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Author(s): Theodore H. Fleming and Brian L. Partridge

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## On the analysis of phenological overlap

Theodore H. Fleming and Brian L. Partridge

Department of Biology, University of Miami, Coral Gables, FL 33124, USA

**Summary.** We briefly review current methods for detecting nonrandom patterns in the temporal overlap of flowering and fruiting curves. We discuss the assumptions behind these methods and propose a new method of analysis using computer simulations to measure *n*-wise, rather than pair-wise, temporal overlap. We quantify the extent to which observed *n*-wise overlap differs from minimum possible *n*-wise overlap and apply our method to several data sets to test the hypothesis that interspecific competition for animal visitors has produced flowering curves whose overlap is less than that expected by chance. Results of our analyses provide little support for this hypothesis but suggest alternate criteria by which the species may be selected.

### Introduction

Several hypotheses have been put forth to explain the phenological patterns of plants that interact with animal pollinators, seed dispersers, and/or seed predators. For example, competition for limited high quality animal visitor services has been used to explain the divergent flowering/fruiting schedules of sympatric plants in a wide variety of habitats (e.g. Snow 1965, Mosquin 1971, Heithaus et al. 1975, Heinrich 1976a, Waser 1978). In contrast, convergent flowering/fruiting schedules of sympatric plants have been described as adaptations for tracking seasonal changes in animal visitor abundance (e.g. Brown and Kodric-Brown 1978, Schemske 1981) or for satiating seed predators (Smythe 1970, Beattie et al. 1973, Janzen 1978, Augsburger 1981).

As a first step in evaluating these evolutionary hypotheses, one needs to know whether or not observed phenological overlap differs significantly from random expectations. The competition hypothesis predicts significantly less, while the predator satiation hypothesis predicts significantly more, overlap than expected by chance alone. Unless statistically significant departures from chance expectations are found, there is no need to necessarily invoke specific biotic interactions as having an important influence on phenological patterns (Rabinowitz et al. 1981).

In this paper we briefly review current methods of detecting nonrandom phenological patterns before describing a new method which we have applied to several data sets. Because most interest in the literature has been on tempo-

rally-divergent flowering schedules that ostensibly reflect the outcome of interspecific competition for pollinators and/or avoidance of hybridization, we will direct most of our attention to testing the competition hypothesis with these data.

### *Methods for detecting nonrandom flowering and fruiting patterns*

Prior to the late 1970s, nonrandom patterns of flowering and fruiting were identified qualitatively. Most authors (e.g. Snow 1965, Heithaus et al. 1975, Heinrich 1976a, Stiles 1977) plotted the periods of flower/fruit availability along a time line beginning with the earliest flowering/fruiting species. Lack of total overlap between temporally adjacent species was thought to constitute sufficient evidence for competition-induced spreading of flowering/fruiting times. None of these studies asked whether or not observed phenological overlap was actually less than (or greater than) that expected by chance.

Statistical analysis of phenological patterns was inspired by Stiles' (1977) publication of the flowering times of hummingbird-pollinated plants in a Costa Rican wet tropical forest. Poole and Rathcke (1979) challenged Stiles' (1977) conclusion of regularly-spaced flowering times by comparing the separation of flowering peaks (the mid-points of periods of peak flower numbers) with that expected if peaks were randomly-placed. Results of their analysis indicated that actual flowering peaks were either aggregated (into dry and wet season bloomers) or were randomly-arrayed, a conclusion also supported by Gleeson's (1981) analysis of the same data.

Following Stiles' (1979) suggestion that there exists two groups of bloomers (dry and wet season bloomers), Cole (1981) separately analyzed these groups using Poole and Rathcke's (1979) method and found that flowering peaks within seasons conformed to predictions of the competition hypothesis. Furthermore, by independently casting pairs of flowering periods onto line segments the length of the dry or wet "growing seasons" (cf. Stiles 1979) and comparing observed overlap with that generated by random expectations, Cole additionally concluded that overlap between species was less than expected by chance.

The methods of phenological analysis devised by Poole and Rathcke (1979) and, more recently, by Simberloff and Boecklen (1981) rely on qualitative data (i.e. dates of first

and last flowering/fruiting or periods of peak flower/fruit numbers) and are mainly concerned with the position of peak or mean blooming times and not with the degree of overlap of entire temporal distributions. We agree with Gleeson (1981) that more meaningful comparisons of phenological patterns should take into consideration both the mean and variance of temporal activities. That is, phenological analyses should be based on quantitative data consisting of counts of flower/fruit availability on census plants or in plots censused at frequent intervals during a study period. Such data produce flowering or fruiting curves that can be subjected to other kinds of statistical analyses, e.g. degree of temporal overlap, using standard ecological overlap indices.

This approach has been utilized by Pleasants (1980) and Thomson and Rusterholz (1982) in their studies of Rocky Mountain plants. Pleasants (1980) compared the observed pairwise overlap between the standardized flowering curves of several guilds of bumblebee-pollinated herbaceous perennials (each guild included plants visited by the same *Bombus* species) with the overlap generated by randomly placing the curves within the growing season and recomputing pairwise overlap in 50 computer simulations. Results indicated that in 10/11 guilds observed overlap was less than random values, but statistical significance (at the 0.05 level) was attained in only five guilds.

Thomson and Rusterholz (1982) also used a simulation technique to analyze flowering overlap between Rocky Mountain subalpine plants. Because ecological competitors were not necessarily being analyzed in that study, there was no *a priori* expectation of reduced phenological overlap. They concluded that indices of pairwise overlap were inappropriate for quantifying overlap intensity and suggested that calculations of total overlap of one species against all other species more realistically depict interspecific overlap.

### Assumptions

We support a simulation approach for analyzing phenological patterns. One advantage of such an approach is that programming requires that underlying assumptions be made explicit. In particular, our method and those of studies discussed above make the following major assumptions.

1. The shape of the distribution of flowering/fruiting times for each species is constrained, presumably fixed previously by natural selection. Only the relative timing of the distributions can be altered.
2. The species are equivalent in resource utilization and in their effect on other guild members. Thus, for the purposes of overlap calculations, flowering and fruiting curves can be standardized to an area of 1.0. Thomson (1982) discusses the rationale for doing this rather than using actual values of flower or fruit densities in overlap calculations.
3. There are no absolute constraints upon the possible flowering/fruiting times of species within a guild within the time period studied.

Clearly, none of these assumptions is completely valid in real systems, but no previous study has examined how violation of individual assumptions affects one's predictions or conclusions. Violating any of the assumptions affects the random expectations for phenology distributions within a guild. For example, if assumption 1 is invalid, then one

should expect selection against overlap to change the shape of the flowering/fruiting distributions (e.g. 30 species could have zero overlap in a 60 day growing season if each flowered for only two days). If the distributions are at all elastic, then calculating randomly expected overlap becomes difficult.

There is some evidence that assumption 2 may not be unreasonable for species within a guild. For instance, Pleasants (1980) found that attractiveness of flowers was negatively correlated with the number of flowers produced and suggested that the benefit gained by a plant in terms of insect visitations was the product of attractiveness and flower numbers. Clearly, however, it is naive to believe that all species within a guild are exactly equivalent and that if, for example, species A overlaps with both B and C, each will exert an identical influence upon it.

Assumption 3, that there are no absolute constraints on the possible flowering/fruiting times of aggregate species of a guild, is violated whenever a limited growing season exists. The implicit assumption of previous studies is that all times within the season are equally favorable. However, few, if any, of the possible environmental constraints on flowering times will be uniform over even a restricted portion of the year, and the effect that this has on the true random expectation may be considerable.

### Our simulations

We employed several methods for computing between-species overlap in the guilds we analyzed. Each of these methods and their assumptions are described below.

1. *Pairwise overlap.* Overlap was computed for all possible pairs of species within a guild using Pianka's (1974) symmetrical index

$$O_{jk} = \frac{\sum_{i=1}^n P_{ij} P_{ik}}{\sqrt{\sum_{i=1}^n P_{ij}^2 \sum_{i=1}^n P_{ik}^2}}$$

in which  $P_{ij}$  and  $P_{ik}$  refer to the proportion of flowering/fruiting of species  $j$  and  $k$  that occurs in time block  $i$ ; this index ranges from 0 (no overlap) to 1 (complete overlap). Slobodchikoff and Schultz (1980) discuss the advantages of using this particular overlap index rather than others. We tested observed overlap indices against a distribution of indices generated by Monte Carlo simulation. Expected overlap would be difficult to calculate because the shapes of the distributions of flowering times for the various species were not identical. By assigning the observed distributions randomly to time slots within the real growing season, however, an estimate can be made of the overlap expected if the timing of actual distributions was random. Ninety-nine such simulations were made for each pair of distributions and an overlap index was calculated for each. The position of the observed  $O_{jk}$  in the distribution of overlaps generated by the simulation gives an exact probability of obtaining an overlap index less than (or greater than) that observed by chance alone.

A pairwise Monte Carlo simulation makes several assumptions about the phenological distributions. First, it assumes that while the timing of the onset of flowering of a particular species is variable (and presumably could be

altered by selection for divergence between species), the shape of the distribution is immutable and is independent of starting time in the season. The latter assumption is supported by data. For example, there is no evidence of greater skewness of distributions for plants flowering early or late in the season in the data presented by Parrish and Bazzaz (1979) and Pleasants (1980). However, Thomson (1980) and Rabinowitz et al (1981) reported significant positive skewing in certain Rocky Mountain and Missouri plants.

The second assumption concerns the random positioning of phenological distributions in the simulation. Some arbitrary decision must be made about whether distributions will be allowed to overlap the ends of the growing season. In data sets which encompass an entire year, it seems reasonable to let distributions move freely through the year. In those encompassing a restricted growing season, the limits imposed by the season itself may be appropriate. With such data, we ran the simulations in two ways, first with random positioning of distributions constrained so that the entire flowering occurred within a single season and then with distributions permitted to wrap-around to the start of the next season. The two methods yielded similar results with a few exceptions which will be noted below.

The major difficulty which we see with the pairwise comparison method is that it grossly overestimates the degree to which divergence of flowering or fruiting could occur. In real guilds all species are potential competitors, and several species might simultaneously compete. Thus, while calculations of pairwise overlap might indicate that a species could have zero overlap with each of the other guild members separately, it would be impossible to do this with all species simultaneously. To model *n*-wise interactions, we calculated overlap indices for each species with the sum of the distributions of the others as described below.

2. *Total overlap.* As for pairwise comparisons, we carried out a Monte Carlo simulation comparing observed values with those obtained after randomization of the onset of flowering of the species in question. Total Overlap,  $O_T$ , was calculated between the distribution of a particular species and a distribution representing the sum of the phenological curves of the remaining species. Each simulation was carried out for unrestricted movements of distributions and for constrained movements in which distributions were not allowed to wrap around the growing season.

3. *Overlap simulation.* Both pairwise and total overlap calculations are static methods. Neither takes into account that while one species might potentially shift its distribution in time, this would not be an isolated event. If competition results in divergence of flowering/fruiting times, then one should expect a dynamic process. In assemblages of several species, movement of a species' distribution to a position of less overlap with one species may result in higher overlap with another species. We simulated this process by allowing each species to "find" the position of lowest overlap with all other species and to shift its phenology accordingly. The next species then did likewise and so on until each guild member had shifted once. Additional iterations were run until stable values of minimal overlap were obtained for all guild members. To see if the identity of the initial species influenced the final distribution of minimally overlapping distributions, we ran simulations starting with different members of the guild. In our data sets, similar results

were obtained regardless of which species was allowed to shift its phenology first.

### *The data sets*

The ideal data set for studies of phenological overlap should include quantitative data on flower/fruit abundance through time for a guild of plants utilizing the same set of animal visitors. Unfortunately, such data are rare in the literature. The focus of most studies that contain quantitative phenological data is usually on specific plant taxa, and hence these studies potentially include only partial guilds. Three of the five data sets we analyzed suffer from this problem. Analysis of partial guilds severely limits the conclusions that can be made regarding (1) the degree to which temporal overlap is greater or less than that expected by chance and (2) whether or not the "guilds" presently are saturated with species. Despite these limitations, we believe the following analyses are instructive in examining the relative importance of competition as a selective force behind phenological patterns.

Details of the five data sets are summarized in Table 1. Except for Hurlbert's (1970) study of *Solidago*, in which data were presented in tabular form, data were taken from flowering curves that were standardized to an area of 1.0 for each species whenever this had not been done by the original author(s). Because they involved only congeners, three of the studies undoubtedly dealt with incomplete guilds. For example, in addition to nine *Heliconia* species, the Costa Rican hummingbird guild includes at least six other species for which flowering curves have not been published (Stiles 1975, 1977). The two remaining studies were not restricted to specific plant taxa and more closely approximated actual guilds. Pleasants (1980) specifically defined his plant assemblages on the basis of their major bumblebee pollinators and recognized six plant guilds.

## **Results**

### *Do observed overlap values differ from random expectations?*

Data summarizing the results of pairwise and *n*-wise Monte Carlo simulations are presented in Table 1. As discussed earlier, most prior work has examined niche overlap relationships in pairwise fashion whereas we contend that the more meaningful comparison is *n*-wise overlap relationships. In our data sets, however, both approaches yield similar results and conclusions. In the case of pairwise comparisons, observed overlap deviated significantly from chance expectations in 42 of 416 cases. In each of these cases, overlap was significantly greater than expected. Regarding observed *n*-wise overlap, a total of 15 deviant cases out of 109 was found, 14 of which displayed greater overlap than expected (Table 1). These results do not provide strong support for the competition hypothesis. Instead, they suggest that flowering times in some guilds are more clumped than expected by chance.

Our results regarding niche overlap in Colorado bumblebee pollinated guilds run counter to those of Pleasants (1980), who reported that mean pairwise overlap was significantly less than expected by chance in five of 11 guilds. In these five guilds, we recorded no differences from chance expectations in two guilds and more overlap than expected in three instances in pairwise analyses and in two instances in *n*-wise analyses (Table 1). When we reanalyzed these

**Table 1.** Summary of flowering overlap statistics as analyzed by Monte Carlo simulation

Guild	Location and source	No. Species	No. pairs	X $\pm$ S.E. Overlap		Ratio of Observed N-wise overlap Min. N-wise overlap	No. of deviant overlap values <sup>a</sup>		Previous pairwise concl. <sup>b</sup>
				Pairwise	N-wise		Pairwise	N-wise	
<i>Solidago</i> (Goldenrods)	New York Hurlbert (1970)	10	45	0.64 $\pm$ 0.49	0.78 $\pm$ 0.073	0.78/0.45 = 1.75	21 >	6 >	
Winter annuals	Illinois, Parrish and Bazzaz (1978)	6	15	0.082 $\pm$ 0.050	0.23 $\pm$ 0.062	0.23/0.18 = 1.33	1 >	0	
Summer annuals	Illinois, Parrish and Bazzaz (1978)	3	3	0.68 $\pm$ 0.090	0.74 $\pm$ 0.068	0.74/0.51 = 1.44	0	0	
Early prairie community	Illinois, Parrish and Bazzaz (1978)	3	3	0.36 $\pm$ 0.13	0.45 $\pm$ 0.10	0.45/0.19 = 2.32	0	0	
Prairie community	Illinois, Parrish and Bazzaz (1978)	17	136	0.17 $\pm$ 0.026	0.35 $\pm$ 0.031	0.35/0.28 = 1.26	9 >	0	
<i>Bombus appositus</i> 1	Colorado, Pleasants (1980)	4	6	0.13 $\pm$ 0.078	0.19 $\pm$ 0.074	0.19/0.070 = 2.78	0	0	Obs. < Exp.
<i>B. appositus</i> 2	Colorado, Pleasants (1980)	4	6	0.20 $\pm$ 0.15	0.33 $\pm$ 0.13	0.33/0.11 = 3.06	0	0	Obs. = Exp.
<i>B. appositus</i> 3	Colorado, Pleasants (1980)	3	3	0.35 $\pm$ 0.21	0.46 $\pm$ 0.16	0.46/0.18 = 2.60	0	0	Obs. = Exp.
<i>B. flavifrons</i> 1	Colorado, Pleasants (1980)	7	21	0.37 $\pm$ 0.077	0.55 $\pm$ 0.087	0.55/0.39 = 1.40	1 >	2 >	Obs. < Exp.
<i>B. flavifrons</i> 2	Colorado, Pleasants (1980)	5	10	0.58 $\pm$ 0.097	0.71 $\pm$ 0.12	0.71/0.36 = 1.95	0	1 >	Obs. $\approx$ Exp.
<i>B. bifarius</i> 1	Colorado, Pleasants (1980)	7	21	0.27 $\pm$ 0.72	0.42 $\pm$ 0.046	0.42/0.29 = 1.44	1 >	0	Obs. < Exp.
<i>B. bifarius</i> 2	Colorado, Pleasants (1980)	9	36	0.52 $\pm$ 0.053	0.68 $\pm$ 0.079	0.68/0.39 = 1.76	2 >	2 >	Obs. = Exp.
<i>B. flavifrons</i> , front	Colorado, Pleasants (1980)	5	10	0.28 $\pm$ 0.10	0.43 $\pm$ 0.14	0.43/0.27 = 1.58	0	0	Obs. = Exp.
<i>B. flavifrons</i> , back	Colorado, Pleasants (1980)	5	10	0.48 $\pm$ 0.10	0.60 $\pm$ 0.091	0.60/0.40 = 1.50	1 >	0	Obs. < Exp.
<i>B. kirbyellus</i>	Colorado, Pleasants (1980)	4	6	0.46 $\pm$ 0.12	0.60 $\pm$ 0.14	0.60/0.31 = 1.93	0	0	Obs. $\approx$ Exp.
<i>B. sylvicola</i>	Colorado, Pleasants (1980)	3	3	0.64 $\pm$ 0.13	0.72 $\pm$ 0.10	0.72/0.20 = 3.61	0	0	Obs. < Exp.
<i>Heliconia</i> species	Costa Rica Stiles (1975)	9	36	0.56 $\pm$ 0.048	0.72 $\pm$ 0.077	0.72/0.56 = 1.28	4 >	3 >	
<i>Piper</i> species	Costa Rica Fleming (in press)	5	10	0.13 $\pm$ 0.052	0.19 $\pm$ 0.78	0.19/0.11 = 1.85	1 >	1 <	

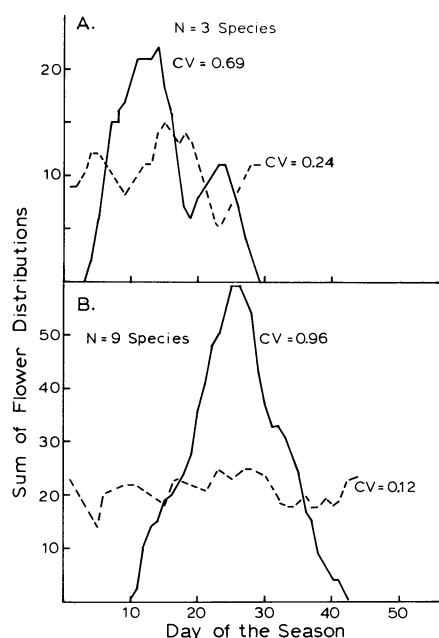
<sup>a</sup> Number of cases significantly ( $P < 0.05$ ) greater (>) or less(<) than expected by chance

<sup>b</sup> Conclusions of original author. Obs = observed. Exp = expected

five guilds using a simulation program with temporally-constrained random starting times, 15 (nine with greater and six with less overlap) of 132 pairs differed from chance expectations. Overall, our results do not suggest that temporal overlap is less than that expected by chance. Placing temporal restrictions on randomized starting dates appears to increase the number of apparently deviant cases but not necessarily in the direction predicted by the competition hypothesis. Thomson (1982) also questioned the validity of Pleasants' (1980) conclusions.

In summary, our two methods of analysis, pairwise and n-wise overlap, produce similar results which suggest that temporal flowering overlap deviates from random expectations in a minority of cases and tends to deviate towards more overlap than expected in the data sets we have examined.

*The "evenness" of floral distribution through time.* A corollary of the competition hypothesis is that flower/fruit availability should be relatively uniform through time within a guild of plants. Under the assumption that niche breadths do not systematically change with changes in guild size (i.e. they might be expected to decrease with increasing guild size), evenness should increase with increasing guild size because of potentially increased competition in larger guilds. The assumption regarding changes in niche breadth is correct for our data sets. Mean niche breadth, as measured by the Shannon-Weiner index ( $B = -\sum P_i \ln P_i$ ), was not correlated with guild size ( $P > 0.05$  in a corner test). We estimated evenness by calculating the coefficient of variation (CV) of mean height of the summed flowering curves of all guild members on each census date for the original data and for the simulated guilds after minimal n-wise over-



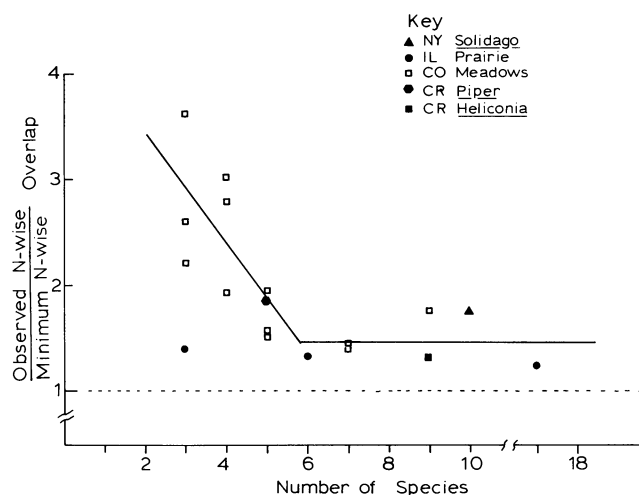
**Fig. 1.** Comparison of observed (solid line) and simulated (dashed line) evenness of flowering distributions in two Colorado bumblebee-pollinated flower guilds **A** Three species guild pollinated by *Bombus appositus*, site 3; **B** nine species guild pollinated by *B. bifarius*, site 2. Data are from Pleasants (1980). CV = coefficient of variation

lap had been attained. A low CV reflects a high degree of evenness and vice versa. We plotted the relationship between guild size and (1) CV of the original data, (2) CV of the simulated data, and (3) the difference between original and simulated CVs. We also examined the speed with which final simulated CVs were attained for guilds of different sizes in terms of the number of iterations of the overlap simulation program required to produce stable values.

Results of these analyses generally did not support the prediction of the competition hypothesis (viz. that observed CV should decrease with increasing guild size). Observed total flower distributions generally were more strongly peaked than final simulated distributions (Fig. 1). Observed CVs were significantly larger than simulated CVs (observed  $\bar{x} = 0.77 \pm 0.05$  (S.E.) vs. simulated  $\bar{x} = 0.27 \pm 0.05$ ;  $t = 8.65$ ,  $df = 17$ ,  $P < 0.001$ ), and original and simulated CVs and the differences between them were not correlated with guild size ( $P > 0.05$  in corner tests). In most guilds, maximal evenness was attained in three or less iterations, and stabilization speed was not related to guild size.

## Discussion

The testing of observed patterns of community structure against random expectations has become increasingly important in ecological studies (e.g. Connor and Simberloff 1979, Strong et al. 1979). Computer simulations have been extensively used to erect and test null hypotheses, but considerable controversy has arisen concerning the construction of biologically-reasonable null hypotheses (e.g. Grant and Abbott 1980, Feinsinger et al. 1981, Alatalo 1982). In this paper we have advocated the use of dynamic computer simulations to analyze observed phenological patterns but



**Fig. 2.** Plot of the ratio of mean observed n-wise overlap to mean minimum n-wise overlap against plant species number in five data sets. The negative relationship below a guild size of 6 is significant ( $r = -0.67$ ,  $0.05 > P > 0.01$ )

stress that the assumptions behind simulations and other methods still need careful scrutiny. A first step in such a scrutiny obviously involves a complete enumeration of explicit and implicit assumptions behind the simulation or other analytical technique. We agree with Stiles (1979) that uniform distributions of flowering/fruitleting curves or peaks are not necessarily reasonable expectations upon which to base a statistical analysis of the existence of competition (cf. Pool and Rathke (1979) and Simberloff and Boecklen (1981)).

Given our list of basic assumptions, what new insights or advantages over other methods does our analytical method provide? We feel that our method offers two major improvements over other techniques. First, our method stresses n-wise, rather than pairwise, comparisons. Results of pairwise and n-wise comparisons were basically similar in the data sets we analyzed, but we feel that n-wise comparisons more closely approximate the ways in which species interact in nature. In the case of plants competing for a limited supply of pollinators, it clearly does not benefit a pair of species to diverge temporally from each other if by doing so they experience increased competition from other guild members. Divergence must be considered in the context of the entire guild simultaneously rather than in pairwise fashion.

A second improvement is that our method produces a quantitative statement as to how closely observed phenological overlap approaches theoretically minimum overlap for a given set of flowering/fruitleting curves. Results of our analysis (Table 1, Fig. 2) suggest that guilds become more tightly packed as species number increases up to a point (5–6 species in this study) beyond which degree of temporal packing is independent of guild size. This point occurred at a ratio of observed n-wise overlap/minimum n-wise overlap of 1.50, i.e. observed overlap averaged 50% greater than the minimum value. This result is not surprising because one should not necessarily expect plants to display minimum possible phenological overlap, even in intensely competitive guilds. Other biological factors such as effective mutualism (sensu Waser and Real 1979), seasonal changes in the availability of animal visitors, and physiological con-

straints will oppose pressures to minimize phenological overlap. For example, in the case of the Costa Rican *Piper* species, flowering times that minimized n-wise overlap probably are not physiologically feasible because they would result in succulent fruits being produced at times when plants are under water stress (Fleming in press). Thus, minimal values of flowering/fruitlet overlap will probably seldom occur in actual guilds.

Finally, our technique allows us to test a corollary of the competition hypothesis, viz. that the abundance of flower/fruit resources is relatively even throughout the reproductive season as a result of regularly-spaced phenological curves. Comparisons of observed and simulated distributions of the summed values of the flowering curves in our data sets revealed strongly peaked, rather than uniform, distributions (Fig. 1). Along with results summarized in Table 1, these peaks suggest that flowering distributions are more likely to be clumped than uniformly spread out in nature. Similar results were reported by Anderson and Schelfhout (1980). While temporal aggregation of resources does not necessarily eliminate interspecific competition as a major factor in the evolution of phenological patterns, it does suggest that other factors such as temporal variations in the availability of animal visitors (e.g. Heinrich 1976b, Thompson and Willson 1979, Zimmerman 1980) and/or favorable physiological conditions (e.g. Borchert 1980, Reich and Borchert 1982) or seed predators may be equally important evolutionary factors.

Despite the failure of our analyses to provide strong support for the competition hypothesis, we cannot conclude that competition is unimportant in the evolution of angiosperm phenological cycles for at least three reasons. First, such a conclusion must await the availability of a greater number of studies of complete guilds of potential plant competitors. Out of necessity, our analyses included several incomplete guilds, but their inclusion probably renders our conclusions conservative because partial guilds are likely to exhibit less temporal overlap than actually exists in complete guilds. The general absence of significantly-reduced overlap in our partial guilds offers little hope that low values of overlap characterize the complete guilds from which our data were drawn.

A second reason is that null hypotheses of random overlap become increasingly difficult to reject as guild size decreases (Fleming in press, Schoener 1983). Owing to chance alone, very low or no overlap becomes increasingly likely as guild size decreases. A final reason is that our simulations are based on the premise that it is biologically reasonable to randomly assign the starting times of phenological events within a growing season. If this assumption is false, then our null expectations are unreasonable.

Rigorous statistical tests of the competition hypothesis must await more complete field studies. Ideally, these studies should include experimental tests of the hypothesis and its predictions. Without direct experimental evidence, statistical inferences about the existence of competition will always be open to question. Most importantly, however, analyses such as those reported here offer several alternate hypotheses to that predicting divergence of flowering time, including (1) uniform overlap (which provides pollinators with a steady supply of flowers) or (2) optimal overlap in which the total number of flowers at any one time tracks the number of pollinators available at that part of the season.

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