Pollination, Gathering Nectar and the Distribution of Flower Species

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A model of pollination, having one species of bee and several species of flower, is presented. The foraging bee monitors the size of the nectar standing crops of the various flower species and, using a learning procedure described in the paper, tends to visit more frequently the species with the larger nectar standing crops. The differential visitation rates affect the relative reproductive success of the flower species. Steady-state flower distributions are derived and it is proved that such equilibria exist. The model explains some general features found in the pollination market, such as why bees lack innate preferences for certain flower species, the equilibrium allocation of flower resources between display and reward, and the conditions that permit deceptive flowers.

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1. Introduction

Bees and flowers are an ecological example of a two-sided natural market (Heinrich, 1979; Peleg & Shmida, 1992). Bees and flowers may be viewed as engaging in an exchange of nectar for pollination service that is analogous to exchanges in human economic markets. In each natural community there are many species of bee and many species of flower. Each flower tries to obtain more effective visits (Selten & Shmida, 1991) in order to obtain more fertilization and to deliver more of its pollen to other flowers.

How many flower species will coexist in the same community? How will the learning policy of the foragers influence the characteristics of flowers (e.g. the nectar production and display size)? In a previous study, Peleg & Shmida (1992) analyzed the interactions of bees and flowers in a model with several species of each and described the equilibrium pattern with which the several bee species visited the flower species (the

equilibrium behavior of the bees and flowers). However, there were no dynamics in that work; that is, there was no attempt to describe the way that either the flower species or the bee species would adjust their behavior over time if they were not at equilibrium.

In the present paper, we describe a dynamic competitive interaction on one side of the market—among the flower species—in a model having only one species of bee. Bees are modeled as being able to learn from experience and to adjust their foraging patterns so that flower species providing more nectar are visited more frequently. Our focus is on the adaptation of the flower species. We model (i) bee behavior that changes over a season in response to changes in the nectar standing crops of the several flower species, (ii) the pollination activity of the bees, and (iii) the effect of bee behavior on the reproductive success of the flowers from season to season. A distribution of flower species that has no tendency to change over time is a steady state of the model. Such a steady state is dependent upon the nectar production rate of each flower species and their respective displays (i.e. their corollas). Conditions are shown under which deceptive flowers can coexist with high nectar

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producers. Overall, the model explains two contra-dictory aspects of pollination markets observed in nature: On one hand, bees forage in a way that directs their efforts toward flower species offering nectar rewards, but, on the other hand, we observe steady state equilibrium behavior in which bees continue to visit flowers that provide relatively small nectar rewards.

We develop a model of pollination having one species of bee and several species of flower. Each flower species is distinguished by its rate of nectar production and the resources it devotes to display. The flowers and bees are assumed to have identical lifetimes that comprise a number of days within a single year. At the start of the year the bees, lacking experience and being in their naïve phase, are attracted to flowers according to the relative sizes of the flowers' displays; however, the bees soon become experienced and continually monitor the nectar standing crops of each species, altering their visiting habits over time so that they always tend to visit most frequently the flower species having the largest nectar standing crop. This, in turn, tends to equalize the nectar standing crops across species. From one year to the next the relative abundance of the flower species can change in accordance with the comparative reproductive success of each species (Roubik, 1989). This, in turn, depends upon the number of visits by bees to the flowers of each species, the amount of energy devoted to reproduction, and the relative abundance of each species in the preceding year. We make no attempt to model the absolute number of bees or of flowers, but do assume the ratio of bees to flowers is the same from one year to the next. The model described below has been programmed so that it is possible to run simulations.

The major result of the paper is to prove that, for a very large class of models, a steady-state equilibrium exists. We also compute several simulations with the model which demonstrate that the dynamic processes of the model can lead over time to a steady state and the simulations provide some examples of steady states that could arise.

The remainder of the paper is divided into five sections. Section 2 gives some biological background that influences the design of the model. The model itself is described in Section 3 where it is seen that the model is quite ambitious and complex. Then the existence of steady-state equilibrium flower distri-butions is proved in Section 4. This is the main result of the paper. The computer simulations are presented in Section 5, giving some hint about the scope and variety of possible equilibria. Section 6 concludes.

2. The Biological Background of the Model

Some basic facts about the foraging activities of bees should be elucidated. The assumptions of our model are based upon these biological phenomena; however, we do not follow these phenomena in every detail. The ways in which the model diverges, and reasons for the differences, are given after the biological facts are presented. (Non-biologists are referred to Selten & Shmida, 1991; Peleg & Shmida, 1992; Cohen & Shmida, 1993; Kadmon et al., 1992; and Shmida et al., 1993.)

1. Most wild bees are solitary, particularly in the Mediterranean region and in the desert. Each individual lives between four and six weeks. Each female has her own nest and raises her brood alone. There is no exchange of information about foraging between bees; hence, each solitary bee can be regarded as a "rational Darwinian individual." (Hammerstein & Selten, 1992).
2. Field observations reveal, on the one hand, a strong preference of bee species for specific flower species, but, on the other, that the same bee species visits several different flower species (Teras, 1985). Individual bees show similar patterns; within short periods of time, an individual sometimes shows a strong preference for one species and sometimes switches frequently among species (Heinrich, 1979).
3. Bees appear to lack any innate preference for particular flowers (Menzel, 1985; Waser, 1983) and their foraging patterns appear to be influenced by experience (i.e. "learning by doing": Real, 1991). The bees could learn by doing in either or both of two respects. The first is that they learn from experience which flowers will yield more nectar per unit time that they expend (Heinrich, 1979). The second is that, by specializing on a particular species, a bee can reduce its handling time (the time it takes the bee to land on the flower and to suck the nectar: Laverty, 1980).
4. Bees visit flowers to collect nectar and pollen as food resources. Each round trip of a female bee from its nest is called a bout. The female bee leaves its nest with an empty nectar tank (crop) and visits many flowers from few individuals in order to fill its crop with nectar and to collect pollen (O'Toole & Raw, 1991). Male bees spend most of their time looking for females and during this process they visit many flowers for nectar.
5. The individual flowers of many of the species we investigated live for between 3 and 5 days (A. Shmida, unpublished data). An individual plant may have many blooming flowers and the total blooming time of a plant is between 8 and 15 days.

The population of one plant species will bloom for 3 to 5 weeks.

6. Plants produce nectar only to attract pollinators. Pollen is produced for the fertilization of other plants, but it is also collected by female bees as a protein resource primarily for raising their young (Waser, 1983).

7. During its lifetime a flower produces nectar only while blooming (i.e. when the sex organs are functional). We will assume that nectar is produced continuously at a constant rate through the daytime and at a lower constant rate through nighttime (Kadmon & Shmida, 1992).

8. Flowers are the only nectar source for bees; however, the nectar is hidden from view so that the bee can learn about different flowers' nectar standing crops only by sampling. At the beginning of a bee's life, before experience is gained from sampling flowers, the display of a flower attracts a bee's attention.

Our model conforms to the preceding specifications in many, but not all, ways. The model is based upon solitary bees with no distinction being made between male and female bees and no account taken of the mating activities of bees (Shmida *et al*., 1993). Field observation suggests that, even when bees change flower species frequently, they typically remain within one flower species during each bout. Our model conforms to this visitation practice; however, we assume that each plant has only one bloom, which is relevant to the computation of the number of effective visits to a flower species (Selten & Shmida, 1991). We totally ignore the value of pollen to bees; rather, we assume that they are only interested in nectar. In the model individual plants bloom for three days in each season. An assumption of the model is that the lifetime of a bee and the total duration when a flower species is in bloom are both about the same—roughly 4 weeks. The foraging activity of a solitary bee is typically temperature-sensitive; therefore it can vary through the day according to whether or not it is raining or whether the sun is behind clouds. We ignore these within-day variations. While such variations may be very important, we believe that the elements incorporated into our model are sufficient to make the model interesting and we would hope to expand this research in various ways in the future. We assume no innate preferences for particular flower species. At first, the bees in our model are attracted by flowers' displays. Then, as they gain information on nectar standing crops by means of sampling, their experience affects their visitation choices. Their choices are continually being modified by their experience; however, no matter how little nectar is found in a given

species, the bees will always *minor* (that is, they always spend some time visiting all other species in the field including those that yield the least nectar) and sample any species from time to time (Heinrich, 1979).

3. The Model

We start with a fixed number, n, of flower species. The subscript i refers to a species. These species differ in the amount of energy they devote to a display (D_i) and the rate at which they produce nectar per daylight hour (r_i). Time is divided into years, days, and periods. These are indexed by y, d, and π, respectively. Each year contains a number of active days (T_d) during which the flowers bloom and bees forage. We assume that the T_d active days constitute a season during which all species bloom according to the same pattern. That is, the individual flowers of all species are assumed to bloom for 3 days. The number of plants of each species will change from season to season, but is constant throughout any single season. The number of blooming plants of a species is exactly the same on all days of the season except the first two and the last two. Thus, the population of plants of a single species is divided into T_d-2 cohorts of equal size. The first cohort blooms on days $d=1$, 2 and 3. The second cohort blooms on days $d=2$, 3 and 4, and so forth up to the last cohort (number T_d-2) that blooms on days $d=T_d-2$, T_d-1, and T_d. Consequently, the first and last days of the season have only a third the number of blooming plants as days 3 through T_d-2, and days 2 and T_d-1 have two-thirds as many. The cohort that blooms during days d, $d+1$ and $d+2$ is referred to as cohort d. The bees are assumed to be born on the first day of the season and to live precisely for the duration of the season. Consequently, any parameters of a bee's activity that are determined by the very early stages of life are learned at the start of the season.

Within the lifetime of the flowers and bees, each day is 24 hours long and is divided into σ active hours and $24-\sigma$ inactive hours. The active hours constitute daytime when the bees are active while the inactive hours are night-time. The flower species i produces nectar at the hourly rate r_i throughout the daytime hours and at the hourly rate $r_i/2$ throughout nighttime. As a computational convenience daytime is further divided into periods. The total energy of a flower is defined to be one unit per period. Energy is divided between reproduction, display and nectar production. The cost per period of display is D_i for species i and D_i is also taken as a measure of the size of the display. With respect to nectar production, the situation is a little more complicated because r_i is naturally measured in units such as fl (femtoliters) per hour. The

total nectar production in a 24-hr period is $r_i[\sigma + 1/2(24-\sigma)] = r_i(12+\sigma/2)$, and it is reasonable to suppose that the cost to the flower in energy of one day's nectar production is strictly proportional to its total nectar production in the day. Thus if the cost of nectar production is c per fl for any species, the total cost for the day is $cr_i(12+\sigma/2)$. If there are T_p periods in the active part of the day and we wish to do our energy bookkeeping on the basis of active periods, then the cost per active period is $cr_i(12+\sigma/2)/T_p = kr_i$ where k is defined as $k = c(12+\sigma/2)/T_p$.

3.1. THE FLOWER DISTRIBUTION OVER TIME

The abundance of each flower species at the start of year y is denoted $\phi_y = (\phi_{1y}, \ldots, \phi_{ny})$. The model does not keep track of the total population of each species; instead only relative population sizes are computed. Thus $\Sigma_{i=1}^n \phi_{iy} = 1$ at all times. The fitness of a species depends on the energy allocated in display, energy allocated in nectar production, and on the number of effective visits by bees to flowers of each species during the year. An effective visit by a bee to a flower of species i is a visit that is immediately preceded by a visit to a flower of the same species, so that the visit brings pollen from one flower of the species to another. The number of effective visits to cohort d of species i in year y is denoted V_{iyd}. The flower distribution in year $y+1$ is given by eqns (1) and (2).

$$\phi_{i,y+1}^* = \sum_{d=1}^{T_d-2} \phi_{iy}^{e_i}[1-kr_i-D_i][\mu_i V_{iyd}^{1/2}$$

$$+(1-\mu_i)V_{iyd}] = \sum_{d=1}^{T_d-2} \phi_{i,y+1,d}^* \quad (1)$$

$$\phi_{i,y+1} = \frac{\phi_{i,y+1}^*}{\sum_{j=1}^n \phi_{j,y+1}^*} \quad (2)$$

The symbol $\phi_{i,y+1,d}^*$ in eqn (1) measures the relative reproductive success of cohort d of species i in year y. Equation (1) is the sum of the $\phi_{i,y+1,d}^*$ over all the cohorts of species i in year y, giving $\phi_{i,y+1}^*$, the relative reproductive success of species i in year y. The relative reproductive success of species i is given by eqn (2) in the form of a normalization that ensures that the flower distribution sums to 1. Equation (1) bears more examination; $\phi_{i,y+1,d}^*$ can be decomposed into three pieces:

(i) $$\phi_{iy}^{e_i},$$

(ii) $$1-kr_i-D_i,$$

and

(iii) $$\mu_i V_{iyd}^{1/2} + (1-\mu_i)V_{iyd}.$$

Term (i) is the previous year's relative population of species i raised to a power, e_i, that is between zero and one, which gives a slight relative advantage to species that are not very numerous. Term (ii) is the energy that remains to flower after deducting the energy expended on nectar production and on display. As noted above, total energy is normalized at one, D_i is the energy used for display, and kr_i is the energy used in nectar production with k being the cost parameter described above. Thus the residual energy is what is devoted to reproduction. Term (iii) gives the effect on fitness that is due to the number of visits. This term has two parts, one is $\mu_i V_{iyd}^{1/2}$ representing female fitness, and the other is $(1-\mu_i)V_{iyd}$ representing male fitness. Generally, male fitness is proportional to the number of visits, but female fitness increases at a decreasing rate as the number of visits rises (Willson, 1990).

3.2. ACTIVITY WITHIN THE DAY

Most of the complex interaction between bees and flowers portrayed in our model is described in this section. As seen above in eqns (1) and (2), the number of visits by bees to the flowers of a given species is important as is the amount of energy remaining available for reproduction after deducting the energy used for display and for nectar production. In this section, we analyze how display and nectar production influence the visits of bees to flowers, determining the critical values V_{iyd}.

During each of the T_d days of the year when flowers are open and bees are active, time is further divided into σ hours of daytime when the bees are out foraging and nectar is being produced at a high rate, and $24-\sigma$ hours of night-time when the bees are not foraging and nectar is being produced at a low rate. The σ hours of foraging are divided further into T_p time periods of length $\delta = \sigma/T_p$. The period length is unimportant as long as it is sufficiently small. Ideally, we would use continuous time; however, that appeared too difficult. Thus our use of a short time period, δ, is intended to give a reasonable approximation to continuous time. At the start of the first period of the first day we assume $R_{iy11} = 2r_i$; that is, the initial nectar standing crop (R_{iy11}) is equal to the amount of nectar that the flower can produce in two daytime hours. Throughout the active part of the day bees are visiting the flowers and taking nectar while the flowers are continually producing more nectar. The bees distribute themselves at the start of the first day of each year according to the displays of the flowers and the relative abundance of each species. That is, at the start of the first day of the

year we assume that only the visible display put out by a species will affect the visits of bees. Thus in the first period of the first day of a year the proportion of bees visiting flowers of species i is $p_{iyd\pi}$ where $d=1$ and $\pi=1$

$$p_{iy11} = \frac{D_i\phi_{iy}}{\sum\limits_{j=1}^{n} D_j\phi_{jy}} \tag{3}$$

The bees change their foraging habits according to their experience at gathering nectar through the periods of the day. The more nectar a species yields, the more the bees favor it, but the bees always minor (Heinrich, 1979). The extent to which the bees minor is affected by the size of the species' display. The specific process is described in eqn (4). Let $R^M_{yd\pi}$ be the largest nectar standing crop at time period π of day d in year y (that is, $R^M_{yd\pi}=\max_j R_{jyd\pi}$). The distribution of bees among flowers at period π is

$$p^*_{iyd,\pi+1} = \lambda p_{iyd\pi}$$
$$+ (1-\lambda)\left[\frac{aD_i\phi_{iy}}{\sum\limits_{j=1}^{n} D_j\phi_{jy}} + \frac{(1-a)R_{iyd\pi}\phi_{iy}}{R^M_{yd\pi}}\right] \tag{4}$$

$$p_{iyd,\pi+1} = \frac{p^*_{iyd,\pi+1}}{\sum\limits_{j=1}^{n} p^*_{jyd,\pi+1}} \tag{5}$$

In eqn (4) note that the term in square brackets consists of two terms weighted by a and $1-a$, respectively. The first term reflects minoring with the extent of minoring depending on both the overall minoring weight (a) and the relative visibility of the particular species. The second term, $R_{iyd\pi}/R^M_{yd\pi}$, weighted by $1-a$, reflects the influence of the nectar standing crop. The ratio of species i nectar standing crop to the largest of any species, is necessarily between zero and one; therefore, $R_{iyd\pi}/R^M_{yd\pi}=1$ for the species for which $R_{iyd\pi}=R^M_{yd\pi}$ and $R_{iyd\pi}/R^M_{yd\pi}$ is between zero and one for all other species. Now note that the term in square brackets is multiplied by $1-\lambda$ while $p_{iyd\pi}$ enters the determination of $p^*_{iyd,\pi+1}$ multiplied by λ. The parameter λ indicates the speed of adjustment of the bees to the information that they gather. If $\lambda=0$ they totally adjust within a single period. When $\lambda<1$, total adjustment takes $1/(1-\lambda)$ periods or $\delta/(1-\lambda)$ hours (under stationary conditions). Equations (4) and (5) are an example of a commonly used learning model (Bush & Mosteller, 1955).

Next we must account for the time path of the nectar standing crop of an average flower of each species as

the day progresses and also from day to day. To do this we must first see how much nectar a single bee obtains from each species during each period of the active part of the day. The time for a round trip from the bees' nest to the flower site is τ_0, the time to get in and out of position at a single flower is τ_1 and the time to extract $R_{iyd\pi}$ from a flower is $\tau_2 R_{iyd\pi}$ ($\tau_1+\tau_2 R_{iyd\pi}$ is handling time). Therefore, a bee that visits flowers of species i during period π and that can carry a quantity β of nectar in its crop needs

$$\tau_0 + (\tau_1 + \tau_2 R_{iyd\pi})\frac{\beta}{R_{iyd\pi}} \tag{6}$$

hours to extract an amount β of nectar and make a round trip to the nest. The average number of visits to individual flowers of species i that are needed to collect an amount β of nectar is $\beta/R_{iyd\pi}$ and the number of visits of one bee to flowers of species i during time period π is

$$V'_{iyd\pi} = \frac{\beta\delta}{\tau_0 R_{iyd\pi} + \beta\tau_1 + \beta\tau_2 R_{iyd\pi}}. \tag{7}$$

The number of effective visits is less than $V'_{iyd\pi}$. We suppose that a bee visits only one species on each bout; therefore, the number of effective visits on each bout is precisely one less than the number of visits; that is, $\beta/R_{iyd\pi}-1$ on each bout. The assumption that bees do not switch species during a single bout is not necessary for the model, but we believe that it does only minor violence to bee behavior and, at the same time, affords a useful simplification of the model. Consequently, the average number of effective visits during a single time period by a bee that goes to species i is

$$V_{iyd\pi} = V'_{iyd\pi} - \frac{V'_{iyd\pi}}{\beta/R_{iyd\pi}} = \frac{\delta(\beta-R_{iyd\pi})}{\tau_0 R_{iyd\pi} + \beta\tau_1 + \beta\tau_2 R_{iyd\pi}} \tag{8}$$

Suppose there are N_B bees, N_F flowers in each cohort (summed over all species), and that the bee distribution is $p_{yd\pi}=(p_{1yd\pi},\ldots,p_{nyd\pi})$. There would be $N_{Fd}=N_F$ blooming flowers on days $d=1$ and $d=T_d$, $N_{Fd}=2N_F$ on days $d=2$ and T_d-1, and $N_{Fd}=3N_F$ on all other days. There would be $N_B p_{iyd\pi} V_{iyd\pi}$ individual effective visits by all bees to flowers of species i and, as there are $N_{Fd}\phi_{iy}$ individual blooming flowers of species i, the total number of effective visits to a single blooming flower of species i is $v_{iyd\pi}=N_B p_{iyd\pi} V_{iyd\pi}/(N_{Fd}\phi_{iy})$. The time period δ must be made sufficiently short that $N_B p_{iyd\pi} V_{iyd\pi}/N_{Fd}\phi_{iy}<1$ so that we may think of some individual flowers of species i being emptied of their nectar and others not touched. Our experience with natural flowers and bees suggests that the nectar standing crop of an unvisited flower does not

materially change in 20 min or less. In our simulations, δ has values from about 5 to 16 min. The nectar standing crop in period $\pi+1$ becomes

$$R_{iyd,\pi+1}=\left[1-\frac{N_B p_{iyd\pi} V'_{iyd\pi}}{N_{Fd}\phi_{iy}}\right]R_{iyd\pi}+\delta r_i$$

$$=\left[1-\frac{\beta\delta N_B p_{iyd\pi}}{N_{Fd}\phi_{iy}(\tau_0 R_{iyd\pi}+\beta\tau_1+\beta\tau_2 R_{iyd\pi})}\right]$$

$$\times R_{iyd\pi}+\delta r_i. \qquad (9)$$

After the active part of the day is over, the flowers produce nectar while bees do not make visits. Thus for $24-\sigma$ hours nectar is produced at the rate $r_i/2$. By daybreak the nectar standing crop has risen by $1/2(24-\sigma)r_i$ unless such an addition of nectar would overflow the capacity of the flower. Thus the nectar standing crop of an average flower of species i at the start of a day, $R_{iy,d+1,1}$, is the smaller of R_i^* and

$$R_{iy,d+1,1}=\left[1-\frac{N_B p_{iydT_p} V'_{iydT_p}}{N_{Fd}\phi_{iy}}\right]R_{iydT_p}$$

$$+1/2(24-\sigma)r_i. \quad (10)$$

In summary, eqn (4) shows how the nectar standing crop determines the visiting pattern of the bees within each period. Equations (6) to (9) show how the visiting pattern of the bees within a period determines that path through the daytime of the nectar standing crop and eqn (10) shows the further change of the nectar standing crop at night. Equation (8) shows the total number of visits made by a single bee, on average, to all flowers irrespective of species.

3.3. THE NUMBER OF EFFECTIVE VISITS PER FLOWER LIFETIME TO AN AVERAGE FLOWER

In this section we show how V_{iy}, the number of effective visits received during a year by an average flower of species i, is determined.

$$V_{iyd\pi}=\frac{N_B p_{iyd\pi} V_{iyd\pi}}{N_{Fd}\phi_{iy}}$$

$$=\frac{\delta N_B p_{iyd\pi}(\beta-R_{iyd\pi})}{N_{Fd}\phi_{iy}[\tau_0 R_{iyd\pi}+\beta\tau_1+\beta\tau_2 R_{iyd\pi}]} \qquad (11)$$

is the number of effective visits to an average flower of species i during period π of day d. Therefore,

$$V_{iyd}=\sum_{l=d}^{d+2}\sum_{\pi=1}^{T_p}V_{iyl\pi} \qquad (12)$$

is the total number of effective visits by bees to an average flower in cohort d of species i during year y.

Now that the model is completely specified, some additional comments may be usefully made on it. The bee behavior in eqns (4) and (5) has two implications that deserve comment with reference to deceptive flowers; that is, flowers that have large displays, but that produce little or no nectar. First, the minoring behavior of the bees will ensure that such flowers continue to receive some visits even though the flowers are not very rewarding for the bees. Second, a large display coupled with a large value of λ (slow adjustment to information) will mean that deceptive flowers can have a large number of effective visits from bees. A more realistic model than ours would better show the opportunities for deceptive flowers. For example, if there were new bees emerging at a great rate steadily over the blooming period of a deceptive species, then these flowers could receive a very large number of visits because they could take advantage of the naïveté of the newborn bees (Shmida et al., 1993). Deceptive orchids are common in the Mediterranean region in early Spring. They take advantage of the newly emerging solitary bees. Within our model, a deceptive species would fare better if its period of blooming were shorter than that of the other flower species.

Carrying the preceding argument a bit further, the larger the bee, the longer the blooming period of each species, and the less environmental fluctuation, the smaller the displays are likely to be. Larger bees can forage in more variable conditions and they can fly faster; therefore, they visit more flowers per unit time. Longer blooming periods allow more time to discover deceptive species, and stable environments make less minoring and faster adjustment more profitable. If the foragers are resident and territorial we should expect the flower to have a smaller display and a larger reward.

Another aspect of eqns (4) and (5) is the speed of adjustment, λ. Within our model, the interest of an individual bee is best served by adjusting very quickly, because the nectar standing crops of the flowers will not change very rapidly. If all bees adjusted very rapidly (e.g. if $\lambda=0$), then the nectar standing crops would probably oscillate wildly and most bees would tend to be choosing the same species at any given moment, leading to very low rewards. Although slow adjustment does not seem to be in the interest of the individual bee within our model, it would make sense in a more sophisticated model. Real bees face random fluctuation in nectar standing crops due, for example, to weather patterns. A few days of cold or rain can greatly alter the absolute and relative

nectar standing crops of various species, as compared with continued warm, dry weather. A severe storm may kill off a large portion of one species while doing little damage to others. In addition, the personal experience of one bee will often vary from the mean experience of bees visiting the same species (Heinrich, 1979). That is, a bee may visit a low yielding plant species, but may chance to visit many high yielding individuals. This experience will incline it to return to the same species even though that species is not high yielding on average. All of these considerations suggest that slower adjustment is likely to benefit the individual in a stochastic environment.

Related to the preceding, and also related to eqns (4) and (5), is the observation that there are various forces at work in our model that tend to prevent the attainment of the ideal free distribution (IFD). In addition to the slow adjustment and minoring, present in our model, random elements that we do not incorporate would also tend to preserve some discrepancies from the IFD. Smaller T_d, larger λ, and larger a all will increase deviation from the IFD. Field observation by one of us near Jerusalem confirms that there are some situations in which flowers with large nectar standing crops are not visited for the first 6 to 8 days in bloom while flowers with large displays and small reward are visited frequently.

Field observation also shows that the flower resources (relative distributions of different flower species) vary widely from one season to the next and that certain bee species seem to specialize in different species in different seasons. All of this supports the view that learning behavior, such at that portrayed in eqns (4) and (5), is more advantageous for bees than is an innate preference of bees for particular species. While the ability to learn has a cost in complexity, such cost appears worthwhile due to the gain in adaptability.

4. Steady State Flower Distributions

Taken together, eqns (1–12) describe a continuous function that transforms ϕ_y into ϕ_{y+1}. That is, starting from a flower distribution, these equations describe the activities of bees and flowers through a season. These activities determine the relative fitness of each of the flower species which, in turn, determines the flower distribution for the next season. To see that this is true requires proceeding through a recapitulation of the model. At the beginning of the year ϕ_y is known and the nectar standing crops of the flowers have constant starting values of $R_{y11} = (R_{1y11}, \ldots, R_{ny11}) = 2(r_1, \ldots, r_n) = 2r$. Then $p_{y11} = f_1(\phi_y)$ is specified in eqn (3). All later values of $R_{yd\pi}$

and $p_{yd\pi}$ are determined from ϕ_y and the earlier values of $R_{yd\pi}$ and $p_{yd\pi}$. More precisely, eqn (9) gives $R_{y,d+1\pi}$ as a function of $p_{yd\pi}$, $R_{yd\pi}$, and ϕ_y. For simplicity of notation, this equation can be denoted $R_{y,d,\pi+1} = g_1(p_{yd\pi}, R_{yd\pi}, \phi_y)$ for $\pi = 1, \ldots, T_p - 1$ and $d = 1, \ldots, T_d$. Only the overnight values $R_{yd\pi}$ are unspecified; they are given by eqn (10) and may be denoted $R_{y,d+1,1} = g_2(p_{ydT_p}, R_{ydT_p}, \phi_y)$. Equations (4) and (5) give the values of $p_{yd\pi}$ that follow the initial value. In particular, $p_{y,d,\pi+1} = f_2(p_{yd\pi}, R_{yd\pi}, \phi_y)$ for $d = 1, \ldots, T_d$ and $\pi = 1, \ldots, T_p - 1$. And $P_{y,d+1,1} = f_2(p_{ydT_p}, R_{ydT_p}, \phi_y)$ for $d = 1, \ldots, T_d - 1$. Equations (3), (4), (5), (9) and (10) are all continuous and, starting from ϕ_y, they determine the bee distributions at each period of each day of the season, denoted $p_y = (p_{y11}, \ldots, p_{y1T_p}, \ldots, p_{yT_d1}, \ldots, p_{yT_dT_p})$. They also determine the nectar standing crops of each species of flower at each period of each day of the season, denoted $R_y = (R_{y11}, \ldots, R_{y1T_p}, R_{yT_d1}, \ldots, R_{yT_dT_p})$.

Thus, due to the recursive structure of the model, the flower distribution ϕ_y determines the path of values of the bee distribution, $p_{yd\pi}$, throughout the year y and ϕ_y similarly determines the values of the nectar standing crops, $R_{yd\pi}$, at all time periods during the year. To see this in more detail, note that $p_{y11} = f_1(\phi_y)$ and R_{y11} depends on the nectar production rates, $2r$. Then $p_{y12} = f_2(p_{y11}, R_{y11}, \phi_y) = f_2(f_1(\phi_y), 2r, \phi_y)$, so that p_{y12} depends only on ϕ_y. It is possible to continue in this way, one period at a time, to the last period of the last day showing that each $p_{yd\pi}$ is totally determined by ϕ_y. The same can be done with $R_{yd\pi}$. Therefore, we may write $p_y = f_0(\phi_y)$ and $R_y = g_0(\phi_y)$ to represent the relationships developed recursively above. The continuity of f_1, f_2, g_1 and g_2 imply that the functions f_0 and g_0 are continuous, which permits the following lemma.

LEMMA 1. The functions f_0 and g_0, determined by eqns (3), (4), (5), (9), and (10), are continuous.

Turning now to the determination of $V_y = (V_{1y1}, \ldots, V_{ny1}, \ldots, V_{1yT_d}, \ldots, V_{nyT_d})$, these values are from eqns (11) and (12) and the relationship may be denoted $V_y = h_0(p_y, R_y, \phi_y)$. Using this function together with f_0 and g_0 permits us to specify $V_y = h_0(f_0(\phi_y), g_0(\phi_y), \phi_y) = h_1(\phi_y)$. This latter function is also continuous by construction, permitting the next lemma.

LEMMA 2. The function h_1, given by f_0 and g_0 together with eqns (11) and (12), is continuous.

Now note that eqns (1) and (2) specify $\phi_{y+1} = h_2(V_y, \phi_y)$, which is also continuous.

LEMMA 3. The function h_2, given by eqns (1) and (2), is continuous.

A function transforming ϕ_y into ϕ_{y+1} can now be determined as follows: $\phi_{y+1} = h_2(V_y, \phi_y) = h_2[h_1(\phi_y), \phi_y] = F(\phi_y)$. Thus ϕ_y is transformed into ϕ_{y+1} by a continuous function. This function, F, that transforms ϕ_y into ϕ_{y+1}, has a fixed point; that is, there is a flower distribution ϕ^* that will persist over time if it is once reached (i.e. a flower distribution ϕ^* such that $\phi^* = F(\phi^*)$). This is expressed and proved in the following theorem.

THEOREM. A steady-state flower distribution, $\phi^* = F(\phi^*)$, exists.

Proof. A flower distribution ϕ is at a steady state if and only if ϕ is a fixed point of F; that is, if $\phi = F(\phi)$. The function F is continuous and it maps a compact, convex set, $\Omega = \{x \in \mathbb{R}^n_+ | \Sigma^n_{i=1} x_i = 1\}$ into itself. Therefore, the Brouwer fixed-point theorem applies and F has a fixed point.$\square$

This theorem does not inform us whether the steady-state distribution is unique. Furthermore, the practical relevance of such a distribution is small because the actual path of the flower distribution over time will be affected by elements that are outside of our model. For example, the extent of cloudy or rainy or unusually cold weather will affect the foraging time of bees. More such weather will cut down on foraging time, tending to reduce effective visits to all plant species, but the relative sizes of different flowers' nectar standing crops will also be affected by weather variations, causing changes in the bee distribution. Consequently, some flower species may be hurt relatively more than others by such conditions. Weather also has other effects—the ability of plants to grow will be differentially affected by variations in weather.

We point these things out because we recognize the limitations of the steady-state distributions that come from this model. At the same time, such distributions give a notion of the direction of forces at work in the model and, therefore, such distributions have some interest in spite of their shortcomings. It should be noted that the role of minoring is, in reality, much more important than in our model. The steady, reliable conditions in the model preclude the random variations that, in nature, are likely to make minoring a great aid to survival.

A final point about the results in this section is that they can be generalized considerably beyond the model considered here. Little else was used about eqns (1–12) beyond their being continuous. Many modifications and generalizations could be made to the model without destroying continuity. We have not sought to be as general as possible because we also wished to be able to run computer simulations. Some of these are reported in the next section.

5. Some Calculations

In Tables 1 through 7 below there appear some calculations made with the model. Table 1 shows the baseline parameter values and the long run equilibrium flower distribution that results from those parameters. Three flower species are used in all simulations and the program used a large enough number of years that the flower distribution converges to a long run steady state. The parameters appearing in Table 1 provide an equilibrium distribution in which the three flower species are not greatly different in size. In each of the other tables just one parameter, or parameter set, is changed as compared with Table 1.

The parameters that are varied in the simulations are the display parameters, D_i (Table 2), the nectar production rates, r_i (Table 3), the parameter governing the importance of the bees's initial experience, a (Table 4), and the upper limit of the flower's nectar

TABLE 1
Benchmark simulation

Parameter	Value
n	3
τ_0	0.3
τ_1	0.6
τ_2	0.2
β	0.3
a	0.2
λ	0.2
N_B/N_F	0.4
σ	8
k	50
μ_1	0.8
μ_2	0.7
μ_3	0.87
R_1^*	0.2
R_2^*	0.1
R_3^*	0.4
r_1	0.003
r_2	0.003
r_3	0.005
D_1	0.2
D_2	0.5
D_3	0.1
T_d	30
T_p	80
e_1	0.6
e_2	0.6
e_3	0.6
ϕ_1	0.421
ϕ_2	0.222
ϕ_3	0.357

TABLE 2
Display parameter variations

Flower distribution			Display parameters		
ϕ_1	ϕ_2	ϕ_3	D_1	D_2	D_3
0.421	0.222	0.357	0.2	0.5	0.1
0.448	0.219	0.333	0.15	0.5	0.1
0.387	0.229	0.384	0.25	0.5	0.1
0.394	0.272	0.334	0.2	0.45	0.1
0.448	0.175	0.378	0.2	0.55	0.1
0.399	0.222	0.380	0.2	0.5	0.05
0.446	0.227	0.327	0.2	0.5	0.15

standing crops, R_i^* (Table 5). Variations of these parameters gives a sense of the response of the model to interesting changes in some of their values. Unreported simulations indicate that the number of periods per day could vary quite widely without greatly affecting the equilibrium flower distributions. The effect of varying the number of days per season is curious and discussed in conjunction with Table 6. Lastly, Table 7 reports on variations in the adjustment parameter, λ.

Looking at Table 2 where the display parameters vary, in all cases more display hurts the species. This, then, means that each species is putting too many resources into display (given the values of all other parameters in the model). Display plays a role at the start of the season in attracting bees. This attraction, in turn, determines the initial bee distribution which affects minoring. In our model the value of minoring is, in fact, very low because the random elements that are so important in real life are missing. In addition, the simulations have, apart from those in Table 5, the parameter a set to 0.2, a relatively low value. This parameter is the weight given to first experience, as compared with recent foraging experience, in determining the distribution of bees among flowers. If a were larger, display would be more valuable.

In Table 3 it is clear that as r_1 increases species 1 benefits; however, as r_2 increases species 2 is worse off.

The experience of species 3 is similar to that of species 2. That species 2 is worse off with higher nectar production while the other two species are better off is due to species 2 spending a very small fraction of its total resources directly on reproduction. The fractions for the three species are, respectively, 65%, 35%, and 65%. Resources for reproduction are, for species 2, extremely scarce and increasing them by either lowering r_2 or lowering D_2 helps it. If the nectar production rate is set to zero for one species while it remains at the benchmark value for the remaining two species, the fraction for the species producing no nectar is positively related to the display of the species. Species 2 with the largest display still accounts for 0.159 of all flowers, while species 3 is reduced to 0.014. The substantial population of species 2 in these circumstances is consistent with the observation that a flower can do well as a ''deceiver'' when it has a large display.

The effect of variations in the parameter a is shown in Table 4. As the parameter rises, the first term in the square brackets in eqn (4) acquires increasing value. That is, initial experience based on display increases in importance for determining the distribution of bees to flowers and the recent foraging experience shrinks in importance. Not surprisingly, when $a = 1$ or is close to 1, the flower distribution strongly parallels the relative display strengths. When $a = 0$, the second species, with its very large display, suffers badly.

TABLE 3
Nectar production variations

Flower distribution			Nectar production rates		
ϕ_1	ϕ_2	ϕ_3	r_1	r_2	r_3
0.421	0.222	0.357	0.003	0.003	0.005
0.392	0.235	0.373	0.002	0.003	0.005
0.072	0.349	0.579	0	0.003	0.005
0.426	0.219	0.355	0.004	0.003	0.005
0.414	0.235	0.351	0.003	0.002	0.005
0.460	0.159	0.381	0.003	0	0.005
0.438	0.193	0.369	0.003	0.004	0.005
0.420	0.216	0.364	0.003	0.003	0.004
0.675	0.311	0.014	0.003	0.003	0
0.429	0.231	0.340	0.003	0.003	0.006

TABLE 4
Minoring variations

Flower distribution			
ϕ_1	ϕ_2	ϕ_3	a
0.430	0.155	0.415	0
0.421	0.222	0.357	0.2
0.396	0.316	0.288	0.4
0.357	0.431	0.212	0.6
0.311	0.559	0.130	0.8
0.282	0.667	0.051	1

TABLE 6
Variation in days

Flower distribution			
ϕ_1	ϕ_2	ϕ_3	T_d
0.421	0.222	0.357	10
0.421	0.222	0.357	20
0.421	0.222	0.357	30
0.551	0.266	0.183	31
0.590	0.283	0.127	32
0.630	0.326	0.044	33
0.617	0.318	0.065	34
0.610	0.315	0.075	35
0.610	0.315	0.075	40
0.610	0.315	0.075	50
0.610	0.315	0.075	60

Variations in the capacity of the flowers to hold nectar (R_i^*) are reported in Table 5. The values used in simulations reported above are so large that they are never a source of constraint on the model. Note that our model has no random weather variations of sun, cloud, or rain that might affect the bees; instead our weather is sunny and warm for 8 hours each day and inhospitable to the bees for 16. Consequently, the flowers' nectar standing crops are, through the bulk of the day, very small. They build up overnight when $8r_i$ of nectar is produced with no harvesting occurring. This means that the capacity of a flower must be near to $8r_i$ before capacity becomes a binding constraint (i.e. 0.024, 0.024, and 0.04 respectively).

Equilibrium flower distributions are shown in Table 5 for various values of R_i^*. Notice first that when capacities are (0.03, 0.03, 0.05) there is no change in the flower distribution as compared with (0.2, 0.1, 0.4), the values used in prior tables, which indicates that the flowers never carry more than this. When each new day starts they carry at least (0.024, 0.024, 0.04). To show the effect of R_i^* Table 6 shows flower distributions as R_i^* is reduced. The fraction of species 1 flowers does not drop greatly when $R_1^* = 0.005$, which is much below 0.024. This indicates that daytime nectar standing crops generally run well below the overnight minimum of 0.024. Clearly this is to be expected. At $R_i^* = 0.002$ ϕ_1 is still 0.302 and from 0.002 downward ϕ_1 drops quickly. The final row of the table show the flower distribution for (0.005, 0.005, 0.05). With both species 1 and 2 at notably reduced capacities, species

2 loses very little and species 1 loses much more. The obvious explanation is that species 2 derives much more of its pollination from the effect of its display.

The effect of T_d, the number of days in the season, on the flower distribution is shown in Table 6. From 10 to 30 days, changes in T_d appear to have no effect and from 35 to 60 days changes also have no effect, but within those two ranges the distributions are different. In addition over the interval of 30 to 35 the distribution changes with 33 days looking slightly anomalous. The fewer the number of days, the better off was the flower distribution with the largest display.

Changing the rate of adjustment has predictable effects; when the rate becomes very slow, display takes on relatively greater importance compared with nectar production. This is because a larger display attracts more bees at the start while a slower rate of adjustment means that the bees take longer to move away from a flower with low nectar production. Consequently, the early attraction from display has more scope to aid the flower than when adjustment is faster. With $T_p = 80$ the value of λ must be very near to one if adjustment is going to be "slow". For example, consider the extreme case of a two species model with $r_1 = 0$, $r_2 > 0$, $D_1 > 0$, $D_2 > 0$, and $\phi_1 = \phi_2$. Then the initial bee distribution is $p = D_1/(D_1 + D_2)$ at species 1 and $1 - p$

TABLE 5
Nectar capacity variations

Flower distribution			Flower capacity		
ϕ_1	ϕ_2	ϕ_3	R_1^*	R_2^*	R_3^*
0.421	0.222	0.357	0.2	0.1	0.4
0.421	0.223	0.356	0.03	0.03	0.05
0.373	0.241	0.386	0.005	0.03	0.05
0.302	0.268	0.430	0.002	0.03	0.05
0.173	0.315	0.512	0.001	0.03	0.05
0.100	0.340	0.560	0.0005	0.03	0.05
0.385	0.221	0.394	0.005	0.005	0.05

TABLE 7
Adjustment parameter variations

Flower distribution			
ϕ_1	ϕ_2	ϕ_3	λ
0.421	0.222	0.357	0.2
0.421	0.222	0.357	0.99
0.402	0.262	0.336	0.999
0.296	0.591	0.113	0.9999
0.283	0.660	0.057	0.99999
0.282	0.667	0.051	0.999999

at species 2. In these circumstances, the bee distribution will eventually reach $(p/3, 1-p/3)$. If $\lambda = 0.4$, as in the benchmark simulation, this bee distribution will be reached by the end of the first hour (10 periods). With $\lambda = 0.7$, this eventual bee distribution will be reached by the end of the second hour, with $\lambda = 0.99$ this eventual bee distribution will be reached by the end of the first season, but for $\lambda = 0.9999$, the bee distribution never falls below $(0.9p, 1-0.9p)$ during the course of the season. Adjustment is sufficiently slow that bees continue to make many visits to the species that produces no nectar. We do not consider such slow adjustment to be realistic; these numbers merely illustrate the effect that the adjustment rate can have on visits and on the viability of a species. They also give some feel for what values of λ constitute "slow" or "fast" adjustment.

Examining results for the simulations, Table 7 shows steady-state flower distributions for various values of λ, together with benchmark values for the other parameters. With λ at values of 0.99 or less, the benchmark distributions prevail, but, as λ rises from there, the flower distributions change until species 2 (with the very large display) goes from 0.222 to 0.667 and species 3 drops from 0.357 to 0.051. As noted earlier, if bees were born throughout the season when flowers bloomed, this would increase the value of display and increase the fitness of cheaters (flowers with large displays and small nectar rewards). Thus, steady bee births and slower adjustment speeds have the same effect on flower fitness.

6. Concluding Remarks

We have presented a model in which bees and flowers interact in a relatively sophisticated dynamic environment. Our focus is on the characteristics of the flower species and how the population proportions of the several species respond to the relative sizes of the flowers' displays, nectar production rates, and the costs of both display and nectar. We model detailed behavior throughout a season and then model a succession of seasons for any finite number of flower species. The principal result of the model is the theorem which proves that, for any parameter selection, a steady-state flower distribution exists. Then some simulations based on three flower species are carried out to give the flavor of the model by illustrating several equilibrium outcomes.

It is our contention that this model could prove helpful in describing the field behavior of bees if sufficient data could be obtained to fit the model. By manipulating the parameters, many different behavior patterns and flower distributions could be generated. It should be emphasized, however, that the steady-state distributions that our model would predict are subject to many criticisms. One of the most basic is that the model implicitly assumes that all influences that are not explicitly in the model will operate in exactly the same ways from year to year. Thus, for example, weather conditions will actually vary from year to year, but this does not enter our scheme. In practice, some species whose population is small may thrive in a year in which the weather conditions favoring it occur. If the bee population were to grow or shrink relative to the flower population, the behavior of the model would vary correspondingly. This, of course, could be easily demonstrated by changing N_B/N_F.

The model developed here provides a means of examining the dynamics of the pollination market. There are various directions in which this effort could be extended. For example, suppose a bee gains experience (τ_1 falls) during a bout and consequently has lower handling cost if it visits the same species at the next bout. If the bee switches and then switches back, it loses some of the skill it picked up. Another extention would be to add additional bee species, with each species having some specialization that would fit it relatively better to a particular flower species. Random weather patterns that affect the timing and extent of foraging activity could be added, as could a cost for nectar storage capacity of a flower (R^*). Finally, and very importantly, flower mutations might be incorporated into the model and ESS equilibria examined.

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