 1). Table 1 provides some general information about the individual experiments.

We estimated the abundance of prey populations at the conclusion of each experiment by either complete census (macrobenthos) or inverted-funnel samplers (microcrustaceans). All individuals were identified to the lowest feasible taxon, but related taxa containing similar-sized animals were grouped for analyses (i.e., “small cladocerans” included *Chydorus sphaericus*, *Alona barbulata*, and *Bosmina* spp.; “medium cladocerans” included *Alona affinis*, *A. quadrangularis*, and *Pleuroxus denticulatus*; and “large cladocerans” included *Simocephalus vetulus*, *S. serrulatus*, *Sida crystallina*, and *Eurycerus lamellatus*).

### Hypothesis testing and power analysis

If larval odonates deplete their prey resources, we would expect that: (1) prey densities would be higher in control enclosures with no odonates (NO) than in those containing odonates (HD and LD) and (2) prey densities would be higher in enclosures with fewer odonates (LD) than in those with higher odonate densities (HD). These expectations, referred to henceforth as “Prey Depletion” and “Odonate Density” effects, respectively, are posed as one-tailed alternate hypotheses to the null hypothesis of no effect.

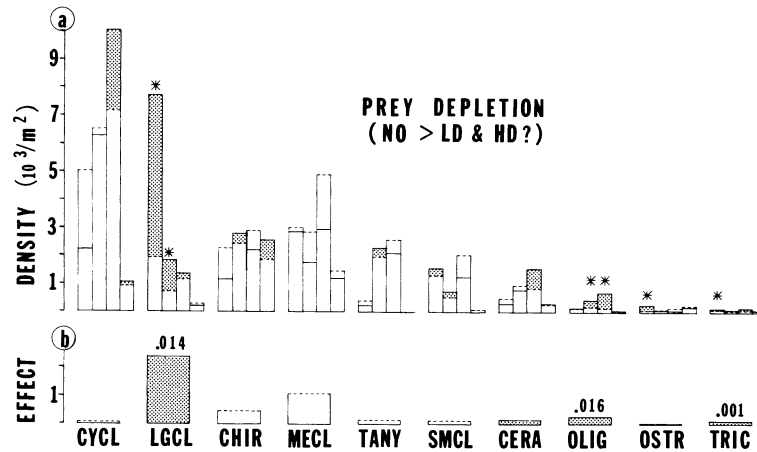


FIG. 1. The mean response of prey populations to the presence (HD and LD) or absence (NO) of manipulated odonate larvae. (a) The four columns for each prey category represent, from left to right, Experiments A, B, C, and D (see Table 1). Two means are presented in each column, corresponding to the contrasted treatments. A solid line represents the mean of those treatments that had the lower density of odonates (NO); a dashed line, those with the greater odonate density (LD and HD). Shaded areas indicate differences whose directions are consistent with the alternate hypothesis that predation reduces prey density (NO > LD & HD). An asterisk above a bar indicates a significant ( $P < .05$ ) Prey Depletion Effect based on 1000 rerandomization runs for individual experiments. (b) Overall Prey Depletion Effects for combined analyses of Experiments A, B, and C. Solid lines, dashed lines, and shading follow the same conventions as above. Actual probabilities associated with null hypotheses are presented where  $P < .05$ . These are based on 1000 rerandomization runs of two-way analyses of variance combining the evidence of three experiments. Prey categories are identified by the following abbreviations: CYCL = Cyclopoida, LGCL = large cladocerans, CHIR = Chironomidae other than tanypodes, MECL = medium cladocerans, TANY = Tanypodinae, SMCL = small cladocerans, CERA = Ceratopogonidae, OLIG = oligochaetes, OSTR = ostracods, TRIC = trichopteran larvae.

In the original publications, responses of prey were evaluated using analysis of variance (all experiments) followed by orthogonal contrasts (Experiments A, B, and C) on log-transformed data ( $y' = \ln[y+1]$ ). Although this transformation is standard procedure and may be the best available for treating multispecies data sets equally (Allan 1984), some groups were not successfully normalized. Furthermore, when data from Experiments A, B, and C were combined, 6 of 10 prey categories had significant heteroscedasticity, despite the transformation.

Difficulties in meeting the assumptions of parametric statistics and with estimating the power of most non-parametric tests, led us to adopt a computer-intensive "rerandomization" approach (Bradley 1968, Edgington 1987) for testing hypotheses and for estimating the power of those tests. In this paper we used rerandomization techniques to re-evaluate the null hypothesis that odonates did not deplete prey densities using a one-way analysis of variance for each experiment and to estimate the power of each experiment to detect 50% prey depletion. We then combined the data from Experiments A, B, and C using a two-way analysis of variance to evaluate the overall Prey Depletion Effect and to estimate the power of this combined analysis to detect specified amounts of prey depletion (10–90%). We took a similar approach to test the Odonate Density Effect.

Analyses were conducted on an IBM PC microcomputer using TurboPascal programs written by the se-

nior author. Power was evaluated by the "naive" method recommended by Gabriel and Hsu (1983). Detailed appendices describing procedures, as well as program listings, are available on microfiche.<sup>4</sup>

RESULTS

Prey depletion effects

*Analysis for individual experiments.* — The responses of prey to control (NO, no manipulated odonate larvae introduced) and odonate (HD and LD, combined high and low densities of manipulated odonates) treatments in all four experiments are presented in Fig. 1a. Statistically significant Prey Depletion Effects ( $\alpha = .05$ ), indicated by asterisks, were found in only 6 out of 39 individual tests. (It is worth noting here that one of those tests, LGCL, Experiment B, was not statistically significant in previous parametric tests. In this case the nonparametric rerandomization approach proved more powerful than its parametric counterpart, presumably because the normality assumptions of the parametric test were violated. Another, TRIC, Experiment B, was significant in the parametric tests, but not [ $P = .095$ ] using rerandomization.) But 14 others had differences in the expected direction (shaded). Could insufficient

<sup>4</sup> See ESA Supplementary Publication Service Document No. 8736 for 21 pages of supplementary material. For a copy of this document, contact the senior author or order from The Ecological Society of America, 328 East State Street, Ithaca, New York 14850-4318 USA.

TABLE 2. Power of analyses of variance to detect 50% depletion of each prey category, based on the number of times that a "critical value" of  $F$  (estimated in a previous rerandomization analysis of the null hypothesis) was exceeded during 1000 rerandomization runs. Boldface numbers indicate power of at least 95%, required for strong inference.

Experiments*	Prey category†									
	CYCL	LGCL	CHIR	MECL	TANY	SMCL	CERA	OLIG	OSTR	TRIC
Power of statistical analysis										
One-way ANOVA										
A	096	831	490	269	263	394	174	517	<b>1000</b>	<b>997</b>
B	496	<b>973</b>	421	266	<b>1000</b>	579	537	880	357	897
C	651	351	610	142	462	099	539	616	123	824
D	<b>990</b>	326	<b>991</b>	221	...	113	423	460	391	459
Two-way ANOVA										
A, B, and C	535	918	860	338	946	161	774	942	461	<b>998</b>
A, B, and C/ [(A + B + C)/3]‡	1.29	1.28	1.70	1.50	1.65	0.45	1.85	1.40	0.93	1.10

\* Experiments A–D are described in Table 1.

† Prey abbreviations are defined in Fig. 1 legend.

‡ The ratio of power for two-way to one-way analyses of variance indicates improvement due to combining the data for Experiments A, B, and C. The no-odonate control treatment was ineffective in Experiment D (see Table 1).

statistical power in individual experiments be masking real differences?

Estimates of power to detect 50% depletion of prey densities by odonate larvae (Table 2) suggested that statistical analyses for individual experiments had insufficient power to be capable of consistently rejecting false null hypotheses. If failure to detect prey depletion in these experiments were due to lack of sufficient power, rather than due to the lack of a Prey Depletion Effect, we might have to reconsider our inference that exploitation competition could not have been important in the enclosures.

*Combined analysis of Experiments A, B, and C.*—In an effort to enhance the power of the test, we combined the data from the three experiments (A, B, and C) for which there was an effective No Odonate control treatment (Table 1). The format was that of a two-way analysis of variance, with  $F$  ratios associated with Prey Depletion Effect, Experiment Effect, and an Interaction Effect. Again we used rerandomization both for testing the significance of these effects and for estimating the power of those tests.

The two-way analyses of variance rejected the null hypothesis of no Prey Depletion Effect for three prey categories (Fig. 1b): large Cladocera, Oligochaeta, and Trichoptera. None of the other seven prey categories came close to showing a significant Prey Depletion Effect ( $.79 > P > .27$ ). Once again, we need to ask whether these failures to reject null hypotheses were attributable to low power or to no effect.

Estimates of power for two-way analyses of variance to detect 50% Prey Depletion Effects ( $\alpha = .05$ ) were compared with estimates of power for individual experiments (Table 2, bottom line). Combining the evidence into one test enhanced the power considerably for most prey categories. The median improvement was  $\approx 35\%$ , and the maximum was 85% for Cerato-

pogonidae. (But note that, in the cases of small Cladocera and Ostracoda, combining Experiment C with its very low power with the others actually lowered the power of the test.)

Has this approach to combining the evidence from three separate experiments improved the power of our tests enough for our purposes? If inferences (e.g., no exploitation competition) are to be made from failure to reject null hypotheses, we should have considerable power associated with statistical tests, perhaps 95% ( $\beta = .05$ ; Toft and Shea 1983). The ability to reject false null hypotheses when means differ by a factor of two (50% prey depletion) has been suggested as a practical limit on the effect size for which benthic insect ecologists can expect to have sufficient power in statistical tests (Allan 1984). Our combined evidence (Table 2) met these two criteria for only 1 of 10 prey categories (Trichoptera), exceeded 90% power for three others (large Cladocera, Tanypodinae, Oligochaeta), and rejected null hypotheses for three of these (Fig. 1b). What are we to conclude concerning the other prey categories?

Rotenberry and Wiens (1985) discuss the inherent difficulty in deciding what Effect Size (e.g., 50% prey depletion) should be specified for power analyses and suggest that a preferable alternative might be calculation of the Comparative Detectable Effect Size (CDES), the minimum possible effect size consistent with  $\beta = \alpha$  (Cohen 1977). In an effort to estimate such effect sizes, we conducted 1000 rerandomization tests for the combined evidence (two-way analyses of variance) after imposing known amounts of prey depletion ranging from 10 to 90% of control means. Fig. 2 presents power curves showing how the probability of rejecting a null hypothesis that was known to be false increased as the size of the hypothetical Prey Depletion Effect was increased for the two-way analyses of variance for each

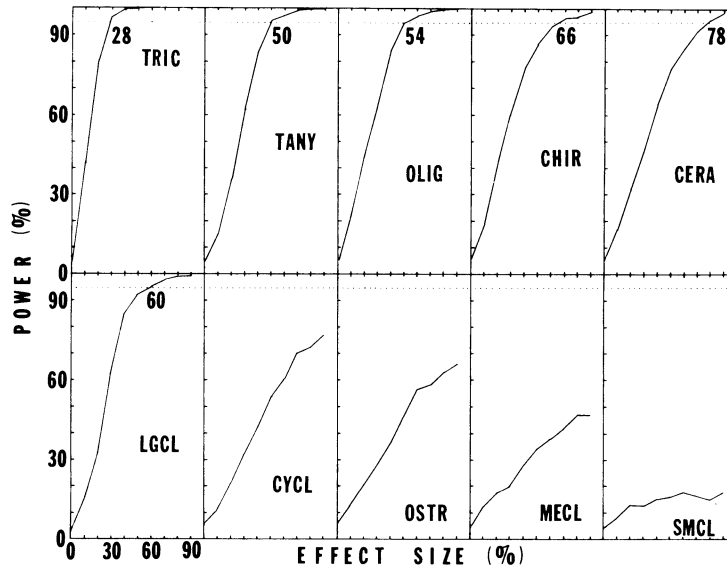


FIG. 2. Power of the two-way analysis of variance to detect Prey Depletion Effects of 10 to 90% for each prey category. Each point represents the result of 1000 rerandomization runs. The goal of 95% power required for strong inference when the null hypothesis is accepted is indicated by a dotted line. Numbers near the intersection of power curves with 95% power indicate the Comparative Detectable Effect Size for each prey category. Prey abbreviations are defined in Fig. 1 legend. Macroinvertebrate taxa whose densities were estimated by complete census of cage contents are presented in the top row; microcrustacea sampled by inverted-funnel samplers are in the bottom row.

prey category. The intersection of these curves with a dotted line indicating 95% power would provide an estimate of the Comparative Detectable Effect Size ( $\beta = \alpha = .05$ ) for each prey category. These estimates suggest that a goal of detecting 66% Prey Depletion Effect with 95% power could have been reached for most macroinvertebrate prey categories (except Ceratopogonidae) as well as for large cladocerans but the variance associated with sampling other microcrustaceans was so high that it precluded detecting even 90% depletion of those taxa.

Despite this evidence that even the combined evidence had little power to detect depletion of microcrustacean densities, inspection of the relative magnitudes of control (NO) and odonate (HD and LD) treatment means for each experiment (Fig. 1a) suggests that there were no additional prey categories, besides the three identified by our combined analyses, for which one might suspect that a consistent real treatment effect was being masked by lack of power. Only for Ceratopogonidae and Ostracoda were the overall apparent Prey Depletion Effects even in the expected direction (Fig. 1b), and in both cases that trend was attributable to only one of the three experiments combined in our analysis (Fig. 1a).

#### *Odonate density effects*

Results of rerandomization tests of null hypotheses in one-way and two-way analyses of variance for the Odonate Density Effect (LD > HD?) are presented in Fig. 3. There was no statistically significant support for the alternate hypothesis that prey densities should be

depleted more by "high" than by "low" odonate densities. In fact, the only two individual tests to reject the null hypothesis involved cases where the relative magnitude of means was in the opposite direction of that expected under the alternate hypothesis (Fig. 3a: MECL, Experiment A; TANY, B). The combined data from Experiments A, B, and C resulted in only 1 of 10 prey categories showing an overall treatment effect in the expected direction (Fig. 3b: SMCL), and that was not even close to being statistically significant ( $P = .37$ ).

## DISCUSSION

### *Prey depletion effects*

The combined evidence from three field experiments indicates that odonate predation consistently reduced the density of three prey categories in our enclosures: trichopteran larvae, oligochaetes, and large cladocerans. Furthermore, our failure to detect significant depletion of other prey categories now seems less likely to have been due to insufficient statistical power. These conclusions are consistent with results of another set of field enclosure experiments (Thorpe and Cothran 1984) that suggest that odonate predation had very little effect on the density of most prey taxa. Interestingly, there was a suggestion of a predation effect on trichopterans (including some of the same genera as in our study) in April–May 1980, and on oligochaetes in January–February 1981. Their paper does not report any results for microcrustaceans.

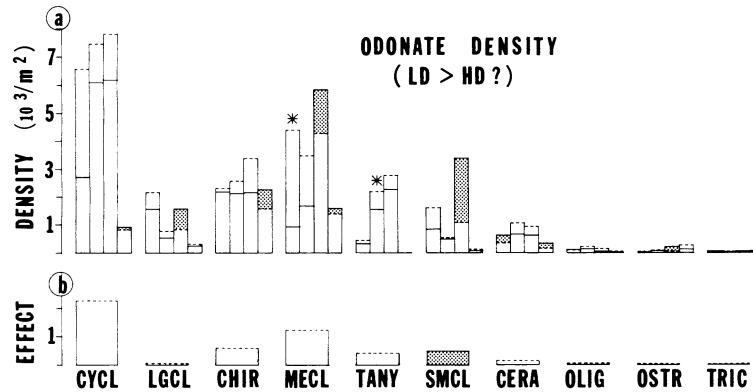


FIG. 3. The response of prey populations to ambient (HD) and half-ambient (LD) densities of manipulated odonate larvae. (a) The response for individual experiments, with data presentation as in Fig. 1. Shaded areas indicate differences whose directions are consistent with the alternate hypothesis that the higher densities of odonate larvae reduce prey densities more than lower densities (LD > HD). (b) Overall Odonate Density Effects for combined analyses of Experiments A, B, and C. Prey abbreviations are defined in Fig. 1 legend.

We have previously attributed competition among odonate larvae to interference rather than exploitation (Johnson et al. 1984, 1985, Pierce et al. 1985) partly on the basis of scanty evidence for prey depletion from individual experiments. The combined analysis supports our interpretation for the following reasons:

1) An analysis of 37 separate estimates (odonate taxon  $\times$  season combinations) of the relative contribution of prey categories to larval odonate diet, based on 3103 items identified in 1188 fecal pellets from individuals collected at Bays Mountain Lake (Johnson et al. 1984: Fig. 2; Merrill and Johnson 1984: Fig. 2; Johnson et al. 1985: Fig. 5; R. E. Bohanan and C. N. Watson, *personal observation*; R. E. Bohanan and D. M. Johnson, *personal observation*), shows that the three prey categories reduced by larvae in these experiments (Fig. 1b) represent less than one-third of the typical larval diet (20% numerically, 31% of biomass). Two categories, oligochaetes and large cladocerans, account for most of this (10 and 9% numerically, 17 and 11% of biomass, respectively). We suggest that when alternate prey that normally constitute two-thirds of the odonate larval diet are readily available, even a large reduction of the abundance of these three categories should have a relatively minor effect on dragonfly growth and survival (see Lawton et al. 1980).

2) Exploitation competition should result in further prey depletion at higher densities (i.e., the Odonate Density Effect in Fig. 3). However, we found that the overall difference between high-density and low-density treatments for Experiments A, B, and C was in the opposite direction than expected due to predation by odonates for 9 of 10 categories. Interference competition is more consistent with this lack of an Odonate Density Effect on prey (see Crowley et al. 1987).

Our combined analysis has identified some potentially important relationships that were obscured in individual experiments due to insufficient statistical

power. The collective evidence strongly suggests that predaceous odonate larvae deplete the densities of certain prey populations within our enclosures: small caddisfly larvae, *Oecetis* (Leptoceridae) and *Oxyethira* (Hydroptilidae); oligochaetes, principally *Chaetogaster* and *Dero* (Naididae), *Lumbriculus* (Lumbriculidae), and *Limnodrilus* (Tubificidae); and large cladocerans, principally *Simocephalus vetulus* and *S. serrulatus* (Daphnidae), and *Sida crystallina* (Sididae). Studies of predator and prey behavior will be necessary to explain why these particular taxa are more vulnerable than others.

#### Combining evidence and power analyses

Logistical constraints on the number of replicates that can be incorporated in manipulative field enclosure experiments have led critics (cf. Toft and Shea 1983) to suggest that statistical analyses of the results of such experiments have relatively little power. Under these circumstances, failure to reject a null hypothesis cannot be considered strong evidence for its validity. But an underutilized advantage of manipulative field enclosure experiments is that they can be repeated, with the possibility of improving statistical power. The computer-intensive rerandomization approach used in this paper can facilitate this approach by permitting straightforward significance tests and power analyses, even for nonnormal data and nonhomogeneous variances. We hope that such "computer-intensive" procedures will eventually be standard features of many statistical software packages. This not only would facilitate utilization but also would standardize the methods used to apply this potentially powerful technique.

#### ACKNOWLEDGMENTS

This research has been supported by National Science Foundation grants BSR-8408543 to D. M. Johnson and BSR-8404424 to P. H. Crowley. Our approach to both power anal-

yses and combining data from several experiments has been influenced significantly by discussions with Jerry Nagel and Tom Woolley from E.T.S.U. The following have made valuable comments on early drafts of the manuscript: Dave Allan, Larry Crowder, Pat Dillon, Stanley Dodson, Bradley Efron, Anne Hershey, David Olfelt, Andy Sih, and Kevin Strohmeier. Peter Chesson and several anonymous reviewers made important suggestions that substantially changed our approach to the statistical analyses.

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