Short Communication

Character Displacement in Flowering Phenologies

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Flower-pollinator systems have increasingly become objects of study in ecology, primarily because the interactions involved, foraging by the pollinators and reproduction by the plants, so directly affect biological fitness. It is in such communities that high degrees of organization would be expected. A recent exchange (Poole and Rathcke 1979, and Stiles 1979) has raised questions concerning the role of competition in interpretations of flowering phenologies. The particular hypothesis in dispute is that competition by plant species for pollinators can cause a divergence of flowering times, resulting in a regular sequence of blooming within a season. Considering blooming time as a quantitative trait, this is essentially a character displacement argument. As Slatkin (1980) has demonstrated, there are two important components of a quantitative character that determine its displacement response; the mean and the variance. Most discussion of flower phenologies has concerned displacement of the means (regularity). This note discusses techniques for assessing relevant patterns in both the means and the variances, and applies them to some published phenologies.

Beginning with Hocking (1968), a number of studies (Parrish and Bazzaz 1979 cite many) have contributed data relevant to the character displacement hypothesis. The ideal system would be one in which a suite of plant species rely exclusively on a single pollinator species during a homogeneous flowering season. Stiles (1977) has most closely approached this ideal in a study of hummingbird pollinated plants in Costa Rica.

A lack of approriate quantitative techniques concealed a basic problem in these studies. As Poole and Rathcke (1979) argued, the very act of ordering blooming times into a sequential phenology produces an impression of regularity. This is illustrated in Fig. 1A, which is a phenology produced by picking 20 pairs of random numbers, with replacement, from an arbitrary blooming period (a uniform distribution), with the lowest and highest number of the pair as the beginning and end, respectively, of a hypothetical species' blooming time. Poole and Rathcke (1979) presented a new statistical method for distinguishing an evenly spaced phenology from such a random one. Applying it to Stiles' data, they determined that in each of the four years the phenology was not significantly different from random and in fact tended toward aggregation. These results are inaccurate, however, due to computational error (R.W. Poole, pers. comm.).

Recomputation of Stiles' data gives results that, while still not significantly non-random, show a tendency toward evenness (for $k=8$; in 1971 $P/E(P)=0.705$, $0.25 < P < 0.5$; in 1972 $P/E(P)=0.683$, $0.25 < P < 0.5$; in 1973 $P/E(P)=0.591$, $0.1P < 0.25$; and

in 1974 $P/E(P)=0.614$, $0.1 < P < 0.25$). The $P/E(P)$ statistic is designed so that clumping will yield values greater than one, and even distributions will yield values less than one. A random phenology will produce an expected $P/E(P)=1$, with a mode $\simeq 0.9$ and a frequency distribution which determines the critical values. P levels for $n \leq 16$ were determined from Table 2 in Poole et al. (unpub.). For more detail, see Poole and Rathcke (1979). Here, P levels are the probability of random $P/E(P)$ values less than observed.

Neither author computed a mean phenology from the four years of data, although this would seem to be a good way to minimize the effects of extrinsic sources of variability. Such a mean phenology was computed by averaging the midpoints and bloom durations of each species (see Fig. 1 B, numbers are the same as in Stiles 1977). It yields a $P/E(P)$ that is as low as the lowest single year value, although still not significant ($P/E(P)=0.598$, $0.1 < P < 0.25$). If the full calendar year is used as the period and the largest interval divided in half to determine the endpoints, the resulting phenology approaches significance at the 0.05 level ($k=10$, $P/E(P)=0.457$, $0.05 < P < 0.1$; this reflects the sensitivity of the test to choice of conventions). In contrast, considering all four years as a continuous phenology does not take advantage of the averaging process and is more random
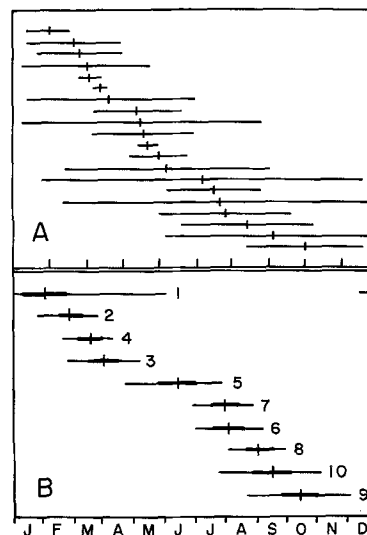

Fig. 1. A A randomly generated 20 species phenology. **B** The 4-year mean phenology computed from Stiles (1977) (see text for details)

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than the mean phenology $(P/E(P)=0.795, \chi^2=30.19, 0.1<P<0.5)$.

The meaning of Poole and Rathcke's test depends on the null hypothesis of randomly spaced mean flowering times. If there were one optimal time to bloom for all plant species, in the absence of competition all species should bloom simultaneously. Certainly Stiles' data is significantly different from a null hypothesis of simultaneous bloom (a random phenology would doubtless be also). Poole and Rathcke's test is more rigorous because its null hypothesis corresponds to the more biologically interesting assumption of an initially disorganized community composed, for example, of species colonizing from a diversity of habitats. Deviation from this condition would then be suggestive of a community that has acquired some organization in response to displacement pressure.

Competition in such a community might result in either competitive exclusion and selective retention of immigrant species, or coevolution by character displacement of the initially random species assemblage (it is not possible to distinguish these two processes with the tests discussed here). In either case there may be various inhibitions to the emergence of a truly even phenology, as Stiles (1979) points out. In addition, it may be that a random (or even aggregated) distribution of times is sufficient to reduce competitive forces to a low level.

More importantly, the second critical feature in a species' phenological response remains to be considered, namely the variance of the trait. Indeed, Slatkin's (1980) results indicate that the variances may be more responsive to competitive displacement pressure. This might be particularly likely if there were some constraint on the response of the means. Reduction of flowering overlap can result not only from a displacement of blooming time in the direction of increased evenness, but also from a compression of the duration of species' blooming periods. If plant species are compressing their blooming periods in response to competiton, one would expect a correlation between blooming duration and some measure of temporal aggregation, that is, the more tightly clumped species are in a season, the shorter their blooming periods. One measure of aggregation might be the mean temporal distance to the nearest competitor (in Poole and Rathcke's symbols, $(y_{i+1}-y_{i-1})/2$). For Stiles' data, the correlation between the mean temporal distance and bloom duration is positive and significant (for both "good bloom", $r=0.725$, and "peak bloom", $r=0.719$; $P<0.05$ for both). As a comparison, the random phenology (Fig. 1 A) has a $P/E(P)=1.02$ (not sig., $P\cong0.5$) and a duration/distance correlation of $r=0.07$ (not sig.).

Other published phenologies are less statisfying as tests of the hypothesis, particularly because of multiple pollinators. Heinrich's (1975) temperate study of bumblebee pollinated bog flowers yields a $P/E(P)=0.77$ ($k=24$, $\chi^2=18.5$, $0.1<P<0.5$) and a duration/distance correlation of $r=0.06$ (not sig.). A study of a tropical bat (seven species) pollinated complex (Heithaus et al. 1975) yields a random $P/E(P)=0.91$ ($k=11$, $P\cong0.5$) and a duration/distance correlation of $r=0.21$ (not sig.). Snow (1966) made a similar argument concerning the evolution of fruiting time, and his data for tropical plants using frugivorous birds for dispersal produce a $P/E(P)=0.689$ ($P\cong0.25$) and $r=0.405$ ($df=16$, $0.05<P<0.1$). These tests used duration midpoints to represent the species and are unlikely to be precise. For example, using the midpoint of "good bloom" (thin line) instead of "peak bloom" (thick line) for Stiles' mean phenology results in an increase in the $P/E(P)$ value (for $k=8$, from 0.598 to 0.634 and for $k=10$ from 0.457 to 0.602).

Alternatively, one could incorporate both dimensions by comparing overlap densities with a null model. However, no analytical test are available and computer simulations must be used. Such an approach has been taken for flowering communities (Parrish and Bazzaz 1979 and Pleasants 1980) and character displacement more generally (Strong et al. 1979). Recently, Cole (1981) has presented another reassessment of Stiles' (1977) phenology in which he breaks the year into dry and wet seasons. He finds both significant evenness and reduced overlap within seasons. This approach assumes that there are two types of flowering strategy in this community, which may or may not be justified. The revision of the full year analysis presented here does not support the assumption of any aggregation (seasonal or otherwise) in this phenology.

What we seek then is not necessarily a strictly even phenology, but evidence for the "escape in time" predicted from natural selection. The most appropriate data set (Stiles 1977) demonstrates a tendency away from randomness toward an even distribution of flowering times, as well as a distinct trend to shorter blooming durations in times of the year when more species are flowering (if the phenology were strictly even, there would be no statistical basis for this correlation). Since both factors would tend to reduce temporal overlap, this suggests a community structure modified by character displacement.

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