Skewed Flowering Distributions and Pollinator Attraction
Author(s): James D. Thomson
Source: *Ecology*, Vol. 61, No. 3 (Jun., 1980), pp. 572-579
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1937423
Accessed: 07/11/2008 17:33

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=esa.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.

Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

http://www.jstor.org

Ecology, 61(3), 1980, pp. 572–579

SKEWED FLOWERING DISTRIBUTIONS AND POLLINATOR ATTRACTION[1]

JAMES D. THOMSON[2]
Department of Zoology, University of Wisconsin,
Madison, Wisconsin 53706 USA

Abstract. The temporal distributions of flowering by animal-pollinated plant populations, "flowering curves," can be viewed profitably as resource utilization functions. A conceptual model of plant competition for pollinators suggests that selection may favor asymmetrical, positively skewed curves, and that such skewness should be most evident in flowers which, at the initiation of flowering, are of a type unfamiliar to their pollinators. Both predictions are confirmed in an examination of 57 species of subalpine meadow plants from the Colorado Rocky Mountains.

Key words: competition; directional selection; flower distribution; niche; phenology; pollination; resource tracking; resource utilization; skewness; time lag.

INTRODUCTION

Ecologists concerned with resource utilization have concentrated on two aspects of the distribution of resources used by a species: the distribution's width or variance, usually used as a measure of niche breadth; and the distribution's location, which is usually considered relative to those of other species and used to generate niche overlap. The higher moments of resource utilization distributions have received much less attention, although Roughgarden (1974) has dealt with the theoretical implications of kurtosis, and Wilson (1975) has discussed the likelihood and possible importance of a particular type of skewed distribution of food size choice. Field studies of skew and kurtosis are rare for at least two reasons: first, many resources cannot legitimately be ordered on a continuous gradient; second, it is usually difficult to measure resource utilization with sufficient accuracy to determine the shape of the curve confidently. One case in which neither objection holds is the distribution of a plant population's flowering in time.

If one graphs the number of flowers in bloom vs. time, the resulting flowering curve can be treated as a resource utilization function. Although pollinator service, not time, is the real resource, time is a gradient along which the use of common pollinators may be partitioned by plant species. This has been widely recognized; the most explicit applications of this theory to field data have been those of Pleasants (1977), Waser (1977, 1978*b*), and Thomson (1978*a*). These authors concur that plant competition for pollination has influenced the sequence and timing of flowering in various Colorado wildflowers. I concern myself here not with the locations of flowering curves of these species but with their shapes, and raise the question whether competition might also affect their skewness. I will assemble a conceptual model (a mathematical version is in Thomson 1978*a*), examine data, and compare the model's predictions with the results in hand.

Theoretical considerations

Several different theoretical treatments of plant competition for pollinators propose that the relation of a species' success to its frequency in a two-species stand should be sigmoidal, such that at frequencies $<$ 0.5 it does very poorly and at frequencies $>$0.5 it does very well (Levin and Anderson 1970, Straw 1972, Thomson 1975, and Waser 1977, 1978*a*). If this minority disadvantage holds over time, one would expect that a species which is bracketed by early and late competitors would do quite poorly until its increasing bloom equals the waning bloom of its predecessor. After that point, its success should rise quickly to a plateau and remain there until, on the decline, its numbers are in turn matched by the succeeding species. If pollinators respond to flower numbers in this way, without time lags in their perception of changing flower numbers, the "success curve" of the species will have the same location on the time axis as the flowering curve, but have steeper sides and a flatter top (Fig. 1). To the extent that pollination is advantageous, this would produce a stabilizing selection acting equally against early and late flowering. But pollinators may lag in their perception of changing numbers of flowers (Thomson 1978*a*) or they may be more likely to continue visiting a familiar resource, one manifestation of "flower constancy." In either case, the success curve may be shifted in time with respect to the flowering curve so that early flowers never do as well as late flowers (Fig. 1b), inducing directional selection. This pattern, a lagged success curve with a plateau, is the most common pattern found in the analysis of per-flower visitation rate in various Colorado wildflowers (Thomson 1978*a*).

If flowering curves were symmetric, such pressure

---

[1] Manuscript received 5 October 1978; revision received 1 May 1979; accepted 19 July 1979.

[2] Present address: Department of Zoology, University of Toronto, Toronto, Ontario M5S 1A1, Canada.

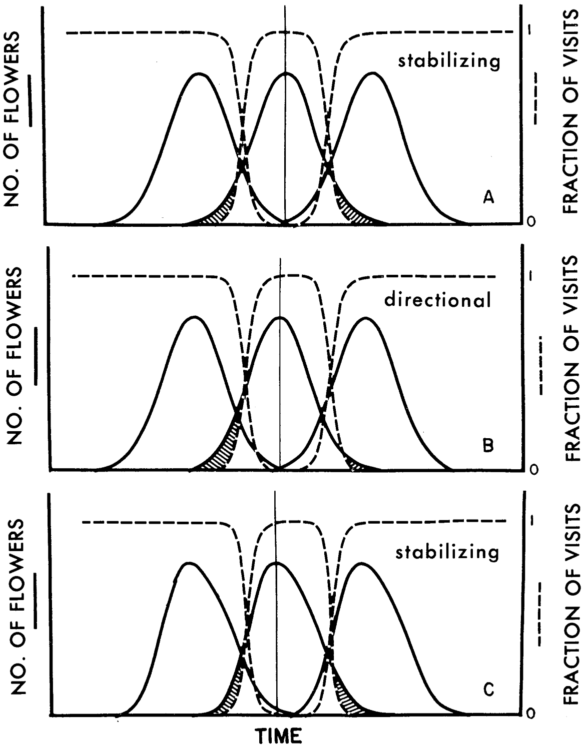

FIG. 1. Each diagram shows three flowering curves (solid lines) and the associated success curves (broken lines). The horizontal axis is time; units of the vertical axis are arbitrary. The center species is of most interest. In (A) flowering curves are normal, evenly spaced in time, and show no time lag. Selection on flowering time of the center species is symmetrical, stabilizing. In (B) a time lag in pollinator response to density changes is introduced. Success curves lag flowering curves by two arbitrary time units. Selection will again be directional but may tend to produce a skewed flowering curve (see text). In (C) the flowering curves are skewed, and selection is nearly stabilizing with a lag time of one unit. Greater lag times require more skewness for selection to be stabilizing. Equations are in Thomson (1978*a*).

might be expected to push flowering later in time. Flowering times of species in nature do not move inexorably backward, however. It is possible to show (Thomson 1978*a*) that a certain degree of positive skewness in a flowering curve can stabilize a particular amount of time lag in the success curve, in the sense that equal numbers of early and late flowers will fail (Fig. 1c; cf. Thomson 1978*a*). This paper seeks first to demonstrate that positively skewed flowering curves predominate in Rocky Mountain subalpine meadow plants, and second, to consider the hypothesis that such skewness is in part an adaptive response to a plant's evolutionary "problem" of attracting pollinators which are accustomed to visiting other species. Thus skewness may be related to plant competition for pollinators.

Other explanations for this curve shape could be proposed, ones that attribute the skewness to nonadaptive but inescapable peculiarities of the development of flowering plants or to the influence of topographical or edaphic variation within the meadow which in turn would influence flowering pattern. For example, one might suppose that most of the plants of a population would be growing in "good" microhabitats, while a smaller number of individuals would occupy marginal areas. If marginal microhabitats tended to delay flowering, perhaps due to slower growth rates there, the population flowering curve would show positive skewness quite independently of pollination success. One could also argue that skewness may reflect nothing more than an inherent tendency of plants to begin blooming heavily as soon as a cue is received and to continue with a diminished vigor as stored resources are depleted. It would be extremely difficult to show that all such effects are negligible, and I will not try to do so. On the other hand, the existence of such effects is in no way incompatible with the suggestion that competition, constancy, and perception lag also influence flowering curve shape.

Predictions

To unravel such multiple causes, it is necessary to consider testable predictions which are peculiar to the competitive hypothesis. These predictions hinge on the contention that the reason for a flowering curve's rapid ascent is to evade the pollinators' reluctance to visit rare and novel flowers. If this is so, flowers which are not *effectively* rare and novel should show less positive skewness. A species may be effectively familiar if pollinators have been accustomed to visit an earlier-blooming species very much like it. Grant (1966), Mosquin (1970), Macior (1971), Thien and Marcks (1972), Bobisud and Neuhaus (1975), Heinrich (1975), Thomson (1975, 1978*a*), and others have suggested that mimicry among flower species may exist as a mechanism for attracting more pollinators by facilitating inconstancy. Viewpoints range from Heinrich's proposition that nectar-poor species are likely to mimic and bloom directly after nectar-rich species in what is roughly a Batesian interaction, to my contention that many somewhat similar species are likely to bloom more or less simultaneously in quasi-Müllerian mimicry rings. I have found support for this notion in visitation rate patterns, behavioral experiments on bees and flies, and analyses of pollinator partitioning by plants (Thomson 1978*a*); there are elements of "cooperation" linking plant species in such broad groups as yellow composites and the like. Of course, a continuum exists between the well-defined pairwise interactions of Heinrich and my comparatively sprawling cooperative groups; examples of both can be found in the data to follow. In a pair of similar species, I would expect the "following" mimetic species to show less positive skew than the leading model. In a multispecies cooperative, I would expect a correlation between earliness of bloom and degree of positive skew; in other words, after pollinators had been well exposed to a particular general flower type, later species could come into bloom less abruptly with a smaller sacrifice in visitation than would otherwise be exacted.

STUDY SITES AND SAMPLING METHOD

Flowering data were recorded during May–September 1977 in subalpine meadows in the Colorado Rocky Mountains near the Rocky Mountain Biological Laboratory at Gothic (Gunnison County, Colorado). Two sites hereafter named LOW (altitude 2900 m) and IB (altitude 3280 m) were chosen for study. The flora of this area is treated by Barrell (1969), the vegetation by Langenheim (1962). LOW's vegetation corresponded roughly to Langenheim's "fescue" vegetation type, while IB was closer to her "spruce-fir" designation.

At each site a regular grid of 108 permanent sample points was arranged in a 6 × 18 rectangle with 10-m spacing between points each way. The long axis of the resulting 50 m × 170 m rectangle in each case cut across the greatest topographical variation in the meadow. At 2-d intervals until mid-July, and at 3-d intervals thereafter, we counted the open flowers (or, in certain cases, heads or inflorescences; see Table 1) of animal-visited flowers in a 4-m^2 quadrat located at each of the permanent grid points. Plant nomenclature follows Barrell (1969).

Sampling was conducted from 29 May through 15 August, by which time all plant species had passed their flowering peaks (1977 was an advanced season) and all but a few had ceased flowering completely. Both sites were censused again on 2 September.

RESULTS

Calculating skewness

While it is not strictly possible to judge the skewness of those plants still in bloom on 15 August because the tails of their flowering and success curves are missing, reasonable reconstructions may be made. If different reconstructions do not change skewness greatly, because the bulk of the curve fell in the well-sampled period, the statistics may be used conservatively with fair confidence. Skewness is computed as g_1 (Sokal and Rohlf 1969). The values are given in Table 1; details of calculation follow.

For species which were in bloom on 15 August (day 77) but not on 2 September (day 96), I computed two measures of skewness. The first used linear interpolation to fill in the missing days, assuming that day 96 was the first "zero" day. The second used the last two days' values to determine the trajectory of the curve, and extrapolated to the day when the density should go to zero. The 13 species so treated are denoted by "interp" in Table 1, where both values are given. Values determined by the first method are called "raw" values indicated by (1) in the Skewness column of Table 1; those determined by the second method are listed as "modified," identified by (2).

For five other species ("inc late" in Table 1) some flowers were still present on day 96. I again computed two values: the first assumes that flowering ceased on day 96 and uses interpolation to provide the values between 77 and 96, while the second extrapolated to an endpoint in the future, as above.

Species already in bloom on the first census day are denoted by "inc early" in Table 1. A few defied reconstruction since they were already blooming at one-quarter or more of maximum density. For these species, Table 1 gives the skewness of the interpolated raw data: these values are unreliable and are not used further. In other species, where only small sections of the distributions appeared to be missing, I calculated the raw values as before, but also calculated a modified value based on extrapolation similar to that described for "inc late" plants but extrapolating backwards in time rather than forwards.

For each of these cases, then, there is a raw value based on minimum assumptions, which ignores the part of the season not sampled, and a modified value which represents a reasonable guess about the unseen part of the flowering curve. In the case of "interp" species, it is probable that the true value lies between these two estimators; in the cases "inc early" and "inc late" this is less certain.

Sample size and significance

In principle, it is simple to test whether a distribution's skewness is significantly different from zero (Sokal and Rohlf 1969: 171). However, the data at hand are not so easily tested, for several reasons. First, the problem of missing tails (above) obviously makes some of the species formally untestable. Second, the fact that census frequency shifted from every other day to every 3rd d in the middle of the season means that some parts of the curve contribute more heavily to the sample than others.

The value N in Table 1 is the number of "flower-days" used to calculate the raw skewness value. This is greater than the number of flowers actually counted (by a factor between two and three) because of the use of interpolation to fill in days between censuses. I arbitrarily excluded from consideration any species with $N < 300$, which ensures that all species treated had at least 100 floral units counted.

Despite the restrictions noted above, I have followed Sokal and Rohlf's procedure for testing significance. The standard error of the statistic g_1 is a function of the sample size, and can be approximated as $\sqrt{6/n}$ for $n > 100$. I have computed s_{g_1} in this way, using $n = N/3$ for a conservative estimate of the sample size. I then applied a two-tailed t test to both the raw and modified values. While the technique is employed loosely, the large samples provide some con-

TABLE 1. Summary of census data. This table gives, for each plant species, the number of flower-days *N* (see text), the mean date of flowering (day 1 = 29 May 1977), and the skewness measures. Some flowering curves were not observed in their entirety. A curve code of "inc early" indicates that the species was in bloom before day 1. A code of "interp" means that the curve was interpolated because the species was in flower on day 77 but had ceased by day 96. Code "inc late" indicates a species which remained in flower on day 96. Code "entire" indicates that the entire curve was observed. Under the heading Unit sampled, "fls" indicates that flowers were counted, "heads" indicates composite heads, "infls" indicates other inflorescences, and "shoots" means that plants with open flowers were the units counted. For some species with curve code "inc early," and all with "interp" or "inc late," a modified skewness was calculated as well as the raw value (see text). Raw values under the Skewness column are indicated by a (1), modified values by a (2). Standard errors and significance levels are calculated as explained in the test. NS = not significant.

		LOW						IB					
	Unit sampled	*N*	Curve	Mean flowering date	Skewness	SE	*P*	*N*	Curve	Mean flowering date	Skewness	SE	*P*
Boraginaceae													
Mertensia fusiformis Greene	fls							8 386	entire	15.1	.433	.0463	.001
M. ciliata (James) G. Don	fls							14 834	entire	42.3	.488	.0348	.001
Campanulaceae													
Campanula rotundifolia L.	fls	1 947	interp	59.8	.563 (1) .506 (2)	.0962	.001						
Compositae													
Achillea millefolium L.	heads	218 812	inc late	65.7	.234 (1) .316 (2)	.0091	.001	412	entire	69.4	.542 (1) .550 (2)	.2090	.01
Agoseris glauca (Pursh) D. Dietrich	heads							13 409	inc late	67.0	.425 (1) .483 (2)	.0366	.001
Arnica mollis Hooker	heads							1 145	interp	68.3	.468 (1) .415 (2)	.1254	.001
Chrysopsis villosa (Pursh) Nuttall	heads							16 424	inc late	71.6	.207 (1) .287 (2)	.0331	.001
Erigeron coulteri Porter	heads							391	interp	65.7	1.147 (1) .713 (2)	.2146	.001
E. elatior (Gray) Greene	heads							385	interp	62.7	.572 (1) .378 (2)	.2162	.01 NS
E. peregrinus (Pursh) Greene	heads							970	interp	60.3	1.283 (1) 1.120 (2)	.1362	.001
E. speciosus (Lindley) DC.	heads	67 273	interp	62.9	.638 (1) .651 (2)	.0164	.001	2 423	entire	64.6	.440	.0862	.001
Helenium hoopesii Gray	heads							5 962	interp	53.6	.703 (1) .578 (2)	.0594	.001
Helianthella quinquenervis (Hooker) Gray	heads	3 232	entire	48.3	.311	.0746	.001	6 730	entire	52.3	.397	.0517	.001
Senecio crassulus Gray	heads							19 679	entire	47.2	.407	.0302	.001
Solidago multiradiata Ait.	heads	37 069	entire	57.6	.481	.0220	.001						
Taraxacum officinale Weber	heads	27 374	entire	15.8	.893	.0256	.001						
Viguiera multiflora (Nuttall) Blake	heads	11 815	inc late	75.4	.022 (1) .141 (2)	.0390	NS .001						
Cruciferae													
Arabis drummondii Gray	fls	1 844	entire	22.5	2.795	.0988	.001	2 445	entire	24.4	1.710	.0858	.001
Draba nemorosa L.	fls	9 126	entire	9.4	.411	.0444	.001	17 853	entire	21.5	.205	.0318	.001
D. spectabilis Greene	fls							76 546	entire	21.9	.355	.0153	.001
Erysimum asperum (Nuttall) DC.	fls	1 380	entire	28.1	1.089	.1142	.001						
Thlaspi alpestre L.	fls							52 020	entire	11.9	.845	.0186	.001
Geraniaceae													
Geranium richardsonii Fisher and Trautvetter	fls							1 087	entire	46.0	.243	.1287	NS
Gentianaceae													
Frasera speciosa Douglas	fls							9 033	entire	36.3	.417	.0446	.001
Gentiana calycosa Grisebach	fls							588	interp	79.6	−.176 (1) −.530 (2)	.1750	NS .01
G. amarella L.	fls							711	interp	70.7	.811 (1) .562 (2)	.1591	.001
Leguminosae													
Astragalus sp.	fls							1 202	entire	35.0	.332	.1224	.01
Lathyrus leucanthus Rydb.	fls	17 436	entire	34.4	.035	.0321	NS						
Lupinus amplus Greene	fls							176 991	interp	53.6	.425 (1) .346 (2)	.0101	.001
Vicia americana Muhl.	fls	4 496	entire	41.7	.870	.0633	.001						
Liliaceae													
Erythronium grandiflorum Pursh	fls							7 817	inc early	9.0	1.154	.048	.001

TABLE 1. Continued.

		LOW						IB					
	Unit sampled	*N*	Curve	Mean flowering date	Skewness	SE	*P*	*N*	Curve	Mean flowering date	Skewness	SE	*P*
Linaceae													
Linum lewisii Pursh	fls	457	entire	40.7	.432	.1985	.05	8 400	entire	41.4	.914	.0463	.001
Polemoniaceae													
Ipomopsis aggregata (Pursh) Sprengel	fls	345	entire	43.1	.404	.2284	NS						
Primulaceae													
Androsace septentrionalis L.	fls	56 304	inc early	14.6	.748 (1) .692 (2)	.0179	.001	101 859	entire	20.5	.728	.0133	.001
Portulacaceae													
Claytonia lanceolata Pursh	fls							24 264	inc early	5.5	.864	.0272	.001
Ranunculaceae													
Aquilegia caerulea James	fls	453	entire	34.3	.135	.1993	NS	833	entire	41.1	.094	.1470	NS
Caltha leptosepala DC.	fls							14 745	inc early	14.8	.749 (1) .706 (2)	.0349	.001
Delphinium barbeyi Huth	fls	4 755	entire	53.5	.198	.0615	.01	8 874	entire	50.9	.396	.0450	.001
D. nelsonii Greene	fls	607	entire	18.9	−.152	.1722	NS						
Ranunculus alismaefolius Geyer	fls							69 025	entire	22.7	.317	.0161	.001
R. cardiophyllus Hooker	fls	1 005	inc early	7.6	1.272 (1) .820 (1)	.1338	.001	344	entire	20.8	1.068	.2287	.001
Rosaceae													
Fragaria ovalis (Lehmann) Rydb.	fls	2 362	entire	15.2	.839	.0873	.001	1 579	entire	26.9	.950	.1068	.001
Potentilla fruticosa L.	fls	12 602	entire	42.9	.394	.0378	.001						
P. gracilis Douglas	fls	198 631	inc late	44.9	.012 (1) .068 (2)	.0095	NS .001						
Sibbaldia procumbens L.	fls							2 076	entire	18.6	.435	.0931	.001
Rubiaceae													
Galium boreale L.	infls	870	entire	48.7	.286	.1438	.05						
Saxifragaceae													
Saxifraga rhomboidea Greene	infls							340	entire	32.7	.262	.2301	NS
Scrophulariaceae													
Castilleja miniata Douglas	infls							1 754	interp	52.1	−.350 (1) −.378 (2)	.1013	.001
C. rhexifolia Rydb.	infls							639	entire	46.5	−.099	.1678	NS
C. sulphurea Rydb.	infls							12 108	interp	48.0	.317 (1) .256 (2)	.0386	.001
Penstemon whippleanus Gray	fls							331	entire	49.5	.222	.2332	NS
Umbelliferae													
Ligusticum porteri Coulter and Rose	infls							9 196	entire	49.3	.472	.0442	.001
Pseudocymopterus montanus (Gray) Coulter and Rose	infls							2 666	entire	27.6	.097	.0822	NS
Valerianaceae													
Valeriana capitata Pallas	infls	1 141	entire	18.2	.361	.1256	.01						
V. edulis Nuttall	shoots							4 139	entire	42.1	.265	.0659	.001
Violaceae													
Viola adunca Smith	fls							627	entire	27.9	.322	.1694	NS
V. nuttallii Pursh	fls							531	entire	19.0	−.556	.1841	.01

fidence that the computed skewness does describe the true distribution.

There was a preponderance of positive skew values (Table 1). These indicate curves which rise comparatively rapidly, fall comparatively slowly. Only four out of 57 species (7%) had negative values. Both raw and modified values were significantly positive at the .05 level in 44 species. Eleven of the 53 positive skews and three of the four negative skews are insignificant.

The skewness values, or the curves they describe, must actually be species properties before they can legitimately be viewed as potentially adaptive "utilization curves." They should, therefore, be consistent even when species occur in different habitats, and a logical test is to compare the values computed at both study sites for the 10 species which occur at both. Because general site differences may have effects on skewness independent of pollination and competition

TABLE 2. Comparison of skewness at different sites.

	LOW		IB	
	Raw skewness	Modified skewness	Raw skewness	Modified skewness
Arabis drummondii	2.795	2.795	1.710	1.710
Ranunculus cardiophyllus	1.272	.820	1.068	1.068
Fragaria ovalis	.829	.839	.950	.950
Androsace septentrionalis	.748	.692	.728	.728
Erigeron speciosus	.638	.651	.440	.440
Linum lewisii	.432	.432	.914	.914
Draba nemorosa	.411	.411	.205	.205
Helianthella quinquenervis	.311	.311	.397	.397
Delphinium barbeyi	.198	.198	.396	.396
Aquilegia caerulea	.135	.135	.094	.094

TABLE 4. Skewness and time of bloom in yellow composites. Day 1 = 29 May 1977.

	Mean date of flowering	Skewness	Modified skewness
Taraxacum officinale	23.9	.893	.893
Senecio crassulus	47.2	.407	.407
Helianthella quinquenervis	52.3	.397	.397
Helenium hoopesii	53.6	.703	.578
Solidago multiradiata	59.6*	.481	.481
Agoseris glauca	67.0	.425	.425
Arnica mollis	68.3	.468	.415
Chrysopsis villosa	71.6	.207	.287
Viguiera multiflora	77.4*	.022	.141

* These species did not occur in the permanent sample grid at IB. To allow comparison with the others, with which they do interact, the LOW census data have been used to calculate skewness. The dates of mean flowering have been increased by 2 d to compensate for the later season at IB.

(above), direct comparison is difficult, but the similarity of the various species' relative skewness was compared, using a rank-order correlation (Table 2). The most skewed species at one site also tended to be the most skewed at the other site ($P < .01$ for the combination of raw and modified values giving the worst correlation; Sokal and Rohlf 1969).

Testing predictions

At the two sites, four pairs of species (Pairs 1–4, Table 3) met the following criteria: they were structurally similar; they co-ocurred spatially within 30 m of each other, or less; they shared the same major pollinators; pollinators passed between them at substantial rates, without great hesitation; and their periods of bloom overlapped substantially (>.25 using Schoener's [1970] overlap measure; Thomson 1978*a*). In each pair the earlier species had a greater tendency toward positive skew, supporting the first prediction based on the competition model.

Two other pairs of congeners (*Delphinium* and *Mertensia,* Table 3, pairs 5 and 6) might be expected to show the same pattern; however, temporal overlaps are small. Each pair's earlier member is visited by bumblebee queens, the later by workers. Thus both later species are still novel to most of their visitors and do not show reduced skewness.

A multispecies group suitable for testing the second prediction is the somewhat heterogeneous collection of yellow composites (Table 4) which are bound together by their common attractiveness to short-tongued *Bombus* (e.g., *B. sylvicola, B. frigidus, B. bifarius,* and *B. occidentalis*), and by the willingness of such bees to pass between the various species with

TABLE 3. Skewness and bloom time in plants with suggested model-mimic relationships. For bloom date, day 1 = 29 May 1977.

Pair number	Site	Major visitors	Temporal overlap	Species in pair	Mean date of bloom	Raw skewness	Modified skewness
1	IB	Solitary bees, flies	.5679	*Caltha leptosepala* *Ranunculus alismaefolius*	14.8 20.8	.728 .317	.706 .317
2	IB	Flies	.2543	*Thlaspi alpestre* *Draba spectabilis*	19.9 29.8	.845 .355	.845 .355
3	LOW	Solitary bees, flies	.8338	*Potentilla fruticosa* *Potentilla gracilis*	42.9 44.9	.394 .012	.394 .068
4	IB	Hummingbirds	.5649	*Castilleja rhexifolia* *Castilleja miniata*	46.5 52.1	−.099 −.350	−.099 −.350
5	LOW	Hummingbirds, long-tongued bumblebees	.0000	*Delphinium nelsonii* *Delphinium barbeyi*	18.9 53.3	−.152 .198	−.152 .198
6	IB	Medium-tongued bumblebees	.0277	*Mertensia fusiformis* *Mertensia ciliata*	15.1 42.3	.433 .488	.433 .488

substantial inconstancy (Thomson 1978*a*). All of these species occur at or within a few hundred metres of the IB sampling grid, but three species, *Solidago multiradiata, Taraxacum officinale,* and *Viguiera multiflora,* were rare or absent in the permanent quadrats. For these species, I used the skew data from LOW and adjusted the mean time of flowering by an increment to correct for the later season at the higher site IB. A rank correlation analysis of the modified data, which happens to be unaffected by the corrected bloom times, of degree of positive skewness with earliness of flowering gives Kendall's $\tau = .556$, and a significance level of .05 (Sokal and Rohlf 1969). The raw data and the "worst combination" both give $\tau = .500$, $P > .05$. If normality can be assumed, a Pearson correlation gives a significant positive relation ($r = .822$, $P = .006$).

DISCUSSION

Competition and skewness

The competitive hypothesis, that skewness should be less in species whose flowers are of a type already familiar and attractive to pollinators, receives additional support from the above correlation, weak though it is. Certainly, "everything else" is not equal in these species; in addition to the possible spatial effects on skewness mentioned earlier, species characteristics such as greater flower attractiveness may lessen the need for a quick rise in abundance. Also, the structural organization of the plants may impel certain patterns of skewness, for example, a plant which begins blooming with single terminal flowers and continues with paired axillary flowers. Finally, the yellow composites form only a loose assemblage. Bumblebees are their most important pollinators, but *Helenium hoopesii,* for instance, is visited more heavily by moths than the others in this group; in *Arnica mollis,* large flies are relatively important. Adaptations to these minor visitors, if they exist, will appear as noise in the correlation. With all these caveats, it is somewhat suprising that any correlation exists. That it does suggests rather strong selection at work and permits retention of the hypothesis that skewness may be adaptive in ensuring pollination in a competitive milieu.

Evolution of flowering curve shape

To shorten the preceding discussion of population flowering curve shapes, I have adopted a manner which suggests the population itself as the unit of selection. Coming into bloom abruptly will almost always benefit the population, but not necessarily individuals. The extent to which skewed curves can be "explained" by individual selection depends on several unstudied relationships. First of these is the interplay of the hierarchial levels of flowering phenology: curve width, location, and shape, not just for populations, but for florets, heads, ramets, and genets. Second is the relation of visitation rate to seed set and eventually to fitness under field conditions, including the potentially harmful effects of foreign pollen deposited on stigmas during periods of overlap (cf. Waser 1978*b*). Third is the relation of visitation and flower number, under competitive conditions, which is likely to be more complicated than the simple sigmoid function modeled here (cf. Thomson 1978*b*).

This much remains, however: the data support the predictions of the competition model regarding the relation between a plant's position in a mimetic group and the degree of skewness of its flowering curve. Thus it appears that at least a component of skewness may be sensitive to community composition, regardless of the possible action of "external factors." Further studies must devote more energy to the study of individual plants, and elaborate the visitation rate/fitness relationship by including measures of seed set, seed survival, and seedling success. This information is required to understand the extent to which pollination-related selection pressures contribute to the shapes of flowering curves.

ACKNOWLEDGMENTS

The study would not have been completed without the assistance of Barbara Thomson, who did more than half the extremely tedious censuses. She also assisted in data transcription and analysis, manuscript preparation and editing, and checked my algebra as well. The ideas presented here have benefited from conversations with Susan Anderson, Edward Beals, James Brown, David Clark, Deborah Clark, Tag Demment, Stanley Dodson, Peter Feinsinger, David Inouye, Peter Kevan, Timothy Moermond, Christopher Plowright, Mary Price, Graham Pyke, Leslie Real, Kurt Rusterholz, Mark Stromberg, Nick Waser, Mary Willson, and Fred Wiman. Two anonymous reviewers provided thorough critiques, and the paper incorporates many of their suggestions.

The fieldwork was supported by Sigma Xi, the Marsh-Henry Fund of the National Academy of Sciences, the University of Wisconsin Zoology Department Davis Fund, Philip and Elizabeth Fowler, and Paul Wroblewski. A field vehicle was provided by Philip and Margaret Hess. While preparing the manuscript, I was supported by a University of Wisconsin Zoology Department fellowship; the Graduate School provided computer time, as did Warren Porter. Final manuscript revision was supported by a Canadian National Research Council grant to R. C. Plowright of the Department of Zoology, University of Toronto.

LITERATURE CITED

Barrell, J. 1969. Flora of the Gunnison Basin. Natural Land Institute, Rockford, Illinois, USA.

Bobisud, L. B., and R. J. Neuhaus. 1975. Pollinator constancy and the survival of rare species. Oecologia **21**:263–272.

Grant, K. A. 1966. A hypothesis concerning the prevalence of red coloration in California hummingbird flowers. American Naturalist **100**:85–97.

Heinrich, B. 1975. Bee flowers: a hypothesis on flower variety and blooming times. Evolution **29**:325–334.

Langenheim, J. H. 1962. Vegetation and environmental patterns in the Crested Butte area, Gunnison County, Colorado. Ecological Monographs **32**:249–285.

Levin, D. A., and W. W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. American Naturalist **104**:455–467.

Macior, L. W. 1971. Coevolution of plants and animals—systematic insights from plant-insect interactions. Taxon **20**:17–28.

Mosquin, T. 1970. The reproductive biology of *Calypso bulbosa* (Orchidaceae). Canadian Field Naturalist **84**:291–296.

Pleasants, J. M. 1977. Competition in plant pollinator systems: an analysis of meadow communities in the Colorado Rocky Mountains. Dissertation. University of California, Los Angeles, California, USA.

Roughgarden, J. 1974. Species packing and the competition function with illustration from coral reef fish. Theoretical Population Biology **5**:163–186.

Schoener, T. W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats. Ecology **51**:408–418.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California, USA.

Straw, R. M. 1972. A Markov model for pollinator constancy and competition. American Naturalist **106**:597–620.

Thien, L. B., and B. Marcks. 1972. The floral biology of *Arethusa bulbosa, Calopogon tuberosus,* and *Pogonia ophioglossoides* (Orchidaceae). Canadian Journal of Botany **50**:2319–2325.

Thomson, J. D. 1975. Some community-level aspects of a bog pollination system. Thesis. University of Wisconsin, Madison, Wisconsin, USA.

———. 1978*a*. Competition and cooperation in plant-pollinator systems. Dissertation. University of Wisconsin, Madison, Wisconsin, USA.

———. 1978*b*. Effects of stand competition on insect visitation in two-species mixtures of *Hieracium*. American Midland Naturalist **100**:431–440.

Waser, N. M. 1977. Competition for pollination and the evolution of flowering time. Dissertation. University of Arizona, Tucson, Arizona, USA.

———. 1978*a*. Interspecific pollen transfer and competition between co-occurring plant species. Oecologia **36**:223–236.

———. 1978*b*. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. Ecology **59**:934–944.

Wilson, D. S. 1975. The adequacy of body size as a niche difference. American Naturalist **109**:769–784.