Effects of Stand Composition on Insect Visitation in Two-species Mixtures of Hieracium

JAMES D. THOMSON

▼

Reprinted from

THE AMERICAN MIDLAND NATURALIST

Vol. 100, No. 2, October, 1978, pp. 431-440

University of Notre Dame Press

Notre Dame, Indiana

Effects of Stand Composition on Insect Visitation in Two-species Mixtures of Hieracium

JAMES D. THOMSON

Department of Zoology, University of Wisconsin, Madison 53706

ABSTRACT: I investigated the effects of host plant distribution on the host plant choice of flower-visiting insects in mixed stands of the hawkweeds *Hieracium aurantiacum* L. and *H. florentinum* All. The way in which pollinators divide their visits among simultaneously blooming plant species determines the outcome of plant competition for pollinators, which may affect community structure. Although the hawkweeds are apomictic, these stands are simple communities that embody many of the assumptions of published models concerning the effects of stand composition on insect foraging. Existing theory suggests that visitation on one of two competing species should increase with its proportion in the stand. Visitation on *H. aurantiacum* follows this relationship, but *H. florentinum* receives more visits with *H. aurantiacum* present than when it blooms alone. Extension of this result to other, non-apomictic species implies that a species may occasionally be benefitted by the presence of an apparent competitor. I propose a tentative explanation based on pollinator inconstancy and foraging habitat selection, and suggest some possible effects of these phenomena on community structure.

INTRODUCTION

In recent years, several papers have appeared in a rather new field, community-level pollination ecology. Their authors have in general followed Cody's (1974) dictum that "the goal of ecology is to provide explanations that account for the occurrence of natural patterns as products of natural selection," and have in the process begun to assemble a body of theory. In particular, the idea that plants often compete for the services of pollinators has been invoked to explain both morphological and phenological attributes of plants by several authors (*e.g.*, Hocking, 1968; Mosquin, 1971; Gentry, 1974; Thomson, 1975; Heinrich, 1974; and Moldenke, 1975), and formalized in the general models of Levin and Anderson (1970) and Straw (1972). This competition theory, as it now exists, depends on the assumption that the number of pollinations received by a species increases with its relative abundance (termed "frequency" in the above models). This basic contention has not been properly demonstrated in the field due to difficult sampling problems. By estimating pollinator activity in carefully chosen, simple plant communities, however, I have obtained some data relevant to this question.

STUDY SITES AND GENERAL METHODS

The Levin-Anderson and Straw models make the simplifying assumption that the system comprises only two competing plant species, which are biologically similar. Few natural situations approach this condition; however, in Vilas Co., Wisconsin, I found numerous roadside or other disturbed areas which supported large stands of two hawkweed species, the orange-flowered *Hieracium aurantiacum* L. and the yellow-flowered *H. florentinum* All. I worked on these stands during 1973-1976. In late June and early July it is easy to find patches in which 99% or more of the open entomophilous flowers (or heads) belong to these species. Furthermore, these stands range from nearly pure orange, through mixtures of the two in various proportions, to nearly pure yellow.

Although both species are apomictic, they attract a considerable number and variety of "pollinating" insects. The same insect species visit both plants, and although the plants are not dependent on the insects, the dependence of the insects on the plants renders the system almost ideal for investigating the effects of plant community composition on the behavior of pollinators. My primary interest is not in whether an apomict gets "pollinated," but in the distribution patterns of flower visitors and the way these patterns would affect plant success in instances where competition for pollinators is important.

Describing these patterns entails estimating the amount of foraging each species receives in different patches of known composition. Since it is necessary to obtain all data within a short time to reduce the effects of changing conditions, and since numerous patches must be sampled, a rapid field method is imperative. Simply watching clumps of flowers is far too slow, and although indirect methods using dyes or fluorescent powders (Thomson, 1975) may reduce field time, they are tedious to use on a large scale and give no indication of the insects involved. Conventional sweep samples estimate relative abundances of insects, but these cannot yield the number of visitors per flower or visitation intensity—which is really the desired information—or even the absolute abundance of insects, which could be converted to visitation intensity. I tried estimating visitation intensity directly by attaching a knife-edged steel rim to a heavy-duty sweep net with a somewhat shortened bag. A sweep through a hawkweed patch with such a net severs the fragile scapes, and with practice I could get both flowers and their insect visitors into the net.

When sampling two-species populations, I made separate collections of yellow and orange flower heads. Although the two species intermingle rather freely, there is enough small-scale patchiness so that careful sweeping can achieve quite pure samples. I discarded any samples which contained more than 3% incorrect flowers. I usually walked three or four transects across the flower patch, did not sample near the edges, and tried to avoid resampling areas which I had disturbed. As the net filled, I emptied its contents into a plastic bag containing a paper towel soaked in ethyl acetate. In the laboratory I determined the total fresh weight of the sample, then weighed a subsample and counted the number of open flower heads in it. I could then compute the estimated total number of open flower heads. I hand-sorted flower-visiting insects from the flowers and debris.

To estimate flower head density I used a wire hoop to delimit 0.3 m^2 circular quadrats. I placed the quadrats at five-step intervals along several transects chosen so as to sample the stand fairly evenly, and counted the open flower heads within the hoop.

The radically different foraging rates of different insects demand that adjustments be made before comparing different collections. To establish standards for comparison, I first followed foraging insects from flower to flower, timing their moves with a stopwatch. The resulting estimates of foraging rate, expressed as the number of flowers visited per unit time, are shown in Table 1 for 11 convenient groups which I could distinguish in the field. *Bombus* queens were the fastest movers, so I expressed other insect's rates in terms of these queens, in *Bombus* Queen Equivalents (BQE). Thus an insect which visited half as many flowers per minute as a queen would be ranked as 0.5 BQE. Of course, this correction is partial; although compensating for differences in the number of flowers visited, it does not reflect differences in the amount of pollen carried to stigmatic surfaces. This would vary with the surface area of the insect, its hairiness, *etc.*, and its behavior on the flower. It would be impractical to try to correct for all of these factors, especially since certain important data (*e.g.*, whether a bee was foraging for pollen or nectar at the time of capture) are impossible to get. The values I used, then, tend to overestimate the effectiveness of small, smooth and indolent pollinators, but this bias should not affect the results greatly as these insects are rather unimportant no matter how the data are treated. The larger bees, especially *Bombus* spp., are certainly the most active visitors in these stands.

TABLE 1.—Foraging rates of various insects in a hawkweed stand. n = the number of flower head to flower head moves recorded. The taxonomic categories include some very broad lumping, *e.g.*, "Large Andrenids" includes some megachilids, etc.

	fls/sec	BQE	n
Bombus spp. queens	0.332	1.0	642
Bombus spp. workers	0.236	0.71	180
"Large Andrenids"	0.153	0.46	181
"Medium Andrenids"	0.126	0.38	263
"Small Halictids"	0.080	0.24	56
Large syrphids	0.021	0.064	28
Medium syrphids	0.0017	0.005	15
Small syrphids	0.0010	0.003	14
Hemaris spp.	0.116	0.35	5
Papilio glaucus L.	0.173	0.52	160
Skippers	0.129	0.39	57

I calculated the visitation intensity on a plant species by summing the BQE values for all the insects in the sweep sample and dividing by the estimated number of heads in the sample. I took this to be a practical estimate of the success of the species in attracting visitation.

MEASURES OF VISITATION INTENSITY

I wished to compare the visitation rates of stands with different proportions of orange and yellow. All such "natural experiments" depend on an "everything else being equal" proviso which is never quite fulfilled. In this case, there was stand-to-stand variation in such matters as stand size and flower density. Preliminary sampling did not turn up any dramatic changes in visitation with rather large changes in patch size or density. Although there were marked changes with time of day, visitation changed little from late morning (0930) to early afternoon (1430) on sunny days.

I chose six sites for intensive sampling during the summer of 1975. All were on roadsides along U.S. Hwy. 51 and county highways M and N, were between 1000 and 4200 m^2 in area, had total mean densities from 77.8 to 118.5 heads/m^2, and were located close enough so that I could sample them all well within the 5 midday hr I had chosen as acceptable. One site was "pure" yellow, one "pure" orange, and the others mixtures of various proportions (Fig. 1). I determined visitation intensity for each species at each site on 3 clear, hot days, having censused open heads at each site the day before. Visitation intensities on each species as functions of its frequency in the stand are displayed graphically in Figure 1.

RESULTS AND DISCUSSION-1

It is an intuitively comfortable notion that a plant species should receive more attention from pollinators when it is common than when it is rare. This idea is developed at some length by Levin and Anderson (1970); Straw's (1972) reworking of the same model agrees in substance, and the results of early field studies (*e.g.*, Betts, 1920; Brittain and Newton, 1933) are at least consistent with this hypothesis. Visitation intensity on the orange hawkweed species shows the expected positive relationship with that species' relative frequency in mixed stands; however, the yellow species receives *fewer* visits per flower when it most dominates the stand (Fig. 1). This is true even though the "pure yellow" stand had the highest mean density (118.5 fls/m^2) and was the second largest (3900 m^2) of all stands. In my preliminary studies over 3 summers, yellow stands always had low visitation intensities; the stand described in this study is not a unique aberrant.

If these species were not apomicts, and if pollinators were in short supply, the yellow species would be in the paradoxical position of doing better when a competitor is present. It may be argued, of course, that "competitor" is the wrong word in this situation, but the orange species does draw insects away from the yellow in orange-dominated stands, and so is at least a potential or part-time competitor. This effect, a product of insect behavior, does not depend on any features peculiar to apomictic plants; thus one would expect that outcrossing plants may show similar patterns of visitation under similar circumstances. Examples of this sort are at odds with the Levin-Anderson and Straw models, which tacitly assume that total visitation in a stand remains constant regardless of stand composition. Figure 2 shows that this is not the case.

Both of the mathematical models are couched in terms of "constancy," "the tendency of individual pollinators to forage within a single species in the presence of other suitable species" (Levin and Anderson, 1970); both then go on to specify probabilistic definitions of constancy whose correspondence to the more general verbal definition is uncertain (Thomson, 1975). In my experiments I sidestepped the problem of constancy to examine the overall pattern of visitation instead. Nevertheless, since insect behavior, including constancy, certainly determines the patterns I have described, and since I have a few applicable data, some discussion of the reasons for those patterns is in order.

Observations on constancy.—In 1974, I followed individual insects in a stand with nearly equal proportions of orange and yellow flowers, recording their flower choices. Of a total of 4460 recorded flower-to-flower transitions, 143 (3.2%) were heterospecific, 68 of these being from yellow to orange, 75 from orange to yellow (Thomson, 1975). The approximately equal numbers of the two types of transfers would be expected if the process were at equilibrium (in Straw's sense). From my observations, however, it seems certain that constancy—at the level of the whole pollinator fauna—is more complicated than the simple representations of the models. There are great differences in constancy between species and great individual differ-

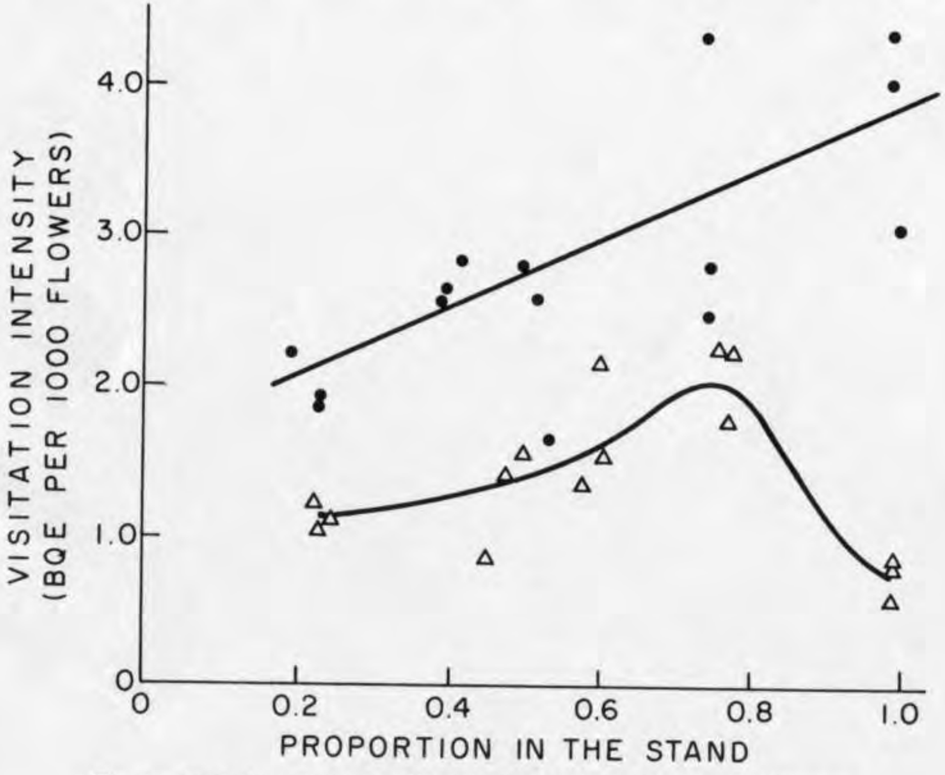

Fig. 1.—Visitation intensity on *Hieracium aurantiacum* (●) and *Hieracium florentinum* (△) as functions of their proportions in mixed stands

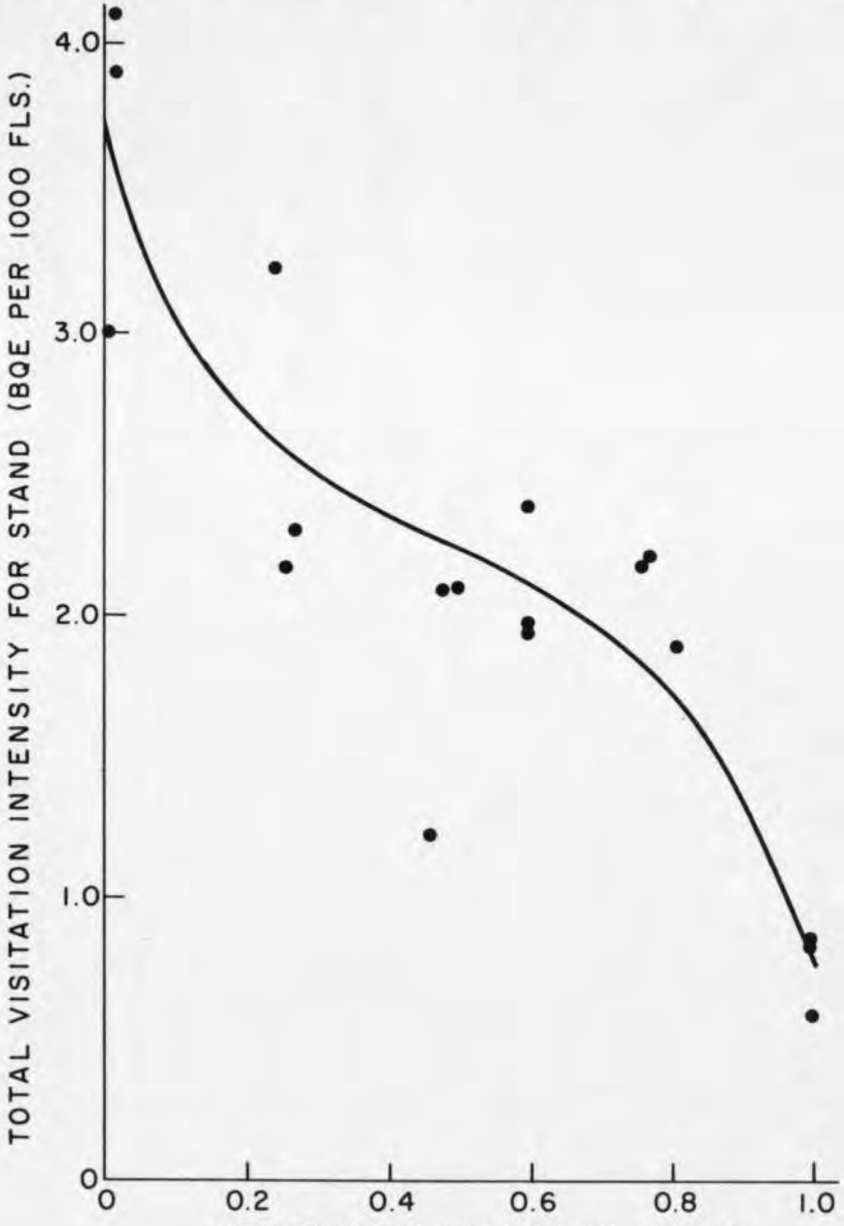

Fig. 2.—Total visitation intensity as a function of stand composition

ences within a species. One *Bombus terricola* queen, for example, visited 114 orange flowers in a row, while another changed species 18 times in 183 flowers. In a few cases, insects appeared to "change their minds," foraging with constancy on one species, then switching and foraging with equal constancy on another. Heinrich (1976) discusses at length the factors promoting such switches.

Knowledge of the intrastand behavior of flower-visiting insects need not depend solely on observations of their movements; analysis of a bee's corbicular load can reconstruct a foraging bout. ***Hieracium aurantiacum*** pollen is yellow-orange while ***H. florentinum*** pollen is yellow. In July 1976 I collected ***Bombus*** spp. workers in a mixed stand (orange = 28.3%, yellow = 71.7%) and compared their loads to reference loads taken in pure stands of each type. Several loads, although homogeneous, appeared intermediate in color between the two extremes; in these cases I presumed that the bee had foraged inconstantly, and termed these loads "mixed." A few bees' pollen pellets were "segregated," following Betts' (1920) terminology; in these, distinct zones of orange and yellow indicated a switch in host plant choice. Table 2 summarizes these results.

Results and Discussion-2

Although ultimately a result of foraging energetics (Heinrich and Oster, 1976), such switches from one species to another are presumed to be facilitated by morphological similarity of the flowers involved. Mosquin (1971), Straw (1972), Gentry (1974) and Heinrich (1974) have all suggested that rare or unattractive flowers may benefit by convergence toward more attractive species, or that rare species converging towards each other can attract more visitors. Bobisud and Neuhaus (1975) and Thomson (1975) used modifications of Straw's model to demonstrate conditions under which convergence is a favored strategy. For such a strategy, pollinators must be neither totally constant nor totally random in their choices but must display a facultative constancy, *i.e.*, show a willingness to change species but retain enough residual fidelity that switches are more likely to be to similar species. I have some evidence that bumblebees do this in semiartificial choice experiments (Thomson, 1975).

Inconstancy and switching partially explain the observed pattern of pollinator distribution. Although the orange species is preferred, the behavior of the bumblebees in particular is such that crossovers could result in a substantial amount of visitation for the yellow in mixed stands, especially if the rewards offered by the orange flowers had been depleted by heavy visitation. The morphological similarity of the flowers may further predispose the insects to visit the yellow species even in stands dominated by orange, but inconstancy of foraging cannot explain the overall distribution curve of visitors (Fig. 2). This curve suggests the hypothesis that foragers are strongly influenced in their choice of foraging sites by the presence of the orange species. A pure yellow stand is much less attractive than a stand with a fraction of orange flowers; once lured to the stand by the orange species, however, the bees forage inconstantly and pay many visits to the abundant yellow species.

Table 2.—Analysis of corbicular loads

	"pure" yellow	mixed	segregated	"pure" orange	other
bees collected from yellow	10 (37%)	6 (22.2%)	3 (11.1%)	7 (25.9%)	1 (3.7%)*
bees collected from orange	2 (10.5%)	1 (5.3%)	0	16 (84.2%)	0

*This insect carried an unknown brown pollen

A visitation model.—To see if the above explanation is adequate, I constructed a simple mathematical model embodying its basic assumptions. I used Straw's Markovian formulation to describe the distribution of visits within a stand, but added a correction factor to account for the differences in attractiveness from stand to stand.

With the assumption that constancy varies directly with frequency—which is certainly oversimplified but cannot be improved upon with the data at hand—Straw's model approximates the proportion of visits on one species A (for a large number of visits) as

$$r_A = \frac{p^2}{1\text{-}2pq}, \qquad \text{(Equation 1)}$$

where p = the frequency of A, q = the frequency of B.

To get a factor for stand attractiveness, I simply assumed that bees would respond to the relative frequencies of the flowers, weighted to show the different attractiveness of each one. Total pollination (in BQE) on species A in a stand would then be

$$T_A = \frac{p^2}{1\text{-}2pq} (K_A p + K_B q), \qquad \text{(Equation 2)}$$

where K_A and K_B are the weighting factors (in BQE) for species A and B. The K values for each species can be determined by the attractiveness of a pure stand of that species. Estimating these values from my data, using the simple mean of the three visitation measurements for each pure stand, I computed the orange K value $K_O = 3.75$ BQE and the yellow value $K_Y = 0.75$ BQE.

Plotting Equation 2 for each species using these values gives the curves shown in Figure 3. That these curves have some similarity to those derived from actual data (Fig. 1) suggests that the hypothesis may have some explanatory value. The major deviation of the model from the data, *i.e.*, the depressed lefthand portions of both curves, is probably due to the inadequacy of the assumption that constancy varies with frequency. This assumption does not mirror reality in that some bees remain inconstant even on species that nearly dominate the stand. Of course, the few visits that are received by rare species may be rather ineffective, since the straying bee may carry little or no proper pollen.

Of course, the stand attractiveness factor $(K_A p + K_B q)$ is also oversimplified; it would predict that a plot of total stand visitation vs. the proportion yellow in the stand should be a straight line of negative slope. In fact (Fig. 2), the data show a more complex curve for this relationship. The tripartite nature of this curve—with its relatively horizontal midsection—suggests that the main visitors may distinguish three types of stands: orange, yellow and mixed. Otherwise, it is hard to explain why a 25% orange stand is almost as attractive as one with 75% orange, and both are less attractive than pure orange.

The analysis of corbicular loads (Table 2) tends to reinforce this inferential argument. There are clear-cut differences in the loads carried by bees collected from orange and yellow flowers. Bees from yellow flowers were more likely to have a past record of infidelity than were orange foragers. In fact, 25.9% of those bees collected from yellow carried virtually pure orange loads. The three segregated loads all showed yellow succeeding orange. These data agree with the hypothesis that foragers observed on yellow in a mixed stand may have been first attracted to the stand by the orange. At this particular site, foraging was heavy on the orange—as usual—even though it was the minority species. Such crowding could help impel switches from orange to the more common but less attended yellow.

In this connection, it is interesting that, according to the model, the less attractive yellow species receives more visits when it is rare than does the orange when it is rare. The yellow is in these circumstances a beneficiary of the orange's great contribution to stand attractiveness; however, the relationship is not reciprocal. This effect does not appear in the actual data, where the great attractiveness of the orange ensures its heavier visitation even at lowered densities. However, I was unable to collect data on species of very low frequency, so there may indeed be such a depression in visitation on orange in orange-poor stands due to a drop in stand attractiveness.

It should be clear that I am only concerned with the number of visits per head and am ignoring any differences in the quality of visits, which might be important in systems where plants require true pollinating visits. Levin and Anderson (1970) and Waser (1977) suggest that heterospecific visits are ineffectual, while Straw (1972) argues that they are fully effectual. Reality probably lies between these extremes, and the value of such visits depends on the specific case. It is true that when the yellow species receives most visits (mixed stands), an unknown fraction

of those visits are heterospecific. In this case of apomictic plants, the "value" of such visits cannot be determined.

Implications and conclusions.—For those who would explain the species make-up, phenology and species morphology of pollination systems largely or wholly in terms of competitive exclusion and character displacement (*e.g.*, Levin and Anderson, 1970; Reader, 1975; Pleasants, 1977), these results present difficulties. That convergence, not divergence, may be advantageous is one problem; that a "competitor" may help other species by acting as an insect magnet is another.

Such phenomena may have effects on community structure. Among self-incompatible plants, pollinator shortages due to competition may have a bearing on fitness and the plants' ability to persist in a community. When simple competition is the main driving force, analysis is comparatively simple, but if such species are functionally interdependent in the manner of the hawkweed example, the problem is quite complex. Certainly one might see a force for maintaining community diversity, given certain frequencies of plants. For instance, a species analogous to the yellow hawkweed might be prevented from dominating a community because of its declining pollination success as its proportions increased. On the other hand, such a species might be hard to eliminate from a community through lack of pollination because of its unexpectedly high visitation rates when rare. At any rate, enough pollination may take place so that the question of persistence shifts to matters of vegetative competition, etc. Bobisud and Neuhaus (1975) theoretically confirm that pollinator inconstancy on favored species may allow longer coexistence of minority species than would otherwise be possible.

Proper understanding of any particular interaction must depend on detailed field studies, not only because of the frequency-dependent nature of neighbor-mediated effects but also because every community will have a different set of neighbors. For instance, the orange *Hieracium aurantiacum,* which bumblebees visited avidly in my Wisconsin experiments, is reportedly "not visited by large bees" near Farmington, Maine, probably because of more rewarding neighbors (Heinrich and Raven, 1972). Despite the unique character of any particular case, however, the results of such investigations can be expected to turn up some principles which bear on general theories of community organization, such as the "magnet species" phenomenon noted here. This phenomenon may operate only in hawkweeds and nowhere else, but there is no reason to suppose this; it may be widespread. Furthermore, the general mechanism of neighbor-influenced interactions is not dependent on morphological similarity of flowers, nor is it restricted to pollination. Some parallel possibilities to be investigated would include the effects of magnet species on the distribution on predators and seed dispersal agents, and the local repercussions in the magnet species' communities. Atsatt and O'Dowd (1976) describe numerous analogous examples from plant-herbivore interactions; palatable plants may be protected directly by noxious neighbors which repel or confuse herbivores, or by neighbors which attract predators or parasites of the herbivores.

Such systems are inherently interesting because their interactive nature results in a closely connected coevolution of the species involved. The system adaptations of those species are likely to be precise, perhaps even striking, and therefore comparatively easy to explain. To the community ecologist, however, there are other stimulating features. A pollination or dispersal or herbivory system has a certain heuristic value for community analysis in that it is a partially independent subcommunity which has been shaped by the same forces which shape whole communities, but is more practical to study.

In this light, pollination systems are particularly provocative because they are uniquely susceptible to quantitative analysis of "success," and because of the involvement of *competition*—either real or apparent, depending on the local species bal-

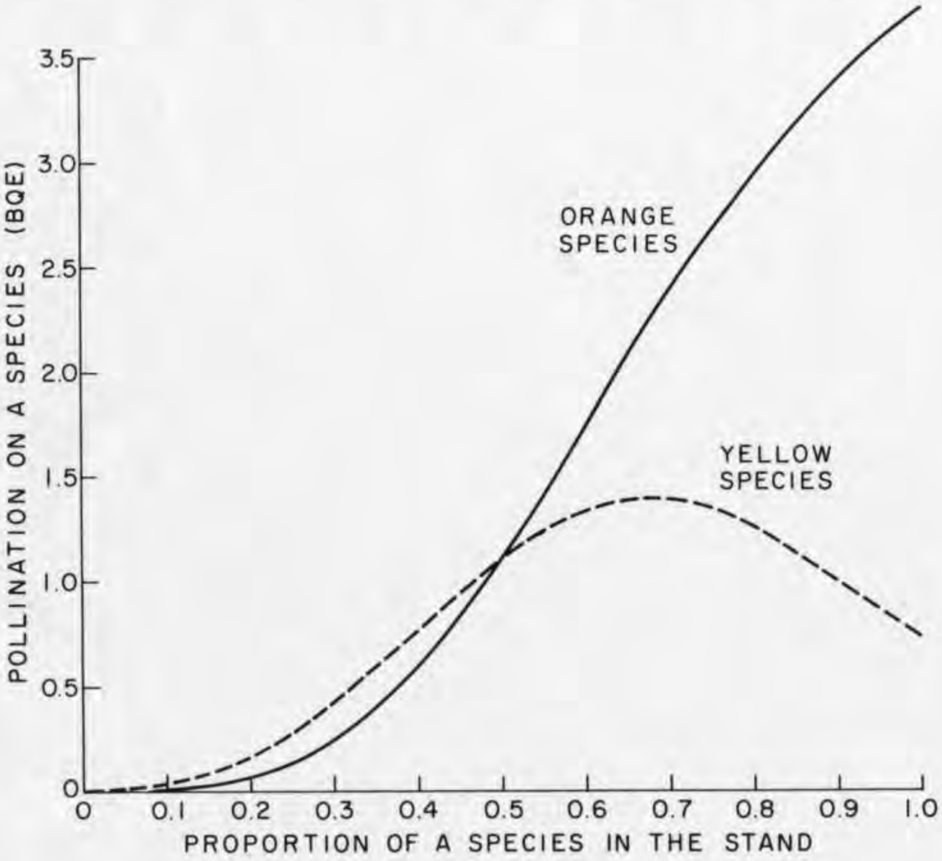

Fig. 3.—Predictions of a model (*see* text) incorporating a factor which permits variable stand attractiveness

ance—for a factor whose distribution is neighbor-influenced.

Acknowledgments.—I am grateful to E. W. Beals, M. J. DeJong, J. S. Denslow, T. C. Moermond and anonymous reviewers for comments on the paper, and to B. A. Thomson for field and clerical assistance.

Parts of the research were supported by a Wisconsin Alumni Research Foundation fellowship and funds from the University of Wisconsin Zoology Department Davis Fund.

LITERATURE CITED

ATSATT, P. R. AND D. J. O'DOWD. 1976. Plant defense guilds. *Science,* **193**:24-29.

BETTS, A. D. 1920. The constancy of the pollen-collecting bee. *Bee World,* **2**:10-11.

BOBISUD, L. B. AND R. J. NEUHAUS. 1975. Pollinator constancy and survival of rare species. *Oecologia,* **21**:263-272.

BRITTAIN, W. H. AND D. E. NEWTON. 1933. A study in the relative constancy of hive bees and wild bees in pollen gathering. *Can. J. Res.,* **9**:334-349.

CODY, M. L. 1974. Competition and the structure of bird communities. Princeton Univ. Press, Princeton, N.J. 318 p.

GENTRY, A. H. 1974. Coevolutionary patterns in Central American Bignoniaceae. *Ann. Mo. Bot. Gard.,* **61**:728-759.

HEINRICH, B. 1974. Bee flowers: a hypothesis on flower variety and blooming times. *Evolution,* **29**:325-334.

———. 1976. The foraging specializations of individual bumblebees. *Ecol. Monogr.,* **46**:105-128.

———. AND P. R. RAVEN. 1972. Energetics and pollination ecology. *Science,* **176**:597-602.

HOCKING, B. 1968. Insect-flower associations in the high Arctic with special reference to nectar. *Oikos,* **19**:359-388.

LEVIN, D. A. AND W. W. ANDERSON. 1970. Competition for pollinators between simultaneously flowering species. *Am. Nat.,* **104**:455-467.

MOSQUIN, T. 1971. Competition between pollinators as a stimulus for the evolution of flowering time. *Oikos,* **22**:398-402.

MOLDENKE, A. R. 1975. Niche specialization and species diversity along a California transect. *Oecologia,* **21**:219-242.

PLEASANTS, J. M. 1977. Competition in plant pollinator systems: an analysis of meadow communities in the Colorado Rocky Mountains. Ph.D. Dissertation, University of California-Los Angeles. 233 p.

READER, R. J. 1975. Competitive relationships of some bog ericads for major insect pollinators. *Can. J. Bot.,* **53**:1300-1305.

STRAW, R. 1972. A Markov model for pollinator constancy and competition. *Am. Nat.,* **106**:597-620.

THOMSON, J. D. 1975. Some community-level aspects of a bog pollination system. Master's Thesis, University of Wisconsin, Madison. 178 p.

WASER, N. M. 1977. Competition for pollination and the evolution of flowering time. Ph.D. Dissertation, University of Arizona, Tucson. 112 p.

SUBMITTED 23 MAY 1977 ACCEPTED 5 JANUARY 1978