OVERLAP, REGULARITY, AND FLOWERING PHENOLOGIES

Stiles (1977) presented the results of a study of the flowering phenologies of 11 tropical plants that are pollinated by hummingbirds. He concluded that the peaks of flowering times were uniformly spaced and interpreted this spacing as the result of competition for pollinating hummingbirds. Competition for pollinators would result in selection for staggered flowering times, and thus a uniform spacing of flowering peaks, to improve the efficiency of intraspecific pollination and minimize interspecific hybridization.

Poole and Rathcke (1979) dispute the observation of Stiles that the flowering peaks are uniformly spaced. They present the results of a statistical test of Stile's data on flowering phenologies. The statistic that they use compares the intervals between dates of peak flowering with the intervals between randomly spaced points.

Their sample statistic P is the variance of distances between the flowering peaks of temporally adjacent species. The expected variance, $E(P)$, under their null hypothesis that flowering dates are randomly assigned, is the expected variance of the broken-stick distribution. For k species, then, $k \cdot P/E(P)$ is distributed approximately as a χ^2 with k degrees of freedom and allows a test of the null hypothesis $P = E(P)$.

Values of the ratio $P/E(P)$ near one indicate that the observed variance equals the expected variance and that the flowering peaks are distributed randomly within the growing season. Values of this ratio less than or greater than one indicate uniform or clumped dispersion patterns, respectively, for the peaks of flowering. Poole and Rathcke obtained $P/E(P)$ ratios of 2.07, 1.85, 2.05, and 2.03 for the 4 yr of data, and concluded that far from being uniformly spaced, the peaks of flowering were clumped.

This result is not surprising in view of the fact that they calculated these ratios on the assumption of a uniform growing season. As Stiles (1979) points out, there is a peak of flowering in the dry season and one in the wet season. Both of these seasons have a characteristic and nonoverlapping set of flowering species.

In order to properly apply the test that Poole and Rathcke suggest, one must break the year into a dry and a wet season. If one follows the same conventions that Poole and Rathcke adopt in their article, but distinguishes the dry season flora and the wet season flora, the conclusion is totally different. Table 1 shows the values for $P/E(P)$ and the degrees of freedom for each growing season and each year.

All but one of the values of $P/E(P)$ is less than one. This suggests that the peaks of flowering are more regularly spaced than one would expect from a random model (a total χ^2 value of 15.31 with 35 df is significant at the 1% level).

Regardless of the results of the previous analysis, one may dispute the use of the variance of the broken-stick distribution as a null hypothesis on two grounds. Of

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TABLE 1

RATIO OF OBSERVED TO EXPECTED VARIANCE

	Dry Season		Wet Season	
	$P/E(P)$	df	$P/E(P)$	df
1971	1.027	4	.696	5
1972	.161	4	.282	5
1973	.115	3	.302	5
1974	.293	4	.529	5

NOTE.—$P/E(P)$ is the ratio of the observed to the expected variance for the null hypothesis of Poole and Rathcke (1979). Values of this ratio less than one suggest uniform spacing of flowering peaks. Aside from splitting the growing season into a dry and a wet season, the conventions used are the same as those used by Poole and Rathcke.

the $k + 1$ terms in the expression for P, $k - 1$ of them are the distances between successive peaks of flowering for two different species. However, two of the terms are one-half the length of the peak flowering period of a single species. There is no a priori reason to suppose that the two types of measurements should be drawn from the same distribution. Thus, there should be an additional variance component included in the expected variance that is used to test the null hypothesis. This is not important in this example because if significant uniformity is found using the test of Poole and Rathcke, significant uniformity would be obtained using a more accurate measure of the expected variance.

The second reason that the null hypothesis of Poole and Rathcke may not be appropriate is that a uniform spacing of flowering peaks need not imply a staggered sequence of flowering periods. It is easy to imagine regularly spaced flowering peaks accompanied by a high amount of overlap of flowering periods. It would be difficult to defend the competition hypothesis if there is a high amount of overlap in the flowering periods of hummingbird-pollinated plants even if the peak dates of flowering appeared to be uniformly spaced throughout the growing season.

A null hypothesis which is perhaps more appropriate to the biological question is that the peak flowering period of each species is a line segment that is thrown at random within another line segment, the growing season. The expected amount of overlap between two segments L_1 and L_2 that are tossed independently within another line segment L may be shown to be (see Appendix)

$$E(d) = L_2\frac{LL_1 - L_1^2 - L_2^2/3}{(L - L_1)(L - L_2)}, \qquad L > (L_1 + L_2), \quad L_1 > L_2.$$

The expected pairwise overlap between the k species of a particular growing season may be computed and compared with the observed amount of overlap. Table 2 shows the observed overlap in days and the expected amount of overlap according to the null hypothesis. In the dry and early wet flowering season for each year of Stiles' study the observed overlap is less than the expected overlap.

A statistical test of these results is not a simple matter. For n flowering periods

TABLE 2

EXPECTED AND OBSERVED PAIRWISE OVERLAP OF FLOWERING PERIODS (days)

	Dry Season		Wet Season	
	Expected	Observed	Expected	Observed
1971	56.3	37	121.6	65
1972	75.6	41	148.6	88
1973	45.9	19	89.5	32
1974	73.4	41	111.7	65

NOTE.—Expected values are calculated on the assumption that the peak flowering periods are line segments thrown randomly into the dry and wet growing seasons.

within any growing season, the expected amount of overlap is calculated from $\binom{n}{2}$ different distributions (because none of the flowering periods are likely to be of the same length).

If the distribution of values for the expected overlap were symmetric, the probability of observing less than random overlap would be equal to the probability of observing greater than random overlap. One could then calculate the binomial probability (with $p = .5$) for observing so deviant an event. The distribution is not symmetric, but the same principle may be applied.

Simulations of the process of randomly placing line segments on a larger line segment were performed to determine the average proportion of events that are less than expected. For line segments that are approximately .3 of the total length (the average in the case of Stiles' data is .31) the fraction of events below the median is about .6. This value is fairly insensitive to changes in the number of segments involved (it declines with increasing segment number) and is rather more sensitive to changes in segment length (it declines with increasing segment length). Thus the probability of observing so deviant an event as that in table 2 may be estimated as $p \simeq .02$.

This result also supports Stiles' observation that flowering periods of hummingbird-pollinated plants are staggered and is consistent with, although certainly does not prove, his hypothesis that competition between plants for the services of pollinating hummingbirds may influence the evolution of flowering phenologies.

It may be pointed out that the expression given above for the expected amount of overlap is applicable to problems other than flowering phenologies. It may be useful as a null hypothesis in exploring resource utilization, size distribution, distribution patterns on ecological gradients or through time, or other one-dimensional patterns.

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APPENDIX

Imagine the situation of two segments of length L_1 and L_2 ($L_1 > L_2$) placed at random within another segment L. It is convenient to designate the position of the "left" end of segments 2 and 1 as x and y, respectively, and to standardize segment L to unit length. If overlap between the two segments occurs, there are two cases, complete overlap or partial overlap.

If complete overlap occurs, the amount of overlap is L_2. If there is complete overlap x can vary between y and $y + L_1 - L_2$. The entire range of x is between 0 and $1 - L_1$. Thus the contribution to the expected overlap is

$$\frac{\int_{y}^{y+L_1-L_2} L_2 \, dx}{\int_{0}^{1-L_2} dx} = L_2 \frac{L_1 - L_2}{1 - L_2}. \tag{A1}$$

If partial overlap occurs, the amount of overlap is given by $x - y + L_2$. For ease of calculation consider the range of x to be from 0 to $y + L_1/2 - L_2/2$, that is, the center of segment 2 lies to the left of the center of segment 1. It is then more obvious that there are two cases. If $y > L_2$, there is partial overlap between $x = y - L_2$ and $x = y$. If $y < L_2$, there must be at least partial overlap. The entire range of x is now between 0 and $y + ½(L_1 - L_2)$ as y varies between 0 and $1 - L_1$. For $y > L_2$ the contribution to the expected overlap is

$$\frac{\int_{L_2}^{1-L_1} \int_{y-L_2}^{y} (x - y + L_1) \, dx \, dy}{\int_{0}^{1-L_1} \int_{0}^{y+\frac{1}{2}(L_1-L_2)} dx \, dy}.$$

For $y < L_2$, the contribution to the expected overlap is

$$\frac{\int_{0}^{L_2} \int_{0}^{y} (x - y + L_1) \, dx \, dy}{\int_{0}^{1-L_1} \int_{0}^{y+\frac{1}{2}(L_1-L_2)} dx \, dy}.$$

When evaluated, the sum of these two quotients is

$$\frac{L_2^2(1 - L_1 - L_2/3)}{(1 - L_1)(1 - L_2)}. \tag{A2}$$

Thus the total expected overlap is the sum of (A1) and (A2), which gives the result in the text after substituting L for 1.

Note that if $L_1 + L_2 > L$, $y < L_1$ is not possible. In this case a different solution is obtained for the expected overlap. While x can still vary between 0 and y, y varies between 0 and $1 - L_1$. The contribution of partial overlap to the expected overlap becomes

$$\frac{\int_{0}^{1-L_1} \int_{0}^{y} (x - y + L_1) \, dx \, dy}{\int_{0}^{1-L_1} \int_{0}^{y+\frac{1}{2}(L_1-L_2)} dx \, dy},$$

which evaluates as

$$\frac{(1 - L_2)(3L_1 - 1 + L_2)}{3(1 - L_2)}, \quad \text{(A3)}$$

and the total expected overlap is the sum of (A1) and (A3).

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