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Analysis of feeding preference experiments

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Summary. Published studies of consumer feeding preferences using foods that experience autogenic change in mass, numbers, area, etc., on the time scale of a feeding trial fail to employ appropriate statistical analyses to incorporate controls for those food changes occurring in the absence of the consumer. The studies that run controls typically use them to calculate a constant "correction factor," which is subtracted prior to formal data analysis. This procedure constitutes a non-rigorous suppression of variance that overstates the statistical significance of observed differences. The appropriate statistical analysis for preference tests with two foods is usually a simple t-test performed on the between-food differences in loss of mass (or numbers, area, etc.) comparing the results of experimentals with consumers to controls without consumers. Application of this recommended test procedure to an actual data set illustrates how low replication in controls, which is typical of most studies of feeding preference, inhibits detection of an apparently large influence of previous mechanical damage (simulated grazing) in reducing the attractiveness of a brown alga to a sea urchin.

Key words: Herbivory – Preference experiment – Statistical analysis

Ecologists frequently design and conduct experiments to learn whether consumers express preferences among alternative food types. Studies of feeding preference are fundamental to understanding basic trophic relationships in all ecosystems: terrestrial, aquatic, and marine. Such investigations are now especially popular among marine scientists investigating the role of herbivory in shaping plant distributions, abundances, morphologies, and evolutionary patterns (e.g. Lubchenco and Gaines 1981). For example, there is presently a substantial research effort directed towards understanding how chemistry is employed by seaweeds as defenses against various types of herbivores (Hay and Fenical 1988). Unfortunately, analyses of feeding preferences are seldom carried out correctly because controls for food changes in the absence of consumers are not properly estimated or incorporated into the formal statistical tests.

Design of preference tests

Experiments designed to detect preferential feeding involve offering a selection of food types to one or more individual consumers. The use of two or more individuals in a feeding trial is less desirable because of the feeding biases that may be caused by interactions (interference, aggression, etc.) between consumers. Ideally, the potential foods are presented simultaneously to the consumer within a single experimental arena so that the consumer has opportunity to express a dietary choice. However, some experimental designs allow individual consumers to feed for a constant time on individually presented alternative foods, which permits comparisons of feeding rates on these different foods. Such an experiment is not a true feeding preference experiment because no food choice is provided, but the results can reflect differences in the attractiveness or palatability of various potential foods that may also be expressed when choices are offered (e.g. Vadas 1977). Although the correspondence between the results of experiments measuring feeding rates on isolated foods and those assessing feeding preferences cannot be assumed without test, we address our comments to each of these designs.

Here we adopt a meaning for feeding preference that allows preference to be measured by quantitative comparisons of amounts eaten. Some alternative definitions of preference may incorporate measures of only the behavioral choice of initiating feeding without also including the subsequent component of how much is then eaten (see Vadas 1977). While this represents a meaningful and insufficiently explored distinction, we are concerned with the analysis of amounts eaten.

If the duration of a feeding trial is short relative to the time required for autogenic change in each of the alternative foods, then estimation of amounts eaten is uncomplicated. Initial measures of food mass, numbers, area, etc. would simply be compared to final measures to produce quantitative estimates of consumption. By use of the term autogenic change, we intend to include all changes in the potential prey that occur independent of the action of consumers. These include reproduction, mortality, growth, respiration, production, water loss or gain, and any other process that may affect the response variable (prey mass, numbers, area, etc.). If the feeding trial were to last long enough for autogenic changes to have occurred in the response variable, then controls without consumers must be employed. Unfortunately, even when autogenic changes do not occur within the time frame of a feeding trial, controls must be conducted to demonstrate their irrelevance. Controls for autogenic change would usually prove necessary for interpretation of experiments assessing the preferential consumption of (1) living microbial or planktonic prey because of their short generation times and rapid turnover, (2) sewaweed biomass

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because of the realistic potential for respiration, production, and change in water content of even excised pieces of macroalgae, and (3) clonal invertebrates because of their potential for continued growth and elaboration of new units (zooids, etc.). Thus, the purpose of controls in feeding preference experiments is to assess the differential magnitude of the autogenic changes in the foods that occur in the absence of the consumers and are presumed to be occurring in their presence. Consumption of each food type can then be estimated as the difference (in mass, numbers, area, etc.) between the controls without consumers and the treatments with consumers (see Pollard 1988 for an example using terrestrial invertebrates).

Table 1. A review of how studies of herbivore preference using seaweeds as foods analyzed feeding preference data

No controls for autogenic change	Controls included for autogenic change	
	Not used in formal analysis	Used to calculate correction factors prior to analysis
Carefoot 1973	Littler and Littler 1980, 1983[c]	Vadas 1977
Nicotri 1980	Brawley and Fei 1987[d]	Zimmerman et al. 1979
Geiselman and McConnell 1981		Sousa 1979
McConnell et al. 1982		Sousa et al. 1981
Himmelman 1984		Anderson and Velimirov 1982
Steinberg 1984		Steinberg 1984, 1985, 1988
Vadas 1985[a]		Hay 1986
Targett et al. 1986[b]		Hay et al. 1986, 1987, 1988b
		Pfister and Hay 1988

[a] This is a methodology paper that describes preference assays but fails to discuss the need for consumer-free controls

[b] Algae in preference assays were offered singly

[c] Statistical methods are undescribed so how the control data were used is ambiguous

[d] No statistical tests were even performed on the preference data

Analytical methods

Previously used analyses

Many otherwise well-conceived studies of feeding preferences of marine algivores fail to employ any controls for autogenic changes in the algae (Table 1). These studies run the risk of confounding differences between algae in respiration/production/change in water content with differences in herbivory, if the algal prey differ greatly in their rates of autogenic change over the course of a feeding trial. Several other studies of preferential feeding on marine algae have incorporated controls into the design (Table 1). Nevertheless, these studies either fail to present and utilize the control data or, more commonly, use the control data to calculate "correction factors" for each species. The correction factor for a given algal prey type is the mean change in mass (or surface area, etc.) observed in the controls. This calculated constant is then subtracted from (or added to, as appropriate) the initial mass (area, etc.) before subjecting the experimental results to formal statistical testing to "correct" for the amount of autogenic change expected to be occurring in the absence of herbivory.

Such a correction procedure is flawed in two ways. We continue to describe these flaws in the context of an experiment with a marine algivore, but they are inherent in all experiments that measure feeding rate or preference. First, the use of a correction factor assumes that the amount of mass (area, etc.) lost (gained) by the controls is also lost (gained) by the experimental algae even though the amount of loss (gain) per unit time is almost certain to vary as a continuous function of the amount of tissue present. Even though a proper design dictates that amounts of food be made equal at the start of a trial, these amounts will differ between controls and experimentals as herbivory acts to remove material. Furthermore, the action of herbivory may itself stimulate differential physiological or ecological changes in grazed plants that are not simultaneously occurring in control plants. Second, calculating a correction constant effectively suppresses all the variability observed among replicate controls. Any subsequent statistical testing is analogous to performing a statistical test on a data set in which all control points are first averaged and then the string of experimental observations compared to a constant control value rather than to a mean with a variance. This suppression of variance in the controls is not rigorous in that it underestimates the error variance and thus overstates the level of statistical significance ultimately reported for the test of whether foods are preferentially consumed.

The magnitude of the underestimate of variance caused by applying a correction constant can be demonstrated readily using theorems concerning (1) the variance in the sum of a random variable and a constant and (2) the variance of a linear combination of independent random variables (e.g. Brownlee 1967). If controls are used to calculate a correction constant (k), then the variance used in statistical testing is:

$$\mathrm{Var}(\mathrm{X}-\mathrm{k})=\mathrm{Var}(\mathrm{X})+\mathrm{Var}(\mathrm{k})=\mathrm{Var}(\mathrm{X}),$$

where X is the random variable of weight loss in the experimentals. If, alternatively, a test procedure is employed that properly compares two random variables, C (weight loss in controls) and X (weight loss in experimentals), then:

$$\mathrm{Var}(\mathrm{X}-\mathrm{C})=\mathrm{Var}(\mathrm{X})+\mathrm{Var}(\mathrm{C}).$$

Consequently, failure to treat the control datum as a random variable underestimates the variance in the difference between control and experimental weight losses by the variance in the controls. As this variance among controls gets small relative to the variance among experimental replicates, the underestimate of variance using the correction factor method disappears. Nevertheless, to the degree that variance exists in the controls the use of a correction factor overstates the reported level of statistical significance.

The recommended analysis

The proper test of whether a consumer exhibits preferential feeding on one of two food types depends upon whether the foods are presented together in a true choice experiment or separately. When the two foods are presented together, the proper statistical procedure is to calculate separately for each replicate container the difference in mass (area, etc.) change (usually loss) between the two foods over the course of the experiment. This procedure yields two sets of differences (experimentals and controls), which can be compared by t-tests or, if assumptions of normality and homogeneity of variances are not met, by non-parametric procedures. The protocol of calculating differences is necessary to produce a single observation for each experimental unit (container). The changes in the two foods when they are held in the same container are not independent and possess correlated errors, making it impossible to analyze them separately. When alternative foods are presented separately, then differences should not be calculated because there is no natural pairing. Instead, the proper test of preferential consumption is the interaction significance in a two-factor (in which food type and consumer presence/absence are crossed) analysis of variance, assuming that the assumption of homoscedasticity can be met. This test asks the question of whether the difference in mass (area, etc.) changes between foods varies with the presence and absence of a consumer.

Both of these analytical solutions make two assumptions that are violated to some degree in practice. First, they assume that the change in the response variable is known without error, when in fact mass loss or area loss is estimated with measurement error by comparing an initial to a final value. We assume here that such measurement error is small. Second, both tests assume that the mass or area change in controls accurately estimates the autogenic changes that also occurred in the experimentals despite concurrent consumption of tissue. The easiest way to minimize the degree to which this assumption is violated is to design a sufficiently powerful experiment to detect small differences in consumption so that the experiment does not run for long enough to allow a large percentage consumption of either of the alternative foods. This protocol also ensures that relative abundances of alternative foods do not change greatly, which could bias the measure of preference depending upon the functional response of the consumer (e.g. Murdoch 1969; Cock 1978). Alternatively, one could design extremely elaborate experiments to assess the role of functional responses of the consumer as amounts of alternative foods diverge, the rate of autogenic change as a function of amount of food, and the degree to which these size-specific rates of "autogenic" change are actually altered by the immediate history of grazing and consumption. A study to isolate these factors would represent a substantial effort but could be quite rewarding.

Results of analyzing a sample experiment

To illustrate the differences between methods for analyzing results of feeding preference experiments, we provide the results of an actual experiment conducted by one of us (P.E.R.). We analyze the results (1) as if there were no controls, (2) using the controls to calculate and utilize the traditional "correction factor," and (3) using our suggested method of comparing differences in mass loss between experimentals and controls. These data were collected to assess whether clipping portions from a brown alga (to simulate herbivore attack) affects its subsequent attractiveness to the omnivorous sea urchin, *Arbacia punctulata.*

Pieces of *Padina gymnospora* were collected from Radio Island Jetty (Bogue Sound, North Carolina) and brought into the laboratory on 25 July 1987. Several pieces were manually damaged by clipping 10–30% of the plant wet mass along the periphery of the thallus creating a pattern similar to that caused by sea urchins. Wet masses were obtained by spinning the algae in a salad spinner (10 revolutions at approximately 120 rpm) to remove excess water and weighing the algae to 0.001 g. Damaged algae were then placed, along with similar-sized undamaged pieces that served as controls, between the strands of a three-stranded rope and were allowed to recover in a flow-through seawater tank for five days. Damaged plants were then reweighed (spun wet mass as above), paired for size with weighed pieces of undamaged algae, and secured to the bottom of 3.8-l glass jars by inserting the algae into holes in a stiff rubber disk. Eleven jars contained 1.0–1.5 l of aerated seawater and one sea urchin that had been starved for one week, while two jars contained only aerated seawater and were designated as controls for mass loss not associated with herbivory. Urchins were allowed to graze until a substantial portion (at least 10% but less than 50%) of one of the pieces in every replicate was consumed (in possible violation of our earlier advice, which reflects the wisdom of hindsight), after which the final spun wet mass of both algae was obtained. Results appear in Table 2.

If no controls had been run to estimate autogenic changes of the algae in the absence of consumers, a paired t-test would imply that urchins prefer undamaged *Padina* to algae that were previously damaged (two-tailed $p = 0.0044$: Table 2). By using controls to calculate a correction factor for autogenic changes in the absence of herbivory, a paired t-test would continue to imply a significant preference for undamaged *Padina,* although the pattern is significant only at the $\alpha = 0.05$ level ($P = 0.013$: Table 2). When, however, our suggested method is employed, taking into account the variability in the controls as well as their means, the apparent feeding preference is no longer statistically significant even at $\alpha = 0.05$. This result was achieved by analyzing angular-transformed differences in proportions eaten, which had the effect of homogenizing variances. Analysis of untransformed differences using a Welch approximation for a t-test assuming unequal variances (Brownlee 1967) also fails to demonstrate significance ($t = 2.26$, $df' = 6.8$, $P = 0.059$).

We present results of t-tests for all three methods in Table 2 because the angular-transformed differences, on which each test was run, met the assumptions of both homoscedasticity (by F-tests) and normality (by the Kolmogorov-Smirnov goodness of fit test) at $\alpha = 0.05$. One could argue that the small sample size limits power to detect even large departures from assumptions in these data. Consequently, we repeated each test with the nonparametric analog to the t-test. The qualitative conclusions are identical, with the Wilcoxon signed rank test revealing significance at $0.05 < p < 0.01$ for both method 1 and method 2 and a Mann-Whitney U-test failing to show significance ($p \geqslant 0.05$) in the preferred method 3.

This example illustrates how our suggested procedure for analyzing data from a feeding preference experiment can fail to indicate significance when the alternative controlled method using a correction factor does not. The failure to detect significance in this example is largely a consequence of the lower power of an unbalanced design, which allocates insufficient replication (2) to the controls without herbivores. For example, if we had run 8 additional control pairs of algae and if they produced differences between damaged and undamaged plants identical to those already

Table 2. Consequences of choice of analysis for data from a feeding preference experiment. This experiment tests whether the sea urchin, *Arbacia punctulata*, expresses any preference for *Padina gymnospora* that was previously unstressed (Non-dam) or stressed by mechanical damage (Dam). Diff is the transformed (2 arcsin $\sqrt{p}$) difference in proportionate loss (Dam minus Non-dam)[a]

	Percent[b] loss or gain (−) in wet mass					
	Experimentals (with herbivore)			Controls (without herbivore)		
Replicate	Dam	Non-dam	Diff	Dam	Non-dam	Diff
1	29.2	36.0	−0.53	−14.5	−7.9	−0.52
2	3.7	49.9	−1.50	−6.2	−7.2	0.20
3	−4.2	14.8	−0.90			
4	−12.9	22.0	−1.26			
5	17.4	24.0	−0.52			
6	−4.2	30.7	−1.26			
7	14.7	24.0	−0.62			
8	−7.0	11.1	−0.88			
9	21.1	−0.7	0.97			
10	−8.2	22.6	−1.18			
11	18.4	33.1	−0.79			
Mean (1 SE)	6.2 (4.3)	24.3 (4.1)	−0.77 (0.20)	−10.4 (4.2)	−7.6 (0.4)	−0.16 (0.36)

Test Results

Method 1: Ignore controls, do paired-sample t-test

$$t=\frac{\bar{x}}{s/\sqrt{n}}=\frac{0.77}{0.20}=3.85$$

$$\mathrm{df}=10$$

Two-tailed $p=0.0044$

Method 2: Use "correction factor (k)", then do paired-sample t-test

$$t=\frac{\bar{x}-k}{s/\sqrt{n}}=\frac{0.77-0.16}{0.20}=3.05$$

$$\mathrm{df}=10$$

Two-tailed $p=0.013$

Method 3: Use t-test on differences

$$t=\frac{\bar{x}-\bar{c}}{s\sqrt{1/n_1+1/n_2}}=\frac{0.77-0.16}{0.50}=1.22$$

$$\mathrm{df}=11$$

Two-tailed $p=0.26$

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[a] The angular transformation produced a variance ratio of transformed differences of 1.69 ($p>0.90$ in F-test with 10, 1 df). Untransformed differences have a variance ratio of 11.97

[b] Data are presented as percentages instead of absolute weights to adjust for variation in initial mass of the pieces of algae used (ranging from 605 to 1145 mg, although paired pieces differed by no more than 7%)

observed in the controls of the actual experiment (i.e., 4 more −0.52's and 4 more 0.20's), the outcome of our suggested test procedure would have been quite different. The t-test in this nearly balanced design (also with greater degrees of freedom) would yield a 2-tailed p of 0.020 (0.029 holding degrees of freedom constant) assuming equal variances. In the hypothetical example, the variance ratio of 3.1 is nonsignificant at $P=0.10$.

In cases where the variance in the controls is small relative to the variance in the experimentals, the correction factor approach underestimates the variance of the difference only slightly. Consequently, if the design were more nearly balanced, our suggested test would produce a similar outcome. In cases where control variance equals or exceeds the variance in experimentals, the use of the correction factor approach would seriously underestimate the variance of the difference and could yield misleading results. However, to achieve sufficient power with our recommended test, controls must be adequately replicated. Most previous studies of feeding preference of marine algivores have used extremely low replication in controls and thus suffer from low power to detect feeding preferences in our more rigorous test procedure. The problem of low replication of controls affects the non-parametric analogs of our suggested t-test even more strongly.

Discussion of preference trials using more than two foods

We have restricted our presentation to preference trials using only two alternative food types because this is a commonly chosen design for feeding preference experiments and because the analysis of the results is tractable. If more than two alternative foods are presented separately to replicate consumers, contrasts among feeding rates on different foods can be achieved by examining the two-factor interaction in an analysis of variance, analogous to the solution we describe for a two-food trial. If, however, more than two alternative foods are used in a true feeding preference experiment, each experimental unit yields more than a single difference between alternative foods, so the t-test on differences suggested for the two-food trial cannot be used. Under these conditions, the appropriateness of any univariate hypothesis testing can be seriously challenged.

Such choice tests using arrays of foods may yield different results from those achieved in tests of pairs of foods and may lead to development of foraging theory on what might be called the "context specificity" of preference. Consequently, it is appropriate to design and conduct such multichoice experiments despite the analytical constraints. Unfortunately, analysis of variance of amounts eaten, comparing two or more alternative prey (food) types, is inappropriate because consumption of one type is not independent of consumption of other types held together within the same experimental arena. Several studies (e.g. Vadas 1977; Anderson and Velimirov 1982; Paul et al. 1987) have, nonetheless, incorrectly applied analysis of variance to feeding preference data. This violates perhaps the most fundamental assumption of analysis of variance. A "non-parametric" analysis of variance of ranks (e.g. Lewis 1985) likewise suffers from the lack of independence of "treatments."

Several alternative solutions to this problem of how to analyze non-independent multichoice data have been developed, although none is especially powerful, elegant, or efficient in its use of available information and all fail to incorporate rigorous means of treating control data on autogenic changes. Holmlund et al. (1989) employed several t-tests on all possible pairs of differences, taking precautions to reduce the α in each test to hold constant the experimentwise α, but this procedure is cumbersome and lacks power as the number of alternative foods increases. Multichoice data have also been analyzed by applying a binomial classification to each species in each replicate trial, categorizing each as either heavily consumed or lightly consumed: then contingency tests were performed to determine whether preferences existed and how prey species differed (Hay et al. 1988a). This classification procedure has the disadvantage of ignoring information on how quantitative consumption differed among alternative prey. A solution to this problem that incorporates the data on quantitative consumption was provided by Steinberg (1988), who selected at random one observation from each experimental trial and then used a one-factor analysis of variance to test for differences among prey in amounts eaten. By utilizing data on only one prey type from any given trial, this procedure establishes independence among "treatments" (prey types), but it requires that a large fraction of the data on hand be ignored in analysis. Because none of these procedures is completely satisfactory and all fail to include rigorous analysis of the control data, one of the biggest current challenges in ecological methodology is the development or discovery of an appropriate, statistical test for analysis of preference data from multichoice experiments. The best test procedure will probably be a multivariate test because multivariate tests are designed in part to handle data classes that are not independent, the intrinsic, yet vexing, characteristic of preference data. Development of a multivariate analog to the two-prey solution that we recommend is not an unrealistic possibility.

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