HANDBOOK OF EXPERIMENTAL POLLINATION BIOLOGY

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COMPONENT ANALYSIS OF COMMUNITY-LEVEL INTERACTIONS IN POLLINATIO SYSTEMS

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ABSTRACT

In studies of communities, one almost always asks broad questions and is usually compelled to pursue these questions rather superficially. I suggest that dissecting pollination systems into components whose interactions can be modeled is the best insurance against making errors of interpretation in studies at this level. I give examples of some characteristics that make pollination systems resistant to coarse analysis, and try to demonstrate that component analysis does more than simply to provide insight into the mechanisms of community-level interactions; when pursued as a systematic research program, it reduces the probability of misinterpretation.

KEY WORDS: Community, competition, component analysis, pollen carryover, bees, foraging, constancy, inflorescence architecture, nectar, mimicry, time lag, scale, presentation.

CONTENTS

FOREWORD

This chapter was originally to be coauthored by Dr. R. C. Plowright of the Department of Zoology, University of Toronto. Much of the original work described was done by him and his students, and the editorial viewpoint he is intended to represent his views as wel mine. Unfortunately, at the last minute he unable to participate in the preparation of chapter, and I have hastily compiled it from rough outlines that we had prepared jointly. Therefore, while Dr. Plowright deserves much of the credit for its contents, he cannot be held responsible for any misrepresentations or faults of exposition, which remain my responsibility.

INTRODUCTION

At least since the work of Robertson (1895), pollination ecologists have been interested in community-level interactions, i.e., ecological and evolutionary connections among species that extend beyond the direct relationship of a plant and its pollinator. Especially within the last decade, pollination community ecology has gained momentum as pollination ecologists have worked their way up from specific to general questions, and as community ecologists have adopted pollination systems as highly quantifiable arenas for study. The recognition that few plants and few pollinators are obligate specialists with regard to pollination compels the conclusion that "pollination webs," like food webs, will often be complex and cross-connected. The success of a particular species is likely to depend in part on its position in this matrix. In this chapter I wish to outline a framework for investigating such phenomena, and to flesh out the framework with a heterogeneous collection of small, but exemplary, case studies. I am concerned only with animal pollination, and my examples will reveal a bias toward bumblebees.

One can identify two extreme strategies for community studies, the "top-down" and "bottom-up" approaches. To illustrate the contrast, consider the case of competition between two plant species for pollinator services, reviewed by Waser (this book). At the broadest, "top-down" level, one may either compute simple measures, such as blooming-time overlaps, which may have something to do with competition, or conduct a large-scale experiment involving removals or additions of the potential competitors, as Waser (1978a) did. Although the experiment is likely to yield an unambiguously interpretable result (and the measurement of overlap is likely not to), neither approach gives information on the mechanism of the interaction. Unraveling mechanisms depends on a more detailed, "bottom-up" analysis of the *components* of the interaction in the style of C. S. Holling. By specifying the behavior of small system subunits, one can proceed to model system behavior, either in a logical, verbal way or explicitly mathematically, in a systems model such as those of Levin and Anderson (1970), Waser (1978b), or Lertzman and Gass (this book).

Lertzman and Gass discuss the general philosophical rationale for constructing this sort of model, and I will therefore not pursue this point. What I wish to stress is that pollination systems contain a number of quirks that seriously impede "top-down" analysis, and that dissection of components may often be necessary, not only to see the details of how the system works, but to avoid erroneous conclusions about the general nature of the interaction under study.

MAJOR COMPONENTS OF PLANT–POLLINATOR SYSTEMS

I first will separate the variables of interest into three major groups. The first of these, and the largest, is the collection of all plant attributes that affect pollination success. I lump all these characteristics under the general heading *plant presentation* (Fig. 22-1). Some of these are apparent to pollinators, whereas others are cryptic. A partial listing of the former would include: density; spatial pattern; timing of bloom; flower morphology, color, and scent; amount, type, and timing of floral rewards; plant height; inflorescence architecture (including flowers per inflorescence and inflorescences per plant, as well as the type of inflorescence); and variation in gender. Aspects that are not apparent to the pollinators but still determine reproductive success include such things as the clonal structure, if any; the genetic neighborhood size; the type of incompatibility system, if present, and the number of incompatibility alleles or mating types; the pollen production and ovule number; the functional response of seed set to varying amounts of pollen; and the seed-maturing resources

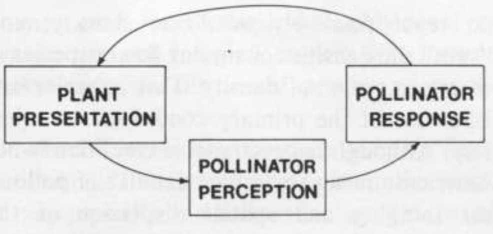

Figure 22-1. The major component categories of plant–pollinator interactions. Components within each category are detailed in the text.

available to the plant and the potential for competition among ovules within a fruit or among fruits within the plant.

A second major category is *pollinator response,* specifically meaning the ways in which pollinators respond to the apparent aspects of plant presentation. A number of these are concerns of optimal foraging theory, including: choice of species to visit and choice of place; foraging site fidelity; movement between plants (direction and distance); speed of working; flowers visited per inflorescence and per plant; degree of flower species constancy and foraging height constancy; extent of sampling of unfamiliar flowers, etc. Other aspects include: recruitment; traplining; territoriality; effectiveness at removing pollen from anthers and applying it to stigmas; and the extent of pollen carryover (treated by Lertzman and Gass elsewhere in this book).

Pollinator response will not, however, be a strict reflection of plant presentation because pollinators will seldom if ever have complete knowledge of all of the relevant characteristics of their potential food plants. Instead, response will depend on the way in which pollinators perceive the plants' presentations, and this perception may encompass a variety of distortions, including mistaken identities, time lags, nonlinearities in response to inflorescence size, and the like. Pollinators' assessments of flower density must involve some spatial scale, which might differ among pollinator species (Thomson, 1981). Structurally complex flowers require visitors to learn proper techniques for reward extraction; at least in bumblebees, some foragers never learn how to handle these flowers and therefore perceive them as nonrewarding, whereas other bees that have perfected their techniques perceive the same flowers as highly rewarding (Heinrich, 1976; Laverty, 1980).

Ultimately, the pollinators' perceptions of the plants' presentations determine their foraging behavior and therefore the reproductive success of the plants. Differential reproductive success of plants with different presentations should in turn exert selective pressures on those aspects of plant presentation that are under genetic control. Pollinator response may also affect plant presentation directly in addition to long-term evolutionary feedbacks. An obvious example is the depletion of nectar by flower visitors, which immediately alters the presentation of the plant. The relationships among these major components are shown in Fig. 22-1.

HYPOTHETICAL AND REAL EXAMPLES OF COMPONENT INTERACTIONS

Clearly, assembling a formal systems model including all the components cited above is a forbiddingly complicated task, especially when one must consider not only a single plant species and single pollinator but a whole community. However, as the chapters in this book repeatedly demonstrate, many aspects of pollination systems can be quantified relatively easily in the field, and I feel that some simple communities can be largely "solved" by long-term studies. As matters stand, no such studies exist. Below, I will discuss a selection of single-component studies from a variety of systems, with the goal of showing how important some largely unstudied, "mechanical" details may turn out to be in lending character to large-scale interactions. The reader may regard the chapter as an annotated checklist of complications. To tie these elements together, I will present them in relation to a particular question: "What is the nature of the interaction between two plant species populations that overlap substantially in time of bloom and in pollinator use?"

The phrasing of the question suggests that interspecific competition for pollination service may be expected between the two species (see

Waser, this book). But the easy equation of ecological overlap and competition has been under attack for some time (e.g., Colwell and Futuyma, 1971; Connell, 1975, 1980; and many others), and certainly cannot be considered to be universally true. With specific reference to pollination systems, several authors now have suggested that similarities in bloom time and use of pollinators may in some cases indicate mutualism rather than competition for pollination, especially when flowers appear similar. In these cases, the similarity of the flowers has been explained as convergence driven by a sort of Müllerian mimicry in which a number of species may all receive better pollination by resembling each other (see Grant, 1966; Macior, 1971; Watt et al., 1974; Brown and Kodric-Brown, 1979; Parrish and Bazzaz, 1979; Thomson, 1980, 1981; Schemske, 1981; Little, this book; Powell and Jones, this book). Thus there have been two outcomes suggested for plant–plant interactions, and they are opposite in effect: competition and mutualism. I am aware of no critical tests of a mimicry hypothesis, but we can identify certain components that are necessary for such a relationship to work. If these component interactions are not present in nature, the mimicry hypothesis is weakened. Proceeding through a series of steps, I will demonstrate the style of the argument.

A hypothesis of Müllerian mimicry first of all depends on a density-dependent or frequency-dependent advantage, such that a dense population receives disproportionately more or better pollination when it comprises a larger fraction of the local flora. Do pollinators behave this way? Such relationships have been described from real systems. Levin and Anderson (1970) review the evidence for "Arnell's dominating flower phenomenon," one expression of frequency-dependent advantage. However, this phenomenon properly describes an increase in flower *constancy* with increasing frequency. More to the specific point is a demonstration that visitation rate on certain insect-pollinated species not only is higher where their density is higher, but increases further where similar flowers of different species coexist (Thomson, 1980, 1981, 1982a). Thus, at least some pollinators, including bumblebees, do react positively to flower density, and "sum" the densities of similar flower species in their perception of density. This behavior satisfies one of the primary conditions for mimicry. Although necessary, this condition is not sufficient, owing to "minor details" of pollinator foraging and spatial dispersion of the plants. It is not certain that increased visitation causes increased fitness, especially in these circumstances, where different species are involved. If pollinators respond to mixed-species arrays of similar flowers by moving inconstantly from one plant species to another, the heterospecific transfer of pollen may actually reduce seed set by various mechanisms described by Waser (1978a,b, this book). Besides the wastage of pollen and the loss of stigmatic surface emphasized in Waser's (1978a) models, "allelopathic" pollen has been found in two genera of Compositae (*Parthenium*, Sukada and Jayachandra, 1980; *Hieracium*, Thomson et al., 1982b). These pollens inhibit successful fruiting in certain other species when applied in mixtures with conspecific pollen grains.

The degree of constancy displayed by the pollinators (an aspect of pollinator response) thus is clearly important to plant–plant interactions (Levin and Anderson, 1970; Straw, 1972; Bobisud and Neuhaus, 1975). It must be emphasized that many wild pollinators may be willing to forage inconstantly, and that the concept of pollinator constancy has perhaps been unduly influenced by the well-studied but unusually high constancy of honeybee workers (Free, 1970; Grant, 1950; Faegri and van der Pijl, 1979, p. 50). Individual bumblebees, for example, commonly visit two or more plant species on a single foraging trip. Such inconstancy may have a sampling function in tracking changes in resources (Heinrich, 1976, 1979; Oster and Heinrich, 1976); in other cases, because individual bees consistently return to the same individual plants in a mixed-species trapline (e.g., *Aralia hispida* and *Rubus* sp., Thomson, Maddison, and Plowright, unpub. ms.), the behavior seems less interpretable as sampling and probably represents simple harvesting. Indeed, in the hypothetical situation under consideration—similar flowers, intermingled to some extent—where

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in most cases the plants yield roughly equal rewards, optimal foraging models that include travel costs usually would predict an inconstant strategy.

When flower-constancy does occur in flexible animals like bumblebees or hummingbirds, it may partially or wholly reflect simple spatial aggregation of flower species ("passive constancy," Thomson, 1982a), which will be especially evident in monocultural crop plantings. If two plant species intermingle in a mosaic of monospecific patches, heterospecific visits will be comparatively rare even if visitors display no active constancy (Levin and Anderson, 1970; Waser, 1978a), especially if the visitors maintain restricted foraging areas that are small relative to the patch size of the plants involved (cf. Solbrig, 1975). However, as patch size increases, any "mimetic" advantages presumably will be dissipated because the pollinators no longer will sum the contributions of the two plant species in deciding where to forage (Thomson, 1981a).

The argument so far should suffice to show that the overall effect of pollinator sharing by plants is not easily predicted without paying careful attention to the fine structure of the interaction. A number of components are involved, and different components have opposite effects; i.e., some tend to produce mutualism and some competition. Figure 22-2 (from Thomson, 1982a) is an attempt to summarize the interplay among spatial pattern, visitation rate, and reproductive success, with the condition of decreasing constancy with increasing intermingling. No existing study has been thorough enough to determine whether any real plant–plant interaction actually fits the curves of Fig. 22-2, but experimental studies have shown that different natural systems occur in different regions of the "success space" depicted (Locations 1 and 2, Thomson, 1982a; location 3, Waser, 1978b).

Another phenomenon affecting plant relationships is pollen carryover, treated extensively by Lertzman and Gass in this book. All empirical treatments of carryover to date have considered one species only, but its importance in heterospecific visit sequences is readily apparent. When a pollinator visits a flower of species A, then B, then A, how much pollen will the second A receive from the first? Although data are lacking, assumptions of published competition models range from Straw's (1972) proposal that carryover is essentially complete, to Levin and Anderson's (1970) view that it is completely lacking. The Levin–Anderson model reflected the then-prevailing view that carryover within a species is generally low, with most pollen being placed on the next flower visited (Levin and Kerster, 1967, 1969). Recent experimental work suggests that carryover is often more extensive than this: In *Erythronium americanum, E. grandiflorum, Clintonia borealis,* and *Diervilla lonicera* (all flowers with open corollas, plentiful exposed pollen, and imprecise channeling of visitors over the reproductive parts), the pollen put on a nectar-feeding bumblebee by one flower declines roughly as an exponential decay with a "grain half-life" of between one and two flower visits. However, the tail of the fall-off curve usually is longer than predicted by exponential decay; i.e., a small fraction of grains travel considerable distances. There is great flower-to-flower variability in deposition,

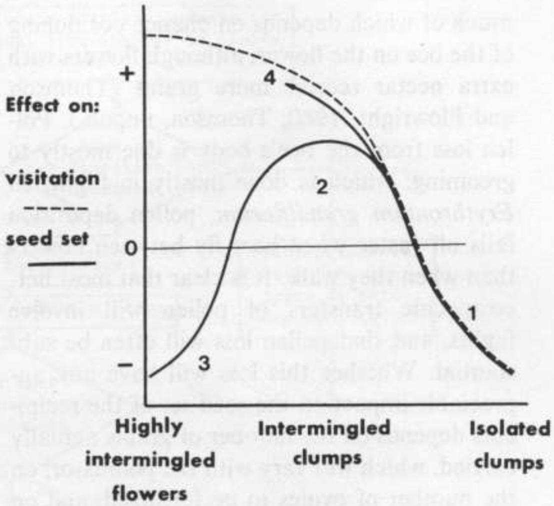

Figure 22-2. A summary of the ways in which spatial intermingling may affect the interaction between two plant species that share pollinators. When plants occur in separate, discrete patches, the patches may compete for visitors. As the species intermingle more, visitation rate may rise as the pollinators respond to the greater density. However, seed set may drop off at extremes of intermingling owing to the increasing fraction of heterospecific visits.

much of which depends on chance positioning of the bee on the flower, although flowers with extra nectar receive more grains (Thomson and Plowright, 1980; Thomson, unpub.). Pollen loss from the bee's body is due mostly to grooming, which is done mostly in flight. In *Erythronium grandiflorum,* pollen deposition falls off faster when bees fly between flowers than when they walk. It is clear that most heterospecific transfers of pollen will involve flights, and that pollen loss will often be substantial. Whether this loss will have any appreciable impact on the seed set of the recipients depends on the number of grains actually carried, which will vary with the pollinator; on the number of ovules to be fertilized; and on the functional response of seed set to pollination intensity. Despite being one of the more important components of any quantitative model of pollination success, this functional response apparently has been described for very few plant species (*Oenothera fruticosa,* Silander and Primack, 1978; *Passiflora vitifolia* and *Geranium maculatum,* A. Snow, pers. comm.). Extensive hand-pollinations in *Clintonia borealis* and *Medeola virginiana* have yielded only a very weak positive relationship between the number of outcross grains applied and the number or proportion of ovules developed (Plowright and Thomson, unpub. data). The weakness of the pollination/seed set relationship for these species is due largely to extensive fruit abortion, which may represent incompatible or semicompatible pollinations (cf. Bertin, 1981), or possibly deficiencies of technique. In view of the general lack of data, the extent to which the seed set response is coupled to pollination should become an active research topic; without such data, the significance of pollination rate and of pollen carryover is very difficult to treat.

The role of grooming in pollen carryover is another poorly understood relationship with important, sometimes elaborate ramifications. Hartling and Plowright (1979a,b; Plowright and Hartling, unpub. ms.) found that a bumblebee could pollinate as many as 50 florets after its arrival on a head of red clover *(Trifolium pratense),* a much larger number than supposed previously. *T. pratense* is self-incompatible, and it had been thought that only a few florets could be fertilized on a new plant before self pollen overwhelmed the outcross pollen on the bee's body (Free and Butler, 1959; Michener, 1974). The outcross pollen that is deposited on clover florets apparently comes from the proboscidial fossa (Furgala et al., 1960; Spencer-Booth, 1965), which must not become overlaid by incompatible self pollen until the bee grooms, after leaving the flower head. Bees seem unable to groom the fossa clean, and they sweep pollen into it during other grooming movements. While not firmly demonstrated, this mechanism is the most likely explanation for the extensive within-head carryover. Bees also regulate the number of florets visited on a head according to the amount of nectar in the florets (Hartling, 1979; Hartling and Plowright, 1979a). If there is layering of pollen from successive heads in the proboscidial fossa, with the depth of each head's stratum proportional to the number of florets visited on the head, and if the amount of pollen removed from the superficial strata during a visit to a head also depends on the number of florets visited, interesting consequences follow. Since nectar-rich plants are the only ones whose stigmas will cut down to the deepest layers and the only ones whose pollen will subsequently be swept into those layers, there can be assortative mating for nectar levels without any discrimination by the pollinators. Nectar-rich plants could also have a larger neighborhood size in that some of their deeply deposited grains may travel considerable distances before being brought to light (see Lertzman and Gass, this book, on the effects of pollen layering).

The connections between nectar secretion and pollinator foraging have been made explicit in a systems model for pollination in red clover assembled by Plowright and Hartling (unpub. ms.) using parameter values from field experiments and the assumption of exponential decay of pollen. A flow chart for this model is given in Fig. 22-3. Although this form of the model does not incorporate the pollen-layering effects discussed above, it does allow one to examine the effects of changing the reward schedule of the flowers, the number of incompatibility alleles in the clover population, and the rules of movement of the bees. Analyzing bee movement in the context of plant–pollinator interaction was, in fact, the original rationale for building the model. Plowright and Hartling used it to show that the flexible foraging behavior actually displayed by bumblebees also resulted in higher seed sets than behavior representing previous casual descriptions of bee behavior (Michener, 1974, p. 327). The model also points out the inadequacy of estimating seed set in a stand of clover from simply determining the frequency of interplant transitions. Behavior that maximizes interplant moves does not maximize seed set.

Manipulations of models of this sort can shed light on other pollination interactions. For example, it is possible to determine the nectar secretion rate that yields optimum seed set. In obligate outcrossers like red clover, this optimum clearly will often involve a "compromise" nectar production, rich enough to prevent visitors from visiting few flowers per plant but not so rich as to make them stay so long that their outcross pollen becomes exhausted or overlaid (see Heinrich and Raven, 1972). The residence time of pollinators on an inflorescence may also vary with the architecture of the inflorescence and with the pattern of nectar secretion. For instance, Pyke (1978) has proposed that many plants with vertical inflorescences present more nectar in the lower flowers, and that this presentation prompts the visitors to move upward and to depart when rewards diminish. Again, analysis of the components of presentation, perception, and response economically reveals the workings of a system subunit and suggests a coevolutionary interpretation. However, one must be very cautious in interpreting inflorescence design as a means of optimizing outcrossing by balancing visitation and carryover as above, since many plants have multiple inflorescences. In such cases, a spike or head that is optimally suited for receiving a pollinator's first visit to the plant will be progressively less suited for successive visits made within the same plant. Theories of inflorescence evolution (e.g., Willson and Rathcke, 1974; Willson and Price, 1977) must reflect this unpredictability as well as the modular nature of most inflorescences (Harper, 1977).

SUMMING UP

As I warned in the introduction, this is primarily a didactic essay. I concede that it also may seem, depending on the tolerance of the reader, either fragmentary and incomplete or simply premature. My main point is to advocate a systems approach, yet I have presented only one real systems model (the clover model), and even that only includes a small subset of the components that I have identified as important. My explanation of this embarrassing situation, as might be expected, has several subunits.

First, I feel that the advantages of a component-analysis approach *in revealing detail* are evident enough in subunit models (such as the red clover model cited here and Lertzman and Gass's carryover models) that one need not wait for a complete community-level treatment to proclaim them. The wait would be long because the intensity of study required to yield the necessary detail means that only small portions of systems usually can be successfully analyzed in the course of a dissertation project. Unless long-term cooperative studies become more common than they are now, our knowledge of community-level interactions will continue to consist of a number of isolated glimpses of various parts of various systems. Of course, this is the prevailing situation in all of community ecology, and if pollination ecologists are forced to draw too many inferences from too few studies—if bumblebees, and *Delphinium* and *Ipomopsis* and *Erythronium*, reach the talisman status of intertidal invertebrates and West Indian anoles—we are no worse or better off than our colleagues. This state of affairs provides one answer to the question, "Why is so much detail needed?" Because we will probably continue to be heavily dependent on a small number of studies, and continue to "solve" other systems by analogy and extension, it is critical to realize that small differences in structure may

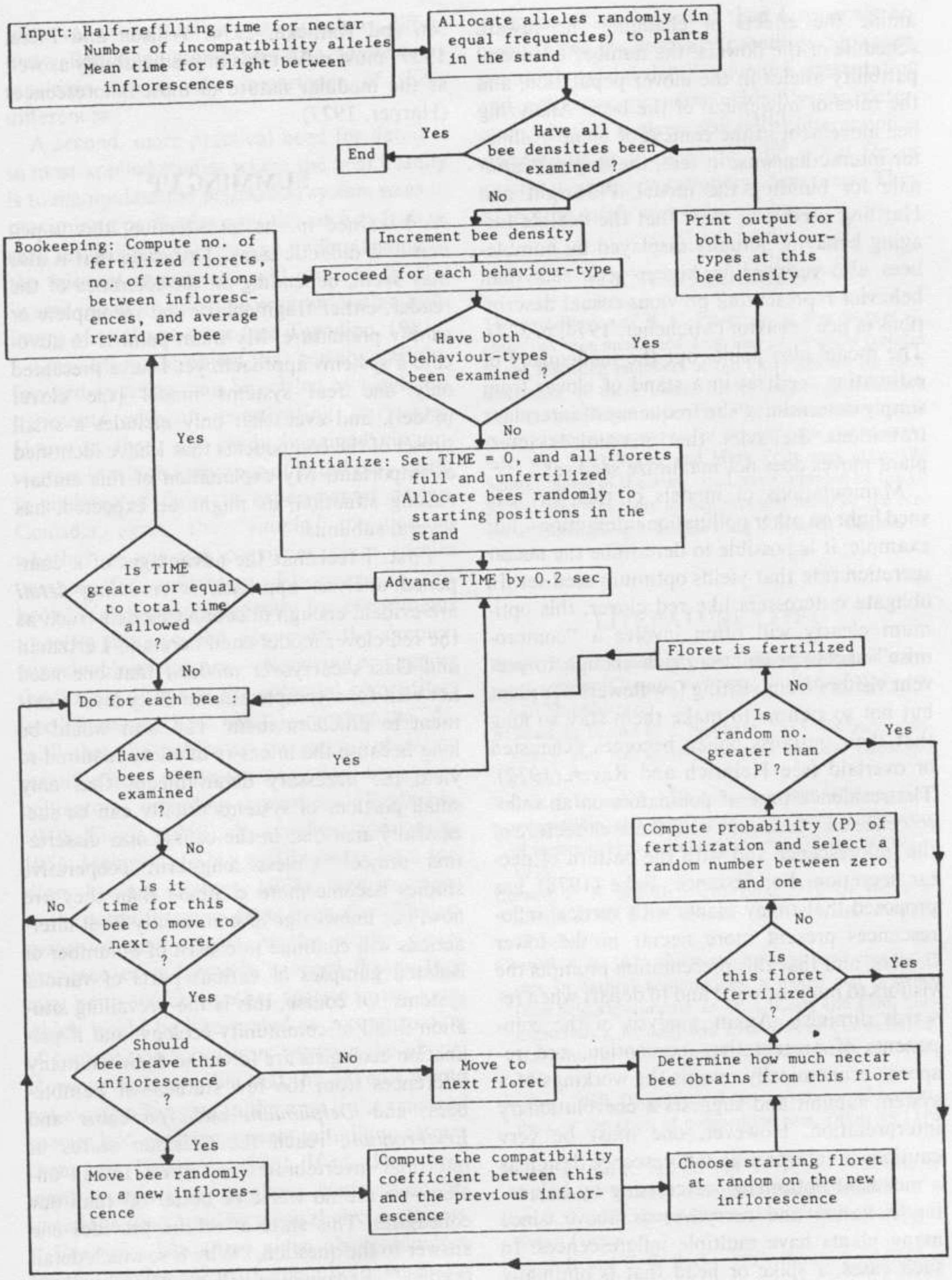

Figure 22-3. A flow chart of the *Bombus–Trifolium* model discussed in the text. Additional details may be found in Plowright and Hartling (unpub. ms.).

make otherwise similar systems behave differently. Breaking interactions into components sensitizes one to the importance of these differences.

A second, more practical need for detail is in most applied studies where the goal usually is to manipulate the pollination system so as to maximize a particular quantity such as fruit or seed set. It is obvious that an understanding of the relevant components will often be helpful in arriving at an effective program with a minimum of trial and error (see Tepedino, 1981).

One still might object that certain straightforward questions can be settled by single experiments without investigating intricacies. However, there are easily imagined circumstances in which ignorance of detail may result in undetected flaws in experimental design. Consider again the "simple" question of whether or not two coexisting plant species compete for pollination. Elsewhere in this book, Waser argues cogently for experiments to settle this question. However, the simplest conceivable experiment—removing or bagging the flowers of one of the potential competitors (see Thomson, 1980, 1982a)—ignores the "detail" that the pollinator community does not reshuffle itself randomly every day. Important pollinators, including honeybees (Ribbands, 1949; Singh, 1950), bumblebees (Manning, 1956; Heinrich, 1976), and birds (at least territory holders, Linhart, 1973), tend to return to the same foraging areas each day. The response of such animals to the sudden disappearance of a formerly favored flower type may be to switch to other species in the area, which would be interpreted as a confirmation of competition for visitors between the plants. However, it is possible that the animals would not even be foraging in the area if the removed species had not been present initially to attract them (see Thomson, 1978). If so, the experiment reveals nothing about competition between the species under natural circumstances.

Examples like those given above convince me that finding the truth about pollination systems usually will require dissection and some amount of model building. My emphasis on detail must not be taken to imply that I find small-scale mechanical processes more interesting or more important than large-scale ecological and evolutionary processes. However, seemingly trivial details of plant presentation and pollinator response evidently can determine whether a given ecological interaction is competitive or mutualistic, and select for or against certain evolutionary directions. They cannot be safely ignored.

ACKNOWLEDGMENT

The contribution of R. C. Plowright to this chapter already has been mentioned. I am also particularly grateful to the following members of the Plowright lab for their discussion of these ideas: Lester Hartling, Lawrence Harder, and Terence Laverty. Many conversations with scientists too numerous to list helped shape this chapter; talks with Nick Waser and Mary Price were especially helpful. Some of the work cited was supported by the U. S. National Academy of Sciences and some by the National Sciences and Engineering Research Council of Canada.

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