

AN ABSTRACT OF THE THESIS OF

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Title: A Model Study of the Alfalfa Leafcutter Bee -  
Seed Production System.

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The behaviors of the alfalfa leafcutter bee - seed production system under imposition of several management regimes were studied through the use of a simulation model that contains mechanisms for the following processes: 1) immature bee development and diapause; 2) immature bee mortality; 3) female bee emergence; 4) nesting tunnel selection; 5) egg-laying; 6) adult mortality; and 7) flowering and seed production.

Management tactics studied through the use of simulation included: 1) varying the number of female bees introduced at the start of the season relative to the flower supply; 2) varying the time of initial bee emergence relative to initial flowering; 3) varying the number of introduced open tunnels relative to the number

of introduced female bees; and 4) varying the time of initial system activities (emergence and flowering).

The annual resolution model outputs, diapause female bee production and seed production, were studied to reveal the following behaviors:

- 1) Bee production increases when the initial emergence and flowering are delayed beyond the standard management time.
- 2) Seed production increases with a two week delay, but decreases with a four week delay.
- 3) With increasing bee introductions, bee production behaves similarly for both delay tactics, but quite differently for the standard.
- 4) With increasing bee introductions, seed production increases rapidly to a maximum and then levels off, for all three tactics.
- 5) The effects on bee and seed productions of asynchrony in first emergence and flowering depend on the timing of the onset of flowering. In almost all circumstances, the flowering delay tactic is better than the standard tactic, but greater asynchrony in the direction of late emergence is best offset by the standard tactic.
- 6) The introduction of open tunnels with small capacities (rather than large) greatly reduces the rate of bee population increase. The population

increase is also greatly reduced when the overall capacity of the introduced open tunnels is insufficient for the population's cell production.

7) Seed production is insensitive to the open tunnel introduction.

The identification of key mechanisms for the above behaviors led to the examination of current knowledge of those mechanisms and to the identification of needed research. The model provides a coherent, whole system perspective for management and research applications.

A Model Study of the  
Alfalfa Leafcutter Bee - Seed Production  
System

by

Steven Bruce Stark

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# A Model Study of the Alfalfa Leafcutter Bee - Seed Production System

## I. Introduction

Modeling provides a basis for the study of complex systems. The complexity of a system in terms of numbers of variables and processes involved in its dynamics is often incomprehensible without the structures imposed by the model. A framework is supplied to provide a context within which the many processes and their interrelations can be understood. Moreover, without a model, a particular behavior is often difficult to comprehend because it depends on certain processes, which are not recognized as important until the whole system is conceptualized. Modeling provides an explicit structural representation of a whole system, as a framework for the organization of thought.

Much information has been accumulated about certain aspects of the biology of the alfalfa leafcutter bee, Megachile rotundata Fabr., which is widely managed for the pollination of alfalfa in the Pacific Northwest. However, as in much of biology, most effort has focused on biological details. Little attention has been paid to the overall system, the level appropriate to complex questions regarding leafcutter bee management. This

paper documents the development and use of such a whole system conceptualization for the alfalfa leafcutter bee - alfalfa seed production system.

The leafcutter bee is usually the pollinator of choice for alfalfa seed production, since it is oligolectic, preferring alfalfa over other plant species, and gregarious, tending to nest in a common area (Stephen 1962). Alfalfa requires cross-pollination for maximum seed production, since it is relatively self-infertile and achieves good seed set only when the flowers are tripped (Carlson 1946, Zaleski 1956). However, as costs of utilization of this bee have increased sharply, a management protocol which could couple greater pollination efficiency with increased bee propagation is sought by the producer. The alfalfa leafcutter bee-seed production system model was constructed to facilitate the development of such effective management by enhancing the system conceptualization and by providing a means for evaluating specific management tactics.

The model includes some mechanisms which are not understood in great enough detail to be associated with precisely estimated parameters. However, these mechanisms are essential to the model's purpose, and, although their parameter values are somewhat subjective, they are felt to represent the current knowledge base. By integrating these mechanisms into a model structure,

their significance in the system behavior can be determined. Future research will benefit by focusing on the significant mechanisms.

The model was constructed to simulate the female population dynamics and the seed production resulting from bee foraging under environmental conditions typical of eastern Oregon and under the imposition of certain management tactics. The anticipated management tactics included those affecting: 1) the flower supply-demand relation; 2) the nesting tunnel supply-demand relation; and 3) the environmental conditions under which bees and seed are produced. The flower supply-demand relation is affected by the tactic of varying the number of female bees introduced at the start of the season relative to the flower supply. This relation is also affected by the tactic of varying the time of initial bee emergence relative to initial flowering, thus altering the coincidence of the trajectories of nesting bees and flowers. (A trajectory is a sequence of values of a system variable over time.) The nesting tunnel supply-demand relation is affected by the tactic of varying the number of introduced tunnels relative to the number of introduced female bees. The environmental conditions under which bees and seed are produced are affected by

the tactic of varying the time of initial system activities (emergence and flowering).

The strategy of model construction reported by Overton (1977) was utilized in this study. This strategy has been used effectively in modeling the dynamics of two herbivore-plant systems, the cinnibar moth, Iyria jacobaeae (L.), controlling a noxious weed, tansy ragwort, Senecio jacobaea L., (Stimac 1976), and the Douglas fir tussock moth, Orgyia pseudotsugata (McDunnough), damaging stands of fir trees (Colbert et al. 1979). Early in the project, a familiarity with the system was obtained through direct experience with the system, discussion with researchers in the field, and a review of the relevant literature. Model objectives were outlined, leading to the identification of key system variables and processes essential for representing the target system behaviors under the anticipated management. The system conceptualization which evolved was then translated into a mathematical model. Finally, the model was implemented on the computer and used in behavioral and sensitivity analyses.

## II. Natural History of the Alfalfa Leafcutter Bee - Seed Production System

The natural history of the leafcutter bee system provided the necessary information base for model development. To facilitate the understanding of the model, a description of the natural history follows.

In the management of the leafcutter bee, populations are established in domiciles distributed in or about the alfalfa fields to be pollinated. Each domicile is provided with a nesting medium, often drilled boards or boxes of drinking straws, in which brood cells are constructed by the nesting females. Within a nesting tunnel, a linear series of cells is constructed by a female, each formed of leafcuttings and provisioned with pollen and nectar. In a cell, a single egg is laid on the provision, the cell is capped, and the next cell in the series is constructed. Fertilized eggs, which develop into females, are laid in the inner cells of the tunnel series and unfertilized eggs, which develop into males, are laid in the middle and outer cells (Gerber and Klostermeyer 1972).

Upon completion of the tunnel series, the tunnel opening is capped with 12 to 50 leafcuttings. Tunnel capping may require up to half of the female's nesting time when shallow tunnels are utilized (Stephen and Osgood 1965b).

This study is oriented towards the use of so-called solid nesting media, e.g. drilled boards and drinking straws, from which the cells are not removed. Other nesting media, from which the brood cells can be individually removed, are also used in bee management to reduce parasites and disease.

Under normal conditions, a single cell is completed in about seven hours, but when weather is unfavorable or forage is limited several days may be required. Temperature and light control adult foraging activity. Klostermeyer and Gerber (1969) found that adult activity under their test conditions is initiated only after the temperature and light intensity reach 21° C and 0.2 langleys, respectively.

Under normal field conditions, the adult female bee lives up to 40 days (Stephen 1973). Stephen (unpubl. data) found that in laboratory populations approximately 75% lived through the third week of adult life, 50% lived through the fourth week, and 10% lived through the fifth week. These data indicate an average adult lifespan of between three and four weeks under laboratory conditions. Lack of food can significantly reduce this lifespan, with starvation occurring in four days at 21° C under laboratory conditions (Stephen unpubl. data). In the field, adult starvation occurs when alfalfa flowers are unavailable or when weather conditions are unsuitable for bee flight.

During her lifetime, the adult female bee produces up to 35 eggs in her ovaries (Stephen 1973). Gerber and Klostermeyer (1972) noted a maximum lifetime production of 35 to 40 cells. Eggs are normally not produced fast enough for the bee to lay more than two eggs per day, although other factors such as temperature, light intensity, or forage availability usually limit the average to less than one egg per day (Klostermeyer and Gerber 1969). Total offspring per female appears to be quite variable, depending on foraging resources, nesting resources and weather conditions. Eves and Johansen (1974) claim that an average of 12 offspring are produced per female, while Klostermeyer et al. (1973) reported three females to produce 19, 23, and 24 cells, respectively.

Nesting tunnel selection by newly emerged females or females which have just completed a tunnel seems to be a fairly complex process. Female leafcutter bees are gregarious and tend to select tunnels in areas of intense nesting activity (Stephen and Torchio 1961). They also tend to select the tunnels from which they emerged (Gerber and Klostermeyer 1972), or tunnels in close proximity (Bohart and Knowlton 1964). Tunnels in which nesting activity previously occurred are also preferred over unused tunnels.

Partially completed inactive tunnels left by the loss of a previous bee may be reoccupied by a second bee. This reoccupation may or may not be followed by the removal of the cells of the previous bee. If the original cells are not removed, the inner bees will probably develop and emerge before those of the second female, resulting in larval mortality (Stephen 1973, Stephen and Osgood 1965b).

A domicile usually contains tunnels of various depths. Tunnel depth is affected by the accumulation of debris and bee cadavers from previous nesting (Pedersen et al. 1972). Bees prefer tunnels of intermediate depths (Gerber and Klostermeyer 1972) and diameters closely approximating body size.

Nesting females are reported to lay a greater percentage of fertilized eggs in deep tunnels than in shallow tunnels (Gerber and Klostermeyer 1972, Stephen and Osgood 1965b). However, these females may not emerge from the tunnel, even if they survive through the immature stages and emerge from their cocoons. Mortality due to tunnel blockage by nesting debris and bee cadavers has been noted (Stephen and Every 1970, Stephen 1962, Stephen and Osgood 1965b). Deep tunnels contain more cells through which the bees must emerge, and, thus, are associated with greater emergence mortality than shallow tunnels. This mortality factor clearly affects female

Good idea to  
clean out  
Bee Boards  
on Time  
properly

bees, which are in the bottom cells of tunnels, more than male bees, which are in the middle and top cells of tunnels. An average of 60% immature mortality with 10% emergence mortality is typical of bee populations propagated in solid nesting media (Stephen, personal communication).

Emergence mortality contributes to a sex ratio dominated by males. Moreover, as bee cadavers and nesting debris accumulate in a tunnel with each successive nesting, the proportion of fertilized (female) eggs laid decreases. The overall result is a highly skewed sex ratio of emerged bees, typically of three males to one female.

The value of the bees in the management system is greatly reduced by the large production of males. Females are responsible for almost all the pollination, males only occasionally tripping a flower while feeding on nectar. Excessive numbers of males interfere with the foraging activities of females by attempting to copulate, and thus reduce female productivity. Moreover, since females need to mate only once and males mate numerous times, the highly skewed sex ratio reflects far more males than are necessary for adequate fertilization.

The developmental rate of immature bees is temperature dependent. The larvae develop at temperatures between 19° and 38° C with a maximum rate at

32° C (Stephen and Osgood 1965a). The relationship between developmental rate and temperature is approximately linear between 19° and 32° C, suggesting the applicability of a simple thermal summation model for predicting development and emergence. Although the size of the provision has been associated with the size of the adult bee (Klostermeyer et al. 1973) no association between nutrition and developmental rate has been reported. Under normal field conditions, eggs hatch in two to four days, and larvae reach maturity with the completion of the cocoon in 14 to 20 days (Stephen 1973). The larvae either develop to the pupal stage and emerge as adults in 10 to 15 days, or enter diapause as prepupae and overwinter. The nondiapause bees thus require from 26 to 40 days to develop from egg to emergent adult.

The facultative diapause in the leafcutter bee is likely induced by environmental cues, thought to be photoperiod interacting with temperature (Stephen, personal communication). When exposed to the appropriate cue, the female lays eggs which develop to the prepupal stage and enter diapause. The percent of larvae which enter diapause increases during the season (Johansen and Eves 1973, Kronic 1972). Currently in field populations of eastern Oregon, 100% of eggs laid after July 20 mature to a prepupal diapause (Stephen, personal communication). Before this date, the percent of diapausing prepupal bees

is increased by cool weather conditions. Under typical eastern Oregon conditions, approximately 50% of the eggs laid by the first generation bee will undergo prepupal diapause. In a Washington population, Johansen and Eves (1973) found 10-30% diapause bees in tunnels completed the last half of June, 47-67% diapause bees in the first half of July, 88% diapause bees in the last half of July, and 100% diapause bees thereafter.

Immature leafcutter bees are hosts to a variety of parasites and predators (Hobbs 1968, Waters 1971). Several wasps, including Monodontomerus obscurus Westwood, Leucospis affinis Say, Tetrastichus megachilidis Burks, and Melitobia chalybii Ashmead, are parasites on the immature bees and may cause substantial losses. The wasp, Sapyga pumila Cresson, consumes the cell provision after destroying the egg, as do the beetles Trichodes ornatus Say and Nemognatha lurida LeConte. A variety of other insects, including dermestid beetles, flour beetles, fruit moths and meal moths, destroy the brood cells and provisions.

Chalkbrood, a fungal disease caused by Ascosphaera aggregata, also affects the leafcutter bee larvae, often causing losses in excess of 40% (Stephen and Undurraga 1978). Infected larvae usually die in the last instar, converting to a chalky cadaver laden with the fungal spores. The disease is spread by the use of contaminated

nesting media and by adult bees which become contaminated when chewing through cadavers during emergence (Vandenberg et al. 1980).

Timing of the female bee activity is an important consideration for effective management. Initial emergence of the first generation is usually timed to coincide with the onset of alfalfa flowering. In eastern Oregon, bees are normally managed so that emergence of half of each population starts approximately June 22. The other half of the population may be held back to emerge a week later, reducing the number of bees flying before the alfalfa has produced adequate flowers for brood cell provisioning. Under controlled incubation, emergence is usually 90% complete in 10 days. Coupled with the five week maximum lifetime of adult female bees, this results in a first generation flight period of approximately seven weeks, ending approximately August 10.

Management of the thermal environment of diapausing bees can also be used to alter the first generation emergence times. A period of exposure to cold during diapause shortens the time until emergence and increases the synchrony of emergence (Johansen and Eves 1973). Early season bee activity can also be delayed without increasing mortality by holding the newly emerged bees

below the activity threshold temperature (Stephen, unpublished data).

In eastern Oregon, the second generation begins emergence when the first generation flight ends. However, second generation flight often extends into periods of inclement weather and limited flower production. Since alfalfa seed must be harvested as early as possible to avoid losses due to fall rains, some second generation bees starve because of insufficient forage, and usually fail to replace themselves.

Thus, the dynamics of alfalfa flowering are of major importance in the bee - seed production system. In leafcutter bee populations managed for seed production, the alfalfa flower provides the primary source of nutrition for both the immature and adult bees. However, alfalfa flowers cannot be viewed simply as an input to the system because the intensity of pollination affects the future course of flowering. A first set of racemes produces flowers from about the last week of June through the end of July under standard management conditions in eastern Oregon. Flowers from a second set of racemes appear toward the end of this first bloom period, after about 30 days from the start of flowering (Stephen, personal communication). However, intense pollination of flowers of the first set of racemes reduces or halts the

production of this subsequent bloom (Stephen, personal communication).

Various tactics are available for managing the timing and duration of alfalfa flowering. Cutting the alfalfa in early spring is used to delay the development and production of flowers until conditions are favorable for bee flight (Drake 1949, Kolar et al. 1968, Zaleski 1956). Flowering increases gradually from the appearance of the first flower to full bloom, a period of about two to three weeks (Todd and Vansell 1952). Vegetative growth is favored over reproductive growth if the soil moisture is high during the flowering period, but seed yields may be reduced (Taylor et al. 1959). Alternatively, stressing the plant by withholding moisture during the flower development period can result in peak bloom one week after initiation of flowering (Stephen, personal communication). Reduced seed yields can result, however, especially if water is withheld too early (Taylor et al. 1959).

Flower availability is also affected by bee foraging behavior. Female bees prefer to forage within the vicinity of the domicile (Bohart 1962), but will forage at greater distances as flowers become scarce. Bacon et al. (1965) found most bees foraging within 100 feet of the domicile early in the season. Later in the season, when flowers became scarce about the domicile, more than

half the females were foraging at 150 to 250 feet, and an occasional female was foraging at 450 to 500 feet. Thus, different spatial patterns of pollination can occur in the field, depending on the location and size of the bee populations, the location and number of flowers produced, and the conditions for bee foraging. The female leafcutter bee trips the alfalfa flower when gathering pollen, which causes the flower to wilt within 24 hours and become unavailable to other females (Palmer-Jones and Forester 1972). An untripped flower remains available for five to ten days, after which it wilts and drops (Todd and Vansell 1952). Thus, the flower availability is determined by the number of flowers opening, the number pollinated, and the number wilted and dropped.

### III. Alfalfa Leafcutter Bee - Seed Production System Model

#### A. Model Overview

Although the alfalfa leafcutter bee-seed production system model operates at the weekly resolution, the various management tactics are best evaluated on annual resolution information. Information on the annual diapause female bee production and seed production is required since both variables are relevant in evaluating tactics.

In addition to other model structures for predicting female bee production, a detailed structure to account for the capacities of nesting tunnels was required. As discussed above, nesting females are reported to lay a greater percentage of female eggs in deep tunnels than in shallow tunnels and to suffer greater mortality due to blocked emergence in deep tunnels. Thus, female bee production depends on the distribution of the total bee production into tunnels of various depths. The importance of this distribution on the dynamics of the female bee population led to the identification of the distribution of tunnels over depths as a key state variable in the model.

The coupling of subsystems, representing system processes, by state variables is illustrated in Figure 1.

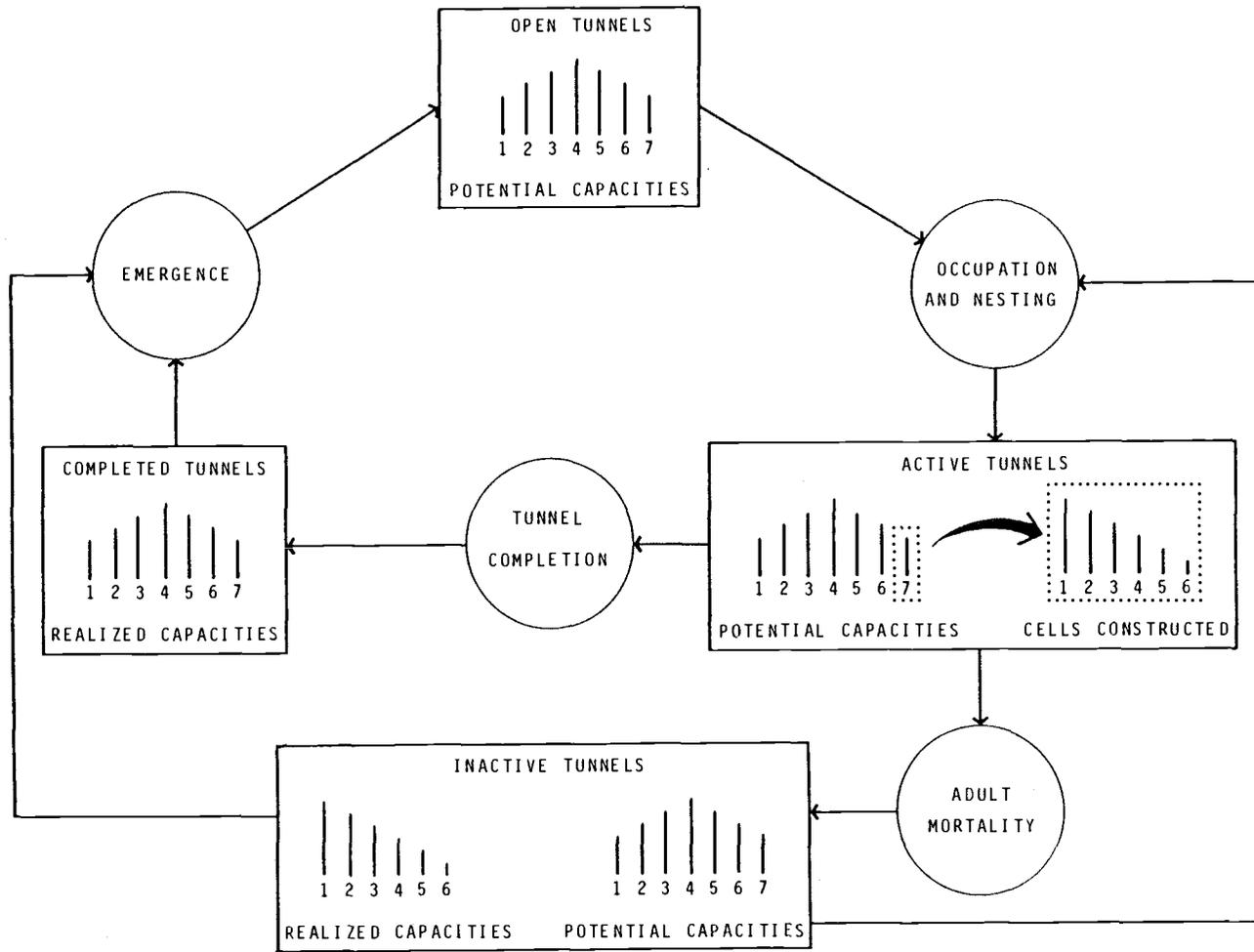


Figure 1. Major processes and state variables of the leafcutter bee system.

The state variables represent the numbers and distributions over cell capacity classes of tunnels of different types. Open tunnels are defined as tunnels lacking both a nesting bee and live brood cells. These tunnels may be partially filled with debris and bee cadavers left from previous nesting and emergence, resulting in a reduced cell capacity of each tunnel. Open tunnels are classified by their potential capacities, the number of cells they are expected to contain upon completion.

Occupation and nesting transforms open tunnels into active tunnels, defined as tunnels occupied by nesting bees and partially filled with brood cells. An active tunnel is classified by the age of the nesting bee. The nesting female population is represented as five weekly cohorts by five sets of active tunnels. Females that have reoccupied inactive tunnels are also represented, as are those that have failed to occupy a tunnel. The completion stage of each active tunnel is classified according to the potential capacity and the number of brood cells in the tunnel.

Tunnel completion transforms active tunnels into completed tunnels, which are defined as tunnels filled to their expected capacities and capped. Completed tunnels are classified by their realized capacities, which equal their potential capacities upon the last occupation.

They are classified as diapause, if the prepupae will eventually overwinter, or nondiapause, if the prepupae develop into adults during the current season. The process of emergence transforms these completed tunnels into open tunnels with reduced cell capacities due to the accumulation of nesting debris and cadavers.

Nondiapause immature bees in tunnels completed during the same week are modeled as a cohort. Overwintered bees in tunnels introduced at the start of the season are also modeled as a cohort. The age of the developing nondiapause bees is determined by the number of weeks since their tunnel was completed or introduced. The development of each cohort of nondiapause bees is represented by a day-degree accumulation. Diapause bees from any week are modeled as a single cohort, and the age of these bees is not accounted for.

Active tunnels are transformed into inactive tunnels if adult mortality occurs before their completion. Inactive tunnels are defined as tunnels partially filled with brood cells, but containing no nesting females. Immature bees in tunnels left inactive during the same week are modeled as a weekly cohort, classified as diapause or nondiapause, and aged by the number of weeks since the death of the nesting bees. Diapause bees in inactive tunnels from all weeks are modeled as a single cohort. The age and development of these bees are not

accounted for. Inactive tunnels are classified by their capacities before occupation (potential capacities) to account for their residual capacities after emergence. To account for the number of females eventually emerging from these tunnels, the total females they contain is determined. The realized capacity of an inactive tunnel is used in this calculation and is defined as the number of cells it contained upon the death of the nesting bee.

Since the inactive tunnel is not filled to capacity or capped, it may be reoccupied by another nesting female, a process which transforms it to an active tunnel. If not reoccupied, the nondiapause inactive tunnel will be transformed into an open tunnel by the process of emergence. The diapause inactive tunnel will overwinter.

Another system representation, shown in Figure 2, provides a different view of the processes modeled in this system. In this, the above processes are included in one of two subsystems, representing either processes associated with emergence or with tunnel filling. The emergence subsystem includes all processes involved in the generation of adult female bees and open tunnels from completed and inactive tunnels. The tunnel filling subsystem includes all processes involved in the generation of completed and inactive tunnels of various types through the activities of nesting bees. The

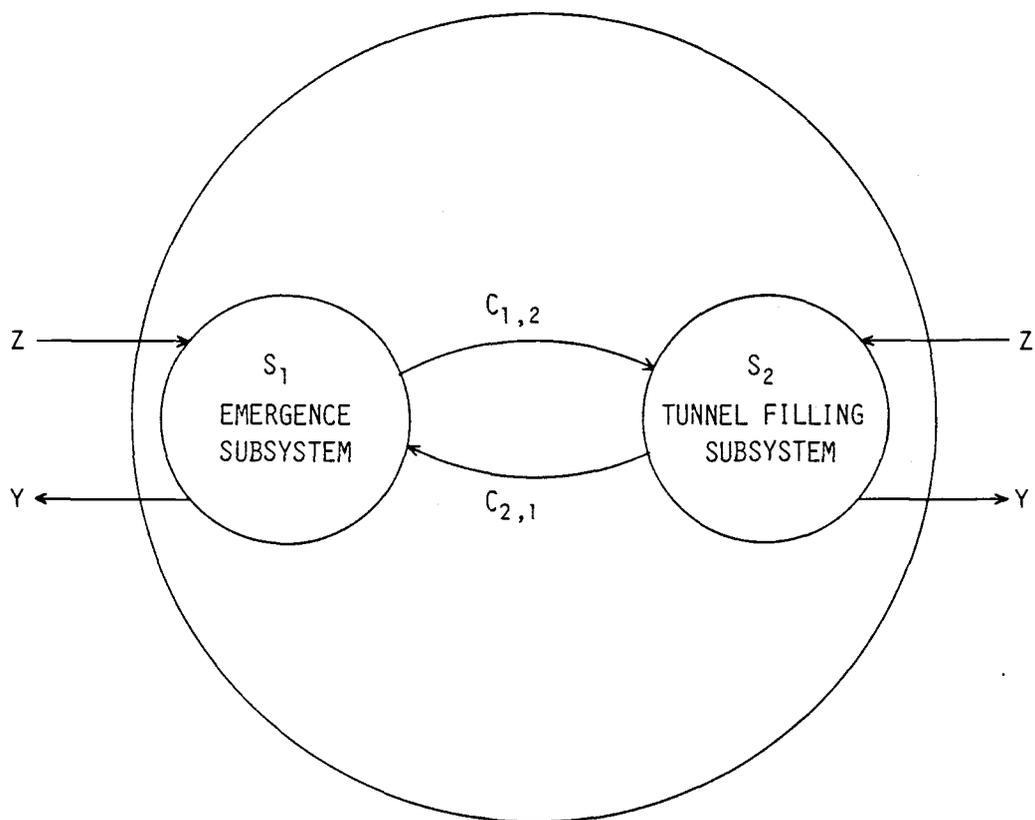


Figure 2. Decomposition of the leafcutter bee system into coupled subsystems.

directed couplings between the two subsystems, the outputs from one subsystem which are necessary for the operation of the other, are also represented. The couplings between the emergence and tunnel filling subsystems are listed in Table 1 along with state variables necessary to account for the performance of the system.

The weekly resolution outputs generated by the tunnel filling subsystem as required for the operation of the emergence subsystem are: 1) nondiapause tunnels with realized capacities of one to seven cells completed this week; 2) nondiapause tunnels left inactive this week; and 3) inactive tunnels cleaned out this week. The completed and inactive tunnels are input to the emergence subsystem to account for their development, mortality, and emergence. As inactive tunnels may be reoccupied and cleaned, thus halting the developmental process, information on tunnel cleaning is a necessary input into the emergence subsystem.

The weekly resolution outputs generated by the emergence subsystem, which are necessary for the operation of the tunnel filling subsystem, are: 1) open tunnels with potential capacities of one to seven cells from this week's emergence; 2) nondiapause inactive tunnels emerging this week; and 3) newly emerged female bees. Newly available open tunnels are produced by

Table 1. Subsystem couplings and state variables of the leafcutter bee system.

Variable Description	Subsystem Couplings		State Variable
	S <sub>1</sub> : Emergence	S <sub>2</sub> : Tunnel Filling	
tunnels with realized capacities of 1-7 cells completed this week (vector)	Z <sub>1</sub>	Y <sub>1</sub>	
tunnels left inactive this week	Z <sub>2</sub>	Y <sub>2</sub>	
inactive tunnels cleaned out this week	Z <sub>3</sub>	Y <sub>3</sub>	
nondiapause tunnels with realized capacities of 1-7 cells introduced this week (vector)	Z <sub>4</sub>		
day-degrees for immature bee development	Z <sub>5</sub>		
immature bee survival from chalkbrood	Z <sub>6</sub>		
immature bee survival from background mortality	Z <sub>7</sub>		
diapause inducing environmental conditions	Z <sub>8</sub>		
open tunnels with potential capacities of 1-7 cells from this week's emergence (vector)	Y <sub>1</sub>	Z <sub>1</sub>	
nondiapause tunnels completed 1-10 weeks ago with realized capacities of 1-7 cells (vector)	Y <sub>2</sub>		X <sub>1</sub>
nondiapause inactive tunnels from the last 1-10 weeks (vector)	Y <sub>3</sub>		X <sub>2</sub>

(Table 1, continued)

Variable Description	Subsystem Couplings		State Variable
	S <sub>1</sub> : Emergence	S <sub>2</sub> : Tunnel Filling	
inactive tunnels emerging this week	Y <sub>4</sub>	Z <sub>2</sub>	
inactive diapause tunnels	Y <sub>5</sub>		X <sub>3</sub>
completed diapause tunnels of realized capacities of 1-7 cells (vector)	Y <sub>6</sub>		X <sub>4</sub>
newly emerged female bees	Y <sub>7</sub>	Z <sub>3</sub>	
day-degrees for immature development accumulated over the past week, 2 weeks, . . . , 10 weeks (vector)	Y <sub>8</sub>		X <sub>9</sub>
introduced open tunnels with potential capacities of 1-7 cells (vector)		Z <sub>4</sub>	
day-degrees for foraging activities		Z <sub>5</sub>	
open alfalfa flowers		Z <sub>6</sub>	
survival rates of adult female bees 1-5 weeks old (vector)		Z <sub>7</sub>	
open tunnels of potential capacities of 1-7 cells (vector)		Y <sub>4</sub>	X <sub>5</sub>
active tunnels of various potential and realized capacities occupied by nesting bees 1-5 weeks old (vector)		Y <sub>5</sub>	X <sub>6</sub>
nesting female bees 1-5 weeks old (vector)		Y <sub>6</sub>	X <sub>7</sub>
eggs laid		Y <sub>7</sub>	X <sub>8</sub>

emerging completed and inactive tunnels and are input to the tunnel filling subsystem for selection and brood cell construction by nesting females. In addition, emerging nondiapause inactive tunnels are no longer available as such for reoccupation, so this information is also required by the tunnel filling subsystem.

Other inputs to the two subsystems are from the environmental subsystem, some of which result from management manipulation. Open and postdiapause completed tunnels can be introduced at various times and in various numbers and distributions over capacities. Flower abundance during the first bloom period can be manipulated through irrigation and preseason clipping. Other inputs, including survival rates of immature and adult bees, are potentially under partial control through management of parasites, predators, and disease.

Several outputs from the two subsystems are state variables (Table 1). These are required to monitor the dynamics of the weekly resolution system. Weekly numbers of open, inactive, and completed tunnels, day-degrees accumulated by the several cohorts of immature bees, nesting female bees of various ages with their active tunnels in various stages of completion, and numbers of pollinated flowers provide necessary information on the within-season system activity.

The annual resolution outputs (seed production and diapause female bee production) required by the management system are obtained from the within-season trajectories of weekly resolution state variables. Annual seed production is obtained as a weighted sum of the numbers of flowers pollinated (computed from the numbers of eggs laid) each week (see  $X_8$  in Table 1). The diapause female bee production is obtained by summing the numbers of diapause female bees in completed tunnels (see  $X_4$  in Table 1), the number of diapause female bees remaining in inactive tunnels at the end of the season (see  $X_3$  in Table 1), and the number of diapause female bees in active tunnels at the end of the season (see  $X_6$  in Table 1). (In computing the diapause females in active tunnels, the tunnels were assumed to contain the same average number of diapause females as the diapause inactive tunnels left at the end of the season.)

#### B. Emergence Subsystem

The coupled subprocesses of the emergence subsystem are illustrated in Figure 3. The  $z$ 's,  $y$ 's, and  $x$ 's represent inputs, outputs and state variables, respectively, identical to those in Table 1 above.

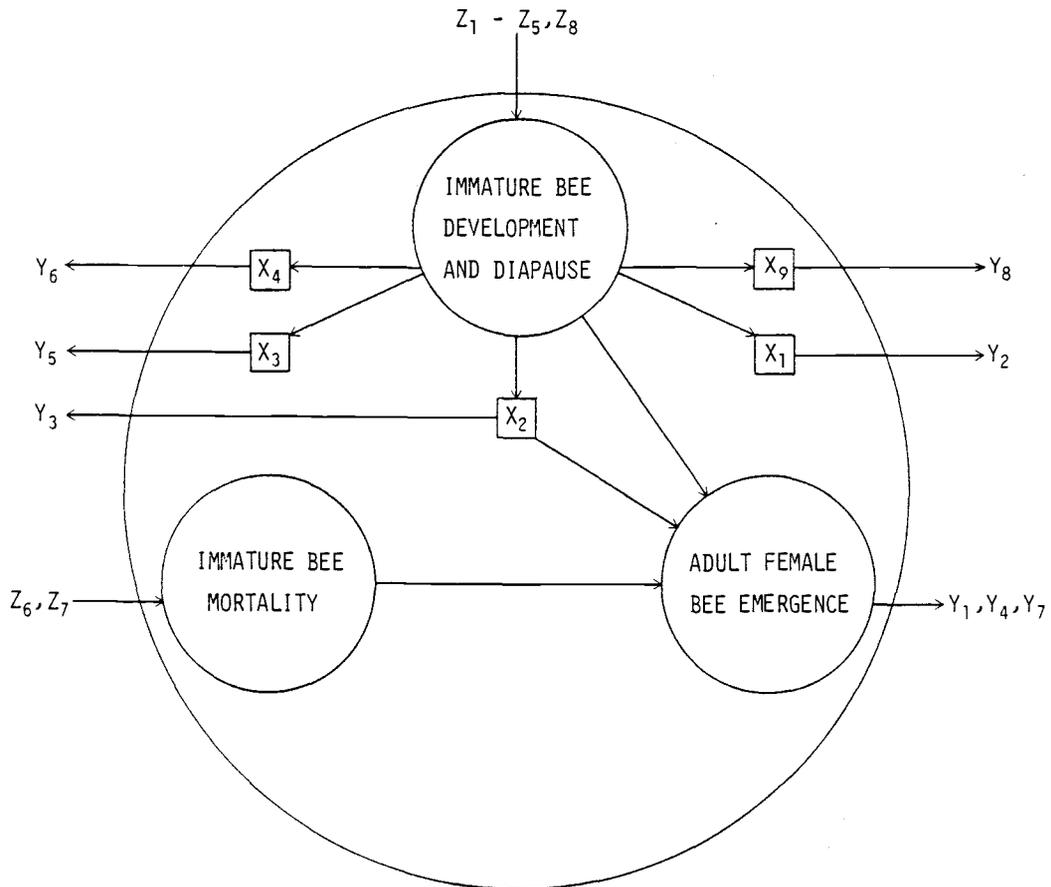


Figure 3. Decomposition of emergence subsystem into coupled subsystems.

Couplings between the subprocesses of the emergence subsystem are shown by internal arrows. Couplings with either the tunnel-filling or the environmental subsystem are also shown as inputs (z's) or outputs (y's).

Immature development is modeled as a temperature-dependent process advancing the stage of development of bees in completed and inactive tunnels. Immature mortality is modeled as a process affected by two mortality sources: 1) chalkbrood, with the level of mortality depending on the inoculum reservoir at the time of tunnel completion, and 2) parasites, predators, and nest destroyers, with the level of mortality depending on the endemic populations and the duration of cell exposure from tunnel completion to emergence. Adult female bee emergence is modeled as a process generating newly emerged females and open tunnels of various potential capacities according to the capacity and type of emerging tunnel (completed or inactive). Immature mortality and adult emergence failure are accounted for at the time of emergence.

#### B-1. Immature Bee Development and Diapause Subsystem

Development of overwintered bees is assumed to resume at the start of the week of introduction. (In the current model implementation, all bees are assumed to be

introduced in a single week.) Development of bees produced during the season is assumed to begin at the start of the week after the tunnel is either capped as a completed tunnel or left as an inactive tunnel. If tunnels are completed or left inactive after a certain date, the tunnels are classed as diapause tunnels for emergence next year. Production of both diapause and nondiapause bees during a week is assumed not to occur.

The developmental progress of a weekly cohort of immature bees is modeled by accumulated day-degrees ( $19^{\circ}$  C threshold). Developmental rates are assumed to be identical among bees in the same tunnel and other tunnels in the domicile at the same time. The day-degree input variable for the week of tunnel introduction is set to a value that accounts for the previous development of the overwintered bees. (For the assumed single cohort introduction, this is equivalent to a prescribed initial condition for the day-degree state variable for the cohort.) Day-degree values for all other weeks represent the actual sums of daily mean temperature above the threshold. Associated with each developing cohort is a state variable that sums the day-degree variable, beginning with the first week of development.

All bees emerging in a week are assumed to emerge at the first of the week. Asynchrony in emergence of an immature cohort is modeled by a ramp function (Figure 4)

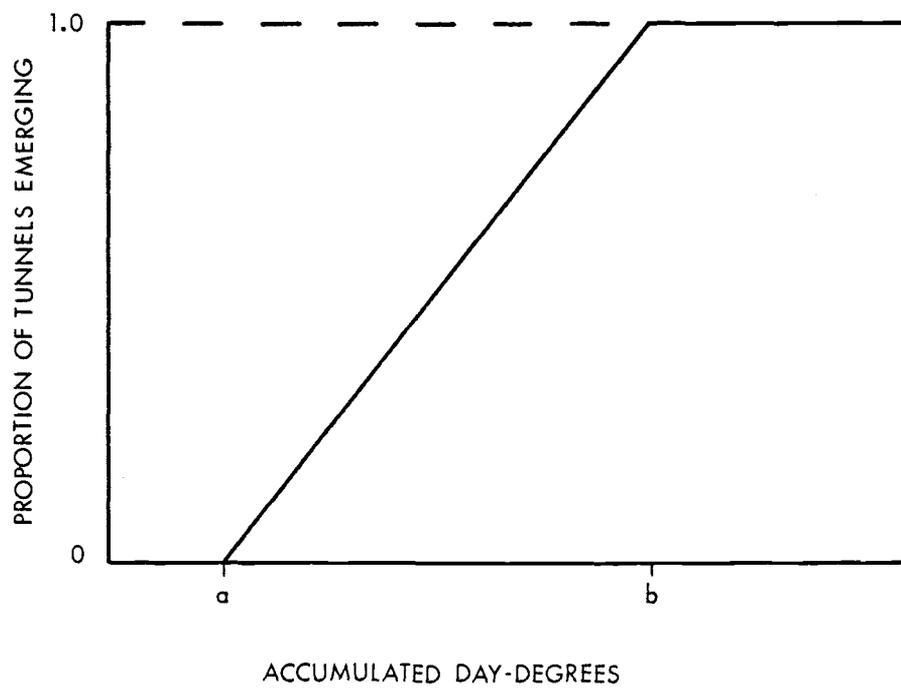


Figure 4. Ramp function for asynchrony in emergence of a cohort.

which provides for emergence of a portion of a cohort's tunnels during a particular week. When the day-degree accumulation for a certain cohort first exceeds the lower threshold,  $a$ , the prescribed proportion of developing tunnels will emerge at the start of the following week. If this accumulation exceeds the upper threshold,  $b$ , the entire cohort will emerge at that time. The cumulative proportion of the original tunnels of a cohort emerged by a certain week is given by the ramp function:

$$c = 0, \text{ if } d \leq a,$$

$$c = (d - a)/(b - a), \text{ if } a < d < b,$$

$$\text{and } c = 1, \text{ if } d \geq b,$$

where  $c$  is the cumulative proportion emerged,  $d$  is the accumulated day-degrees,  $a$  is the lower threshold, and  $b$  is the upper threshold. The proportion to emerge is then given by the difference in  $c$  and the proportion previously emerged.

The cohort of overwintered bees emerges over a longer period than does a cohort produced during the season. The model accounts for this by setting the upper threshold,  $b$ , at a larger value when overwintered bees are emerging.

*To get bees to emerge at one time I may be you could incubate them?*

## B-2. Immature Bee Mortality Subsystem

Immature mortality is accounted for in the model at the time the tunnel occupants are to emerge. The level of immature mortality is assumed equal for all bees beginning development at the same time. Computations regarding bee mortalities use survival rates rather than mortality rates, in accordance with standard methodology. The survival rate corresponding to mortality due to chalkbrood will be referred to as the chalkbrood survival rate and that corresponding to mortality due to parasites, predators and nest destroyers will be referred to as the background survival rate.

Chalkbrood survival is determined by a time-specific rate existing at the time a tunnel was completed, reflecting the assumption that the inoculum level in the domicile at that time determines incidence of the disease. A schedule of anticipated chalkbrood survival rates for bees in tunnels either completed during various weeks of the season or introduced at the start of the season is used to account for this time-varying mortality.

Immature mortality due to parasites, predators, and nest destroyers is considered to be cumulative during the developmental period. No accounting is made of background mortality of diapause bees prior to their

*Check  
Tim & Tom's  
Bee Boards  
for chalkbrood  
probability of getting  
idea not  
to use  
those bees  
because  
of possible  
inoculum  
on bees.*

reintroduction as overwintered bees. The background survival rate,  $s_b$ , for the entire  $k$  weeks, is computed as:

$$s_b = s^k,$$

where  $s$  is the weekly background survival rate. The total immature survival rate,  $s_t$ , is then computed as:

$$s_t = s_b s_c = s^k s_c,$$

where  $s_b$  and  $s_c$  are the background and chalkbrood survival rates, respectively.

### B-3. Adult Female Emergence Subsystem

The generation of newly emerged females and the generation of open tunnels of various potential capacities from completed or inactive tunnels of various realized capacities are the two subprocesses of interest. The numbers of adult male bees are not considered important to leafcutter population dynamics and, thus, only female bees are explicitly accounted for. The open tunnels resulting from emergence are available for nesting; the potential capacities of those tunnels is of great importance because of the effect of depth on the sex ratio of eggs laid within a tunnel. Reduction of open tunnel capacities due to accumulation of nesting debris and cadavers following emergence is therefore

perceived as a key factor affecting bee population dynamics and is given appropriate representation.

The number of females emerging each week and the number and potential capacities of the resulting open tunnels are determined in several steps. For each cohort, the numbers of bees emerging from completed tunnels and from inactive tunnels are calculated and summed. Emerging females from all cohorts are pooled each week into a single cohort of adult female bees. Open tunnels of various residual potential capacities resulting from emergence are added to the appropriate elements of the vector of open tunnels.

The number of females emerging from completed tunnels in a particular capacity class is determined as the product of: 1) the number of completed tunnels of the particular cohort in the capacity class; 2) the proportion of tunnels of this cohort due to emerge the current week (Figure 4); 3) the number of female bees in tunnels of this capacity; and 4) the proportion of female bees surviving and emerging from tunnels of this capacity (Figure 5). This is repeated for all capacity classes and the emerged females are then summed.

The proportion,  $p$ , of female bees successfully emerging from a tunnel (Figure 5) is computed as:

$$p = (s_t - a)/(1 - a)$$

where  $s_t$  is the total immature survival rate and  $a$  is a

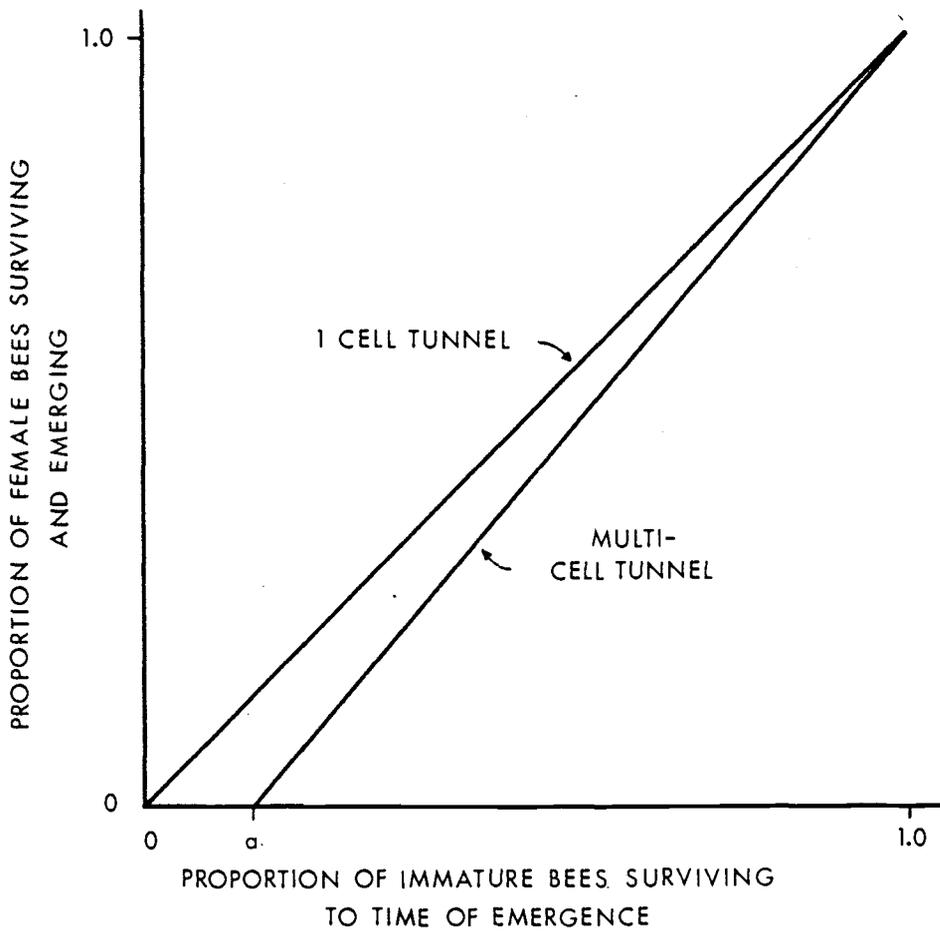


Figure 5. Function for female emergence success as affected by tunnel capacity and immature survival.

lower threshold on the survival rate, prescribed as a function of tunnel depth. In a one-cell tunnel, the proportion of the female bees surviving and emerging equals the proportion of bees surviving to the time of emergence. In deeper tunnels, more females fail to penetrate the debris and cadavers, and, therefore, die in their attempt to emerge. This is reflected in the lower threshold,  $a$ , which increases with increasing tunnel depth. Thus, emergence failure increases with a lower total immature survival, reflecting the greater number of cadavers to penetrate.

The model assumes that emergence failure does not occur in inactive tunnels. Other developmental and mortality processes for bees in inactive tunnels are assumed identical to those for bees in completed tunnels. Also, the realized capacities of inactive tunnels are not explicitly accounted for by a state variable, so the emergence calculation is different. (However, the original potential capacities of inactive tunnels are accounted for by a state variable, used in determining the residual capacities of open tunnels from emergence of inactive tunnels.) The number of females of a weekly cohort emerging from inactive tunnels is calculated as the product of: 1) the number of inactive tunnels of this cohort; 2) the proportion of these tunnels to emerge (Figure 4); 3) the average number of female bees

per inactive tunnel of this cohort; and 4) the total immature survival rate for bees in this cohort.

The numbers and potential capacities of open tunnels resulting from emergence of the completed and inactive tunnels of the cohort are then determined. Figure 6 illustrates the function used in determining the proportion of the original capacity of a completed tunnel remaining after emergence. As immature survival increases, fewer cadavers are left to plug the tunnel, so the proportion of the original capacity remaining after emergence increases. Emergence failure due to blocked tunnels is greater in the multi-cell tunnels than in the one cell tunnels. This results in a greater reduction in the capacity of a deep tunnel than a shallow tunnel, even when both tunnels have the same immature survival. The difference in the proportional reduction in the capacities of the shallow and deep tunnels is greatest when the immature survival is lowest (Figure 6). The potential capacities of the open tunnels resulting from emergence of completed tunnels of a particular capacity are determined by multiplying the capacity by the proportion remaining after emergence and then rounding this product to the nearest integer value.

Again, emergence failure is assumed not to occur in inactive tunnels. Thus, in the model, the emergence of a certain number of inactive tunnels of a particular

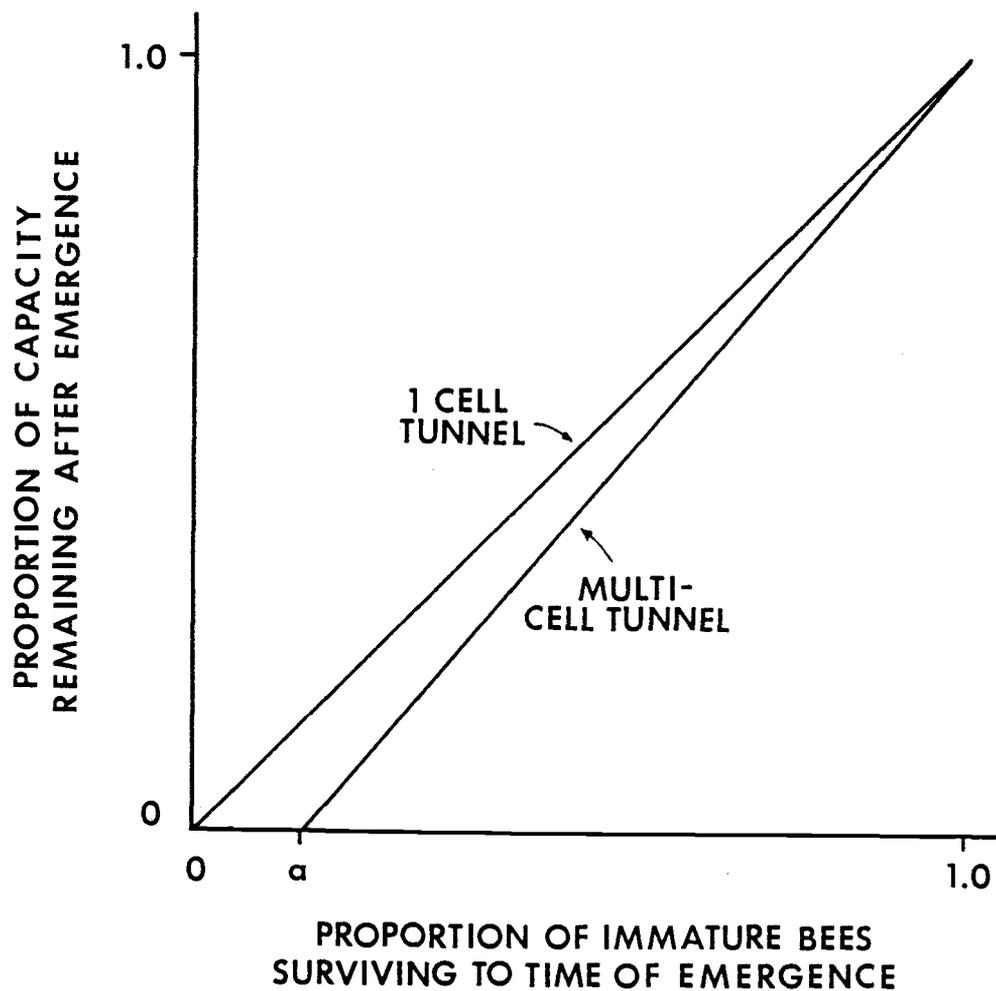


Figure 6. Function for residual tunnel capacity as affected by realized capacity and immature survival.

potential capacity generates the same number of open tunnels of the same potential capacity.

The effects on the emergence process of inactive tunnel reoccupation by a second female are also considered. Reoccupation followed by brood cell construction and tunnel completion is assumed not to affect the emergence fate of the bees produced by the previous female. The model assumes that the inner bees would be able to emerge through the more recently constructed cells. However, if the remaining space in a diapause inactive tunnel is filled with cells by a second female, the entire tunnel is reclassified as a diapause completed tunnel.

### C. Tunnel Filling Subsystem

The tunnel filling subsystem (Figure 7) includes several subprocesses: adult mortality, tunnel selection, and egg-laying. Mortality of an adult female involves the termination of the tunnel filling process, with reclassification of an active tunnel to inactive, and the implied reduction in the age-structured adult female population. The tunnel selection process involves the selection of inactive or open tunnels of various capacities by adult female bees. The egg-laying process

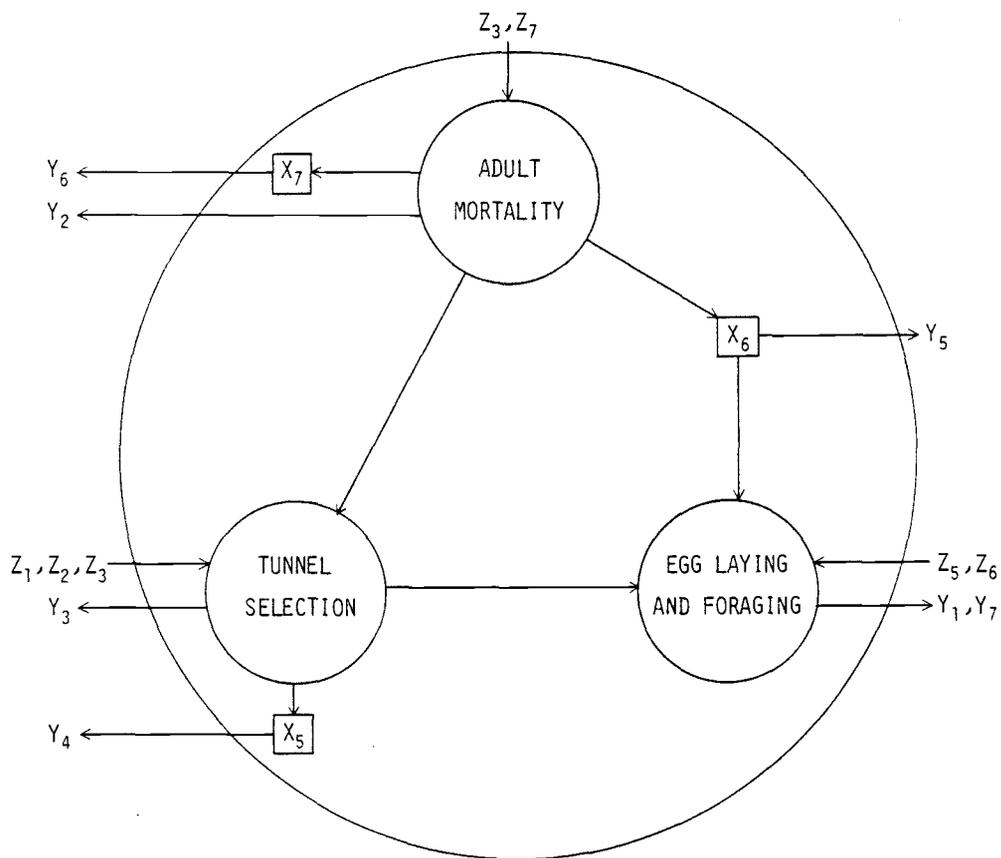


Figure 7. Decomposition of tunnel filling subsystem into coupled subsystems.

involves foraging and oviposition with the egg production rate a function of temperature and flower availability.

Figure 7 illustrates the subprocesses and couplings (internal and external) of the tunnel filling subsystem. Variable descriptions match those in Table 1.

### C-1. Tunnel Selection Subsystem

Two main categories of tunnels, open and inactive, are available to adult female bees which have either recently emerged or completed a tunnel. Female bees are assumed to differentiate and exhibit preferences towards open tunnels and inactive tunnels. Further, for open tunnels, female bees are assumed to differentiate and exhibit preferences towards tunnels of different capacities.

Tunnel selection is modeled as a two-stage process. The first is selection of either the open tunnels as a group or the inactive tunnels as a group. The proportion,  $a$ , of bees selecting open tunnels rather than inactive tunnels is calculated as:

$$a = (n_o p_o) / ((n_o p_o) + (n_i p_i)),$$

where  $n_o$  is the number of open tunnels,  $n_i$  is the number of inactive tunnels, and  $p_o$  and  $p_i$  are relative preference coefficients for open and inactive tunnels, respectively. In the second stage, the bees selecting open tunnels are

further partitioned among the capacity classes by an analogous process. The proportion,  $b_i$ , of these bees selecting the  $i^{\text{th}}$  capacity class is calculated as:

$$b_i = (n_i r_i) / ((n_1 r_1) + (n_2 r_2) + \dots + (n_7 r_7)),$$

where  $n_i$  is the number of open tunnels in the  $i^{\text{th}}$  capacity class and  $r_i$  is the relative preference coefficient for the  $i^{\text{th}}$  capacity.

Bees selecting inactive tunnels are assumed not to distinguish between inactive tunnels of different cell capacities. Selection among inactive tunnels is solely according to relative abundances.

## C-2. Egg-Laying Subsystem

Of interest in the egg-laying process are those subprocesses associated with the utilization of nesting tunnels and alfalfa flowers and the generation of completed tunnels and pollinated flowers. The term egg-laying will be used to represent the construction and provisioning of a brood cell and the process of oviposition. Egg-laying rates are modeled as a function of those factors that affect bee foraging, including thermal conditions and flower availability. Although bee flight and nesting are suspended either by low temperatures or cloudiness, the model only accounts for the effect of temperature. Cloudiness is not provided as

a driving variable, and the realized rates are to be interpreted as averages over the cloud conditions that exist for a given temperature.

The number of eggs laid during a week by a nesting female is assumed to depend upon thermal conditions, flower availability, age of the bee, and availability of nesting tunnels. Egg production by females in each of the surviving cohorts is determined at the beginning of the week, before the actual representation of egg-laying and brood cell construction. The weekly egg production per female in a particular cohort is modeled as a maximum production, reduced by factors accounting for thermal conditions and flower availability.

The reduction factor for thermal conditions,  $r_t$ , is computed as:

$$\begin{aligned} r_t &= 0, \text{ if } d \leq 0, \\ r_t &= d / a, \text{ if } 0 < d < a, \\ \text{and } r_t &= 1, \text{ if } d \geq a, \end{aligned}$$

where  $d$  is the weekly day-degree total, and  $a$  is the day-degree threshold sufficient for maximum egg-laying under optimal conditions of flower abundance. No foraging flights occur at temperatures below  $21^\circ$  C. For simplicity, the model uses the variable,  $d$ , ( $z_5$  in Table 1) computed for the immature development process, which has a threshold of  $19^\circ$  C.

The formula for the reduction factor for flower availability uses a threshold parameter,  $b$ , representing the female population's flower demand under the current thermal conditions. This threshold is the sum over all cohorts of the product of: 1) the number of flowers pollinated per egg laid; 2) the maximum eggs laid per female in the cohort under optimal conditions of flower abundance; 3) the number of adult females in the cohort; and 4) the reduction factor for thermal conditions (above). The reduction factor for flower availability,  $r_f$ , is then computed as:

$$\begin{aligned} r_f &= 0, \text{ if } f \leq 0, \\ r_f &= f / b, \text{ if } 0 < f < b, \\ \text{and } r_f &= 1, \text{ if } b \leq f, \end{aligned}$$

where  $f$  is the total available flowers.

The weekly egg production,  $e$ , representing eggs per female in a specific cohort, is computed as:

$$e = m r_t r_f,$$

where  $m$  is the maximum eggs laid per week per female in the cohort under optimal conditions of flower abundance, and  $r_t$  and  $r_f$  are as defined above. A fractional predicted egg production of, for example, 4.25 eggs is modeled by having 75% of the cohort lay four eggs and 25% of the cohort lay five eggs. Total egg production is required as a coupling variable for determination of flower pollination in the seed production subsystem and

is computed as the sum over cohorts of the products of the number of females and the egg production per bee.

The representation of the egg-laying process depends on the type of tunnel the nesting female has occupied. The simplest representation is used for egg-laying in inactive tunnels, which may either be cleaned of all live brood cells from the previous female, or not cleaned of cells prior to egg-laying. If an inactive tunnel is not cleaned of cells, it is assumed to be completed during the week, regardless of the remaining capacity of the tunnel. The nesting female is assumed to have no residual egg-laying capacity for the current week, and selects a new tunnel at the start of the next week if still alive. If the inactive tunnel is cleaned of cells, it is assumed to be restored by the reoccupying female to its original potential capacity, and the egg-laying process follows that prescribed below for newly occupied open tunnels. A proportion of reoccupied inactive tunnels is assumed to be cleaned of existing live cells prior to egg-laying.

A more detailed representation is provided for the egg-laying process in active tunnels or newly occupied open tunnels. If the number of eggs to be laid during the week by the nesting female exceeds the remaining capacity of the tunnel, it is considered complete. To account for the time spent in capping the tunnel and

selecting another, the residual egg-laying capacity is reduced by one. The female bee then reenters the tunnel selection process, occupies another tunnel if one is available, and enters into the egg-laying process once again. If an open tunnel is selected again, the remaining egg-laying capacity is allocated to the newly selected tunnel. The process continues until the female's weekly egg-laying capacity is exhausted or until she is unable to locate a tunnel for nesting. Females unable to locate nesting tunnels remain in the population for selection of open or inactive tunnels at the start of the following week, after mortality is imposed. Females remaining in incomplete tunnels at the end of the week resume egg-laying at the start of the following week, after mortality is imposed.

Each week, the five cohorts of nesting bees are assumed to do their egg-laying sequentially by age, starting with the oldest cohort, which is beginning its fifth and last week of life. This order of selection was arbitrarily chosen and has little or no impact on model behavior except when tunnels are not available in adequate numbers to satisfy demand.

### C-3. Adult Female Mortality Subsystem

A cohort of adult females remains active in tunnel selection and egg-laying for five weeks, with the number of females in the cohort reduced each week according to a time-invariant, age-specific mortality schedule. As a consequence, each week the nesting female population is represented as five weekly cohorts. Adult mortality is assumed to occur at the start of the week. The death of a nesting bee is represented by the transfer of its previously active tunnel to an inactive tunnel classification. The inactive tunnels resulting from adult mortality are considered both as tunnels containing potentially emergent bees and as tunnel resources for nesting by another female.

The treatment of inactive tunnels will be considered here, since they are generated by adult mortality. To account for the numbers of females that will emerge from inactive tunnels, the average number of females per tunnel and the number of inactive tunnels of the cohort are determined. The determination of the average females per tunnel is based on the original capacities of these tunnels (when open) and their realized capacities (see model parameterization section). To account for residual open tunnels resulting from

emergence, inactive tunnels are also classified by their original potential capacities.

#### D. Flowering and Seed Production Subsystem

Flowers are assumed to be produced during two bloom periods, each five weeks long and each with the same schedule of potential production. The flower production during the second bloom period is assumed to be reduced by the pollination percentage during the entire first bloom period. Thus, the greater the pollination intensity during the first period, the fewer flowers produced during the second period. This model mechanism was used to account for observations by Stephen (personal communication) of termination of flowering following very intense pollination early in the season.

The model assumes a homogeneous distribution of flowers and foraging bees within the alfalfa field. All flowers are assumed equally accessible to the bees, regardless of the distance from the domicile or position on the plant.

Annual seed production is based on the numbers of flowers pollinated during various weeks of the flight season and the proportions of these that produce mature, harvestable seed. The number of flowers pollinated each week has been implicitly determined by the determination

of eggs produced. It is explicitly determined as the product of the number of eggs (cells) produced during the week and the number of flowers required to provision a single cell. (In the current model implementation, the potential egg production, before accounting for time spent in tunnel selection and capping, is used in the computation.) It is noted that availability of flowers has entered the computation of eggs produced.

The proportions of flowers pollinated during successive weeks which produce mature, harvestable seed, increase from early to mid-season and decrease thereafter (see model parameterization section). This schedule implies a fixed harvest time. It is apparent that the schedule will not simply shift as the harvest time is changed because seed maturation rate is weather dependent.

## IV. Model Parameterization

### A. Overview

A set of parameters is associated with each of the model processes discussed previously. Determination of parameter values is detailed in this section. The literature base of many parameters is discussed more fully in the natural history section. Parameter descriptions and values are listed in Table 2.

A weekly day-degree schedule (input variable) for all model runs was computed from daily maximum and minimum air temperature records for Ontario, Oregon, 1974 to 1978 (Oregon Climatological Data). The day-degrees,  $d$ , for a single day was computed as:

$$d = 0, \text{ if } t_2 \leq t_0,$$

$$d = ((t_2 - t_0)^2) / (2 (t_2 - t_1)), \text{ if } t_2 > t_0 \text{ and } t_1 < t_0,$$

$$d = ((t_1 + t_2) / 2) - t_0, \text{ if } t_2 \geq t_0 \text{ and } t_1 \geq t_0,$$

where  $t_2$  and  $t_1$  are the maximum and minimum daily temperatures, respectively, and  $t_0$  is the lower developmental threshold temperature (Lindsey and Newman 1956). The day-degree variable was averaged by date and summed for each seven day period. These weekly sums were used as the weekly resolution input variable (Table 2).

Table 2. Parameter descriptions and nominal values.

DESCRIPTION	VALUE
A. Input Variable	
weekly day-degree schedule (starting week of June 15-21)	225.37 <sup>a</sup> , 24.43, 31.15, 37.79, 40.19, 47.90, 46.23, 37.93, 33.34, 23.30, 21.45, 24.57, 15.30, 10.36, 9.19
B. Emergence Subsystem	
B-1. Immature Bee Development and Diapause Subsystem	
day-degree threshold for first emergence from any tunnel	200
day-degree threshold for last emergence of overwintered bees	260 or 300 <sup>b</sup>
day-degree threshold for last emergence of tunnels containing second generation bees	205
date of onset of diapause- inducing conditions	July 13
B-2. Immature Bee Mortality Subsystem	
immature mortality rate due to chalkbrood	.25
weekly immature mortality rate due to parasites, predators, and nest destroyers	.10

(Table 2 continued)

DESCRIPTION	VALUE
B-3. Adult Female Emergence Subsystem	
proportion fertilized eggs (female bees) laid in open tunnels with capacities of one to seven cells	.14, .16, .19, .21, .24, .26, .29
thresholds of immature survival resulting in 0% female emergence from completed tunnels with one to seven cells	.0, .02, .04, .08, .10, .12, .14
thresholds of immature survival resulting in 0% residual capacity of emerged tunnels that contained from one to seven cells	.0, .02, .04, .08, .10, .12, .14
C. Tunnel Filling Subsystem	
C-1. Tunnel Selection Subsystem	
relative preferences of females for open tunnels and inactive tunnels	.90, .10
proportion of reoccupied inactive tunnels that are cleaned of existing cells	.50
relative preferences of females for potential capacities of one to seven cells (in open tunnels)	.10, .11, .13, .15, .17, .19, .15

(Table 2 continued)

DESCRIPTION	VALUE
C-2. Egg-Laying Subsystem	
day-degrees required for maximum weekly egg-laying	50.00
number of flowers to provision a single cell	2500.00
maximum eggs laid per week by females one to five weeks old	10, 10, 10, 5, 5
C-3. Adult Female Mortality Subsystem	
proportions of an adult cohort alive during weeks one to five	1.00, .88, .75, .50, .10
expected number of immature female bees in inactive tunnels with potential capacities of one to seven cells and realized capacities of one to seven cells	see Table 3
D. Flowering and Seed Production Subsystem	
the potential number (in millions per acre) of flowers produced in each of the five weeks during a bloom period	16.5, 33.5, 50.0, 33.5, 16.5
proportions of flowers producing harvestable seed, as pollinated (11, 10, . . ., 5) weeks before harvest	.2, .4, .6, .8, .8, .6, .4
mg. of seed produced per pollinated flower	7.61

<sup>a</sup>The day-degree variable for the initial week of development is set to account for previous development of overwintered bees.

<sup>b</sup>To obtain approximately equivalent first generation emergence distributions (over time) the first threshold is used with standard management timing and the second is used with the two delay tactics.

## B. Emergence Subsystem

### B-1. Immature Bee Development and Diapause Subsystem

The parameters in this process are: 1) day-degree thresholds for first and second generation emergence; and 2) date of onset of diapause-inducing conditions.

Day-degree thresholds (Figure 4) for first and last emergence of first generation bees were chosen to give emergence times typical for eastern Oregon (Stephen, personal communication) on application of the day-degree schedule. First generation emergence was set for a three week period, with the majority of emergence occurring during the first two weeks. Day-degree thresholds for second generation emergence were chosen so that emergence of a cohort occurred during the fifth and/or sixth week of its development.

Diapause was assumed to occur in all immature bees in tunnels completed or left inactive on or after July 13 and not to occur prior to this time. As discussed in the natural history section, transition is not so abrupt in nature, but this simplification resulted in a diapause bee production for the first generation close to that which would have been obtained with the time-dependent diapause schedule of Johansen and Eves (1973).

### B-2. Immature Bee Mortality Subsystem

The parameters of this process are: 1) the immature mortality rate due to chalkbrood; and 2) the weekly immature mortality rate due to parasites, predators, and nest destroyers (the background mortality rate).

Immature mortality rates were set to typical values for field conditions in eastern Oregon (Stephen, personal communication). Although the chalkbrood rate was conceptualized as a time-varying parameter, a constant 25% chalkbrood mortality and a 10% weekly background mortality were used as nominal values. Over a six week developmental period for bees from the first generation nesting, a total immature survival rate of 40% is obtained using the above rates ( $.9^6 \times .75 = .40$ ).

### B-3. Adult Female Emergence Subsystem

The parameters in this process are: 1) the percent fertilized eggs laid in open tunnels with potential capacities of one to seven cells; 2) thresholds of immature survival used in determining the level of female emergence mortality; and 3) thresholds of immature survival used in determining the reduction in capacity of a tunnel from which bees have emerged.

The assumed percent fertilized eggs laid in open tunnels with capacities of one to seven cells are 14, 16, 19, 21, 24, 26, and 29, respectively. These follow the sex ratios reported by Gerber and Klostermeyer (1972).

The thresholds of immature survival corresponding to 0% female emergence (Figure 5) from tunnels containing one to seven cells were set at 0, 2, 4, 8, 10, 12, and 14 percent, respectively. To illustrate the behavior of the rule under nominal parameter values (under a 40% immature survival rate), the proportion of female bees developing and emerging from tunnels with one cell is 40%, linearly decreasing to 30% for tunnels with seven cells. First generation emergence occurring at the start of weeks two, three, and four were associated with 68, 61, and 55 percent immature survivals, respectively. For one cell tunnels, female emergences were 68, 61, and 55 percent during weeks two, three and four, decreasing with increasing cell capacity to 63, 55, and 48 percent for seven cell tunnels.

The thresholds of immature survival for determining remaining tunnel capacity (Figure 6) were set to 0, 2, 4, 8, 10, 12, and 14 percent for tunnels containing one to seven cells, respectively (the same values as the thresholds for female emergence mortality). To illustrate the behavior of this rule, the proportion of the original capacity remaining in emerged tunnels, which

contained second generation bees with 40% immature survival, decreases from 40% to 30% for tunnels with one to seven cells, respectively. Again, the residual capacity was obtained by rounding, to the nearest integer value, the product of the percent remaining capacity and the original capacity. Under this rule and the 40% immature survival, all one cell tunnels are totally plugged with debris and the seven cell tunnels are reduced to two cell tunnels. First generation emergence, with 68, 61, and 55 percent mortalities in tunnels emerging at the starts of weeks two, three, and four resulted in remaining capacities of 68, 61, and 55 percent for one cell tunnels, decreasing with increasing cell capacity to 63, 55, and 48 percent for seven cell tunnels.

Although the actual threshold values are unknown, the qualitative behaviors of both the emergence failure and the tunnel capacity reduction mechanisms appear reasonable. However, a more appropriate rule would not round the residual capacity to the nearest integer value. As an alternative to rounding, the mechanism could generate, for example, 40% one cell tunnels and 60% plugged (0 cells) tunnels from emerging one cell tunnels with 40% immature survival.

## C. Tunnel Filling Subsystem

### C-1. Tunnel Selection Subsystem

The parameters in this process are: 1) the relative preferences of female bees for open versus inactive tunnels; 2) the proportion of reoccupied inactive tunnels that are cleaned of existing cells before egg-laying by the second female; and 3) the relative preferences of female bees for potential capacities of one to seven cells, in open tunnels.

Relative preference coefficients of .90 for open tunnels and .10 for inactive tunnels were selected on the basis of observations that reoccupation of inactive tunnels occurs primarily when nesting tunnels are limited (Stephen and Osgood 1965b). The proportion of these reoccupied inactive tunnels that are cleaned is unknown and was set at 50%.

The schedule of preference coefficients for capacities of one to seven cells was set at 0.10, 0.11, 0.13, 0.15, 0.17, 0.19, and 0.15. This implies a linearly increasing preference for deeper tunnels up to six cells and a slight drop in preference for seven cell capacity tunnels. Selection against tunnels with small capacities has been noted by Gerber and Klostermeyer (1972) who could get bees to nest in tunnels with a

capacity for 2 cells only when higher capacity tunnels were in short supply. Stephen (unpubl. data) found that a population of bees in eastern Oregon utilized twice as many new four inch deep tunnels with seven cell average capacities as new one inch deep tunnels with one cell average capacities. A decreased preference for new nesting tunnels not previously nested in has been noted; so the seven cell tunnels, representing in large part unused tunnels in the model, are given a preference coefficient less than twice that of one cell tunnels.

#### C-2. Egg-Laying Subsystem

The parameters in this process are: 1) the maximum eggs laid per week by female bees one to five weeks old; 2) the day-degrees required for maximum weekly egg-laying; and 3) the number of flowers required for the provisioning of a single cell.

The maximum age-specific weekly egg productions were set at ten eggs for one, two, and three week old bees, and five eggs for four and five week old bees. This implies a maximum lifetime production of 40 eggs per bee, just over the 35 eggs reported to be produced in the ovaries (Stephen 1973). The egg production schedule is based in part on the findings of Klostermeyer and Gerber (1969) that females usually lay one egg per day and do

not produce them fast enough for laying more than two per day. Using the nominal adult survivorship schedule (below), the predicted mean-maximum lifetime production per bee is 29.3 eggs, close to the estimate of Stephen (personal communication) of 30 eggs for eastern Oregon conditions.

The weekly day-degree schedule described in the section on immature development was used as a driving variable for egg-laying. It was assumed that the temperature regime limited cell and egg production during all weeks, but only to a slight extent during the week with the maximum day-degree value (47.90 day-degrees from July 20 to July 26). An upper threshold of 50 day-degrees was used in setting the effect of the temperature regime on cell and egg productions (the lower threshold is zero). This resulted in a realized egg production of approximately 50% of the maximum potential production during the early and late periods of the flight season, with little reduction during the middle of the season. This is judged to be an appropriate qualitative representation of the effect of temperature conditions on bee productivity.

The number of flowers required to provision a single cell was set at 2500, based on studies of Klostermeyer and Gerber (1969).

### C-3. Adult Female Mortality Subsystem

The parameters of this process are: 1) the adult survivorship schedule; and 2) the numbers of immature females in inactive tunnels of certain potential and realized capacities.

The proportions of an adult cohort alive during weeks two, three, four, and five were set at 0.88, 0.75, 0.50, and 0.10 in the nominal survivorship schedule. This schedule is based on Stephen's studies (unpubl. data) on lab-reared adult bees, as reported in the natural history section.

The number of immature females in inactive tunnels from mortality in all adult cohorts is determined each week, as previously discussed. The expected number of females in inactive tunnels of certain potential capacities and certain realized capacities are used in this determination (Table 3). These values were derived from the numbers of fertilized eggs (female bees) in completed tunnels with capacities of one to seven cells and from the observation that female bees are in the bottom cells of a tunnel (Gerber and Klostermeyer 1972).

Table 3. Expected numbers of immature females in inactive tunnels of various potential and realized capacities.

REALIZED CAPACITY	POTENTIAL CAPACITY					
	2	3	4	5	6	7
6						2.02
5					1.58	2.02
4				1.20	1.58	2.02
3			.86	1.20	1.58	2.02
2		.56	.86	1.20	1.58	2.00
1	.33	.56	.86	1.00	1.00	1.00

#### D. Flowering and Seed Production Subsystem

The parameters in this process are: 1) the potential number of flowers produced in each of the five weeks during a bloom period; 2) the array of proportions of flowers pollinated during each week of the season that produce mature, harvestable seed; and 3) the weight of seed produced per pollinated flower.

Again, flowers are assumed to be produced during two five week bloom periods, with the same schedule of potential flower production during each. The flower production during the second period is directly reduced by the degree of pollination during the first bloom period. The distribution (percent) of total flowers produced per week is (11, 22.33, 33.33, 22.33, 11). This distribution was determined in part from estimates of Stephen (personal communication) and observations of Todd and Vansell (1962) that flowering increases gradually to a peak in about two to three weeks.

The potential total flower production during each of the two bloom periods is assumed to be 150 million flowers per acre, with a combined annual potential of 300 million flowers. This total is based on the calculations of Akerberg (1952) that at least 202 million flowers per acre of alfalfa are produced, and of Pedersen and Nye (1962) that there is a per acre production of 453,330

alfalfa stems, 42.53 racemes per stem, and 17.28 flowers per raceme, for a total annual production of approximately 334 million flowers per acre. Using the total of 150 million flowers per bloom period, there will be 16.5 million flowers per acre during weeks one and five, 33.5 million during weeks two and four, and 50 million during week three.

Two main assumptions were made in developing the relation between seed production and the time of flower pollination. First, flowers pollinated very early in the season are assumed to set seed which has a higher probability of being lost to predation and pod shatter than seed set later. Second, flowers pollinated late in the season are assumed to set seed which has a lower probability of developing to maturity than seed produced earlier.

Although the relation between alfalfa seed predation and time spent on the plant has not been reported, a relation between pod shatter and time has been demonstrated. Smith and Milton (1967) found that later harvest of seed resulted in a greater proportion of fully mature seed pods which had a higher probability of shatter. Harvesting at an earlier stage of development reduced the shatter losses. However, harvesting too soon after flower pollination resulted in a high percentage of immature, unmarketable seed. In eastern Oregon, the

latest flower pollination resulting in production of marketable seed occurs around August 10. Any flower pollination after this time may be of importance to the bee population dynamics, but is unimportant to seed production.

The proportions of flowers that are pollinated eleven to five weeks before harvest and that produce mature, harvestable seed were set at 0.2, 0.4, 0.6, 0.8, 0.8, 0.6, and 0.4. No seed is assumed to be produced from flowers pollinated within four weeks of harvest. September 14 is the assumed harvest date for all model runs. Although the exact proportions are unknown, the qualitative form of the relation seems appropriate, with lower proportions of seed production from pollination occurring early and late in the season.

The weekly seed production was obtained as the product of the number of flowers pollinated, the proportion of these flowers that will produce mature, harvestable seed, and the weight of seed produced per pollinated flower. Values of Pedersen and Nye (1962) of 2.22 mg. per seed and 3.43 seeds per pod imply 7.61 mg. seed per pod. It was assumed that the seed weight per pod figure of Pedersen and Nye (1962) is a maximum, i.e., that the sampled pods had not suffered predation or other effects reducing the total weight of seed.

## V. Model Behavior

Model development has focused on the model structure and on the mechanisms and behavior of the processes that comprise the system. As these parts were constructed, each was validated and evaluated according to the existing knowledge and data base. Assembly of the parts into a representation of the whole system was then followed by a study of behavior of the whole.

The study of model behavior includes several aspects: 1) the development and description of a nominal run whose behavior under typical environmental and management conditions is judged to be a satisfactory representation of typical system behavior (an aspect of model validation); 2) the simulation and comparison of effects of various management tactics on system behavior; and 3) the investigation of the response of certain model outputs to changes in values of selected parameters (sensitivity analysis).

The model run predictions of bee and seed productions were scaled to a single acre of alfalfa by setting the alfalfa flower trajectory at appropriate weekly levels, as previously discussed, and the numbers of introduced completed tunnels of various capacities to appropriate values. The choice of a nominal completed tunnel introduction was based on calculations of Gerber

and Klostermeyer (1972) that 2000 emerging first generation females per acre, producing 16 brood cells each, would result in a 1000 pound alfalfa seed production. Given the nominal mortality rates for immature bees, it was determined that the introduction of 3500 completed tunnels with 500 in each of the one to seven cell capacity classes would result in the emergence of 1938 first generation female bees. The even distribution of tunnels over the seven capacity classes was used to represent a situation where nesting had occurred in previously used materials which were plugged with debris to varying extent. An open tunnel introduction consisting of 7000 unused tunnels with seven cell capacities accompanied the 3500 completed tunnels in the nominal run.

A summary of weekly resolution behavior in the nominal model run is shown in Table 4. Parameters for this nominal run were set to values discussed in the model parameterization section and summarized in Table 2. Table 4 provides: 1) the bimodal temporal distribution of emergence from completed tunnels, with emergence of first generation bees during weeks two, three, and four, and emergence of second generation bees during weeks eight, nine, and ten; 2) the emergence of second generation bees from inactive tunnels during weeks nine and ten; 3) the bimodal distribution of adult females,

Table 4. Weekly resolution outputs of nominal model run.

WEEK NUMBER	DATES	COMPLETED TUNNELS		INACTIVE TUNNELS		EMERGING TUNNELS		OPEN TUNNELS	ADULT FEMALES	FLOWERS (THOUSANDS)		
		NONDIAPAUSE	DIAPAUSE	NONDIAPAUSE	DIAPAUSE	COMPLETED	INACTIVE			AVAILABLE	POLLINATED	DEMANDED
1	15/6-21/6	3500	0	0	0	0	0	7000	0	0		
2	22/6-28/6	2159	0	0	0	1480	0	7444	897	16,500	10,955	10,955
3	29/6-5/7	1855	0	100	0	1425	0	6965	1551	33,500	24,150	24,150
4	6/7-12/7	3275	0	279	0	595	0	5331	1620	50,000	30,616	30,616
5	13/7-19/7	3275	1322	275	257	0	0	4114	1265	33,500	20,902	20,902
6	20/7-26/7	3275	2025	273	631	0	0	3624	681	16,500	10,652	10,652
7	27/7-2/8	3275	2179	272	950	0	0	3610	216	5,800	2,501	2,501
8	3/8-9/8	3185	2219	272	1075	91	0	3682	47	11,775	633	633
9	10/8-16/8	1985	3114	173	1056	1200	96	3331	717	17,575	11,956	11,956
10	17/8-23/8	0	4041	0	1037	1985	173	3199	1879	11,775	11,775	21,889
11	24/8-30/8	0	4501	0	1166	0	0	2900	1632	5,800	5,800	17,450

with first generation flight during weeks two through eight, and second generation flight during weeks eight through eleven; 4) the trajectory of nondiapause completed tunnels (weeks one to nine); 5) the trajectory of nondiapause inactive tunnels (weeks three through nine); 6) the trajectory of diapause completed tunnels, increasing over weeks five through eleven; 7) the trajectory of diapause inactive tunnels, increasing over weeks five through eleven; 8) the decreasing trajectory of open tunnels; and 9) the trajectories of flower supply, demand, and pollination.

The model was judged to be valid for use in behavioral studies on the basis of: 1) the ability of the model to generate system behavior closely resembling the subjectively prescribed nominal behavior; and 2) the inclusion of realistic representation of essential model mechanisms and the conformance of the behaviors of these mechanisms to the knowledge base. The evaluation of annual behavioral conformance was necessarily subjective, as an objective data set at the appropriate resolution does not exist. To compensate for this subjectivity and to give the capacity to respond to manipulation, an effort was made to include mechanisms in the model which realistically represent the way it is thought the system works and which were based on experimental results, when available. A candid assessment of model capability must

acknowledge the inability to accurately predict, quantitatively, the consequence of a perturbation or management tactic. However, the level of realism and conformance with the knowledge base give confidence in the qualitative trends and features of model behavior. As will be seen, these provide strong insights to the management process.

#### A. Evaluation of Management Tactics

Many of the processes of the system model were included to provide the appropriate mechanisms to respond to imposition of practical management tactics. These tactics can be classified into those affecting: 1) the flower supply-demand relation; 2) the tunnel supply-demand relation; and 3) the temperature regime and diapause-inducing conditions to which the bee population and alfalfa plants are exposed. The effects of management tactics were investigated by comparing the annual resolution outputs (seed production and diapause female bee production) from model runs simulating each tactic.

##### A-1. The Level of Bee Introductions and Delay of Emergence and Flowering

The balance of flower supply and demand is a primary management goal. An imbalance is undesirable, since it

results in a lack of pollination or a lack of forage, increasing the likelihood of reduced seed production or bee production, respectively. To achieve a proper balance between flower supply and demand, the proper number of first generation bees must be introduced for the expected flower trajectory. This need is complicated by the dependence of flowering during the second bloom period on the intensity of pollination during the first period. A particular first bloom period pollination intensity may be desirable under certain circumstances but undesirable under others, and thus cannot be judged as an isolated management goal without regard to other factors.

The relation of the time trajectory of bee nesting activities to the time-varying environmental conditions is another primary consideration. Temperature and diapause-inducing conditions have a pronounced effect on the performance of this system, and the potential benefits from certain management tactics, such as manipulating the flower supply and demand, must be judged with regard to the concurrent effects of the environmental regime.

Several relevant management tactics were investigated through the use of the model. The first tactic was to vary the number of introduced completed tunnels, and, therefore, the size of the first generation

female bee population, thus affecting the balance of flower supply and demand. As the level of completed tunnel introduction was increased, the level of open tunnel introduction was increased proportionally, so tunnel availability was not a factor. The second tactic was to vary the timing of flowering and bee flight with regard to the temperature regime and diapause-inducing conditions. This is determined by the time of onset of emergence and flowering, as expressed in weeks of delay relative to June 22, which represents the standard management time in the model runs. Synchrony between the trajectories of flower supply and demand was maintained by simultaneously varying the time of emergence and flowering.

Figure 8 illustrates the general pattern for a reduction in the annual rate of increase in the female bee population as the female introduction is increased. The general result of delaying initial flowering and bee emergence beyond the standard time is a rise in the annual rate. A two week delay results in a substantial rise in the annual rate over that obtained with no delay, while a four week delay results in an annual rate nearly as large as that obtained with the two week delay.

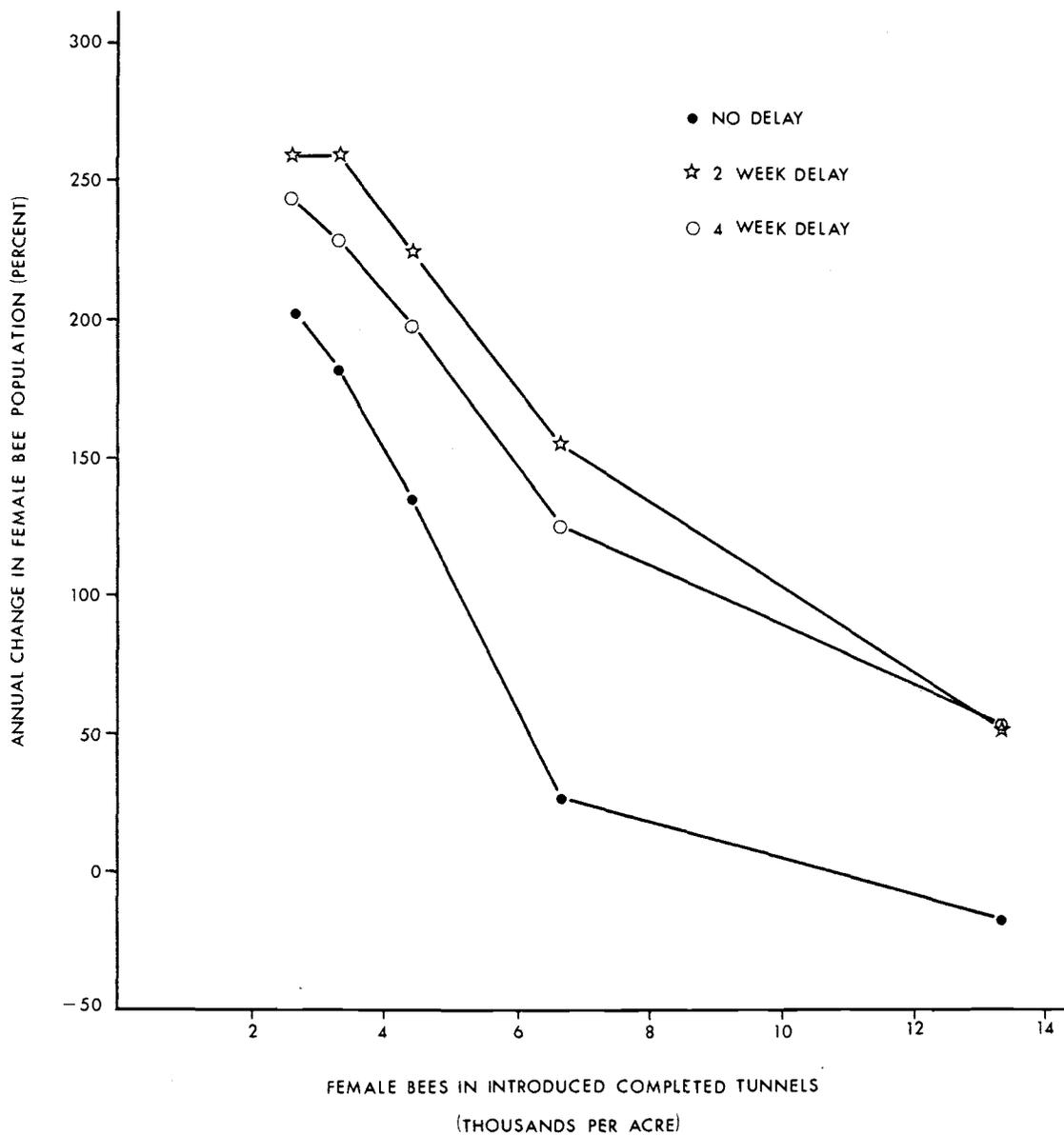


Figure 8. Percent annual change in the female population under several levels of female introduction and under several levels of delay of emergence and flowering. Standard timing (no delay) is June 22.

Figure 9 provides an alternate illustration of these responses, in terms of gross diapause female bee production. The replacement line represents the set of points at which the population exactly replaces itself during the year. Net bee production is given by the difference between the level of gross bee production and the replacement line, and is illustrated in Figure 10. With no delay, the maximum net bee production occurs at about the 3330 bee introduction level. Net bee production rapidly drops thereafter with increasing bee introductions, and above 9400, the population fails to replace itself. However, with both the two and four week delays, the net bee production is relatively constant, with maxima at the 4430 bee introduction level under the four week delay and the 6660 bee introduction level under the two week delay.

Figure 11 shows the pounds of seed produced per acre given different levels of bee abundance and activity delay. The general trend is for increased seed production with increased bee abundance, up to 6660 bees, with little or no change thereafter. The delay tactic results in a moderate increase in seed production for a two week delay but in a sharp decrease in production for a four week delay, relative to the nominal situation.

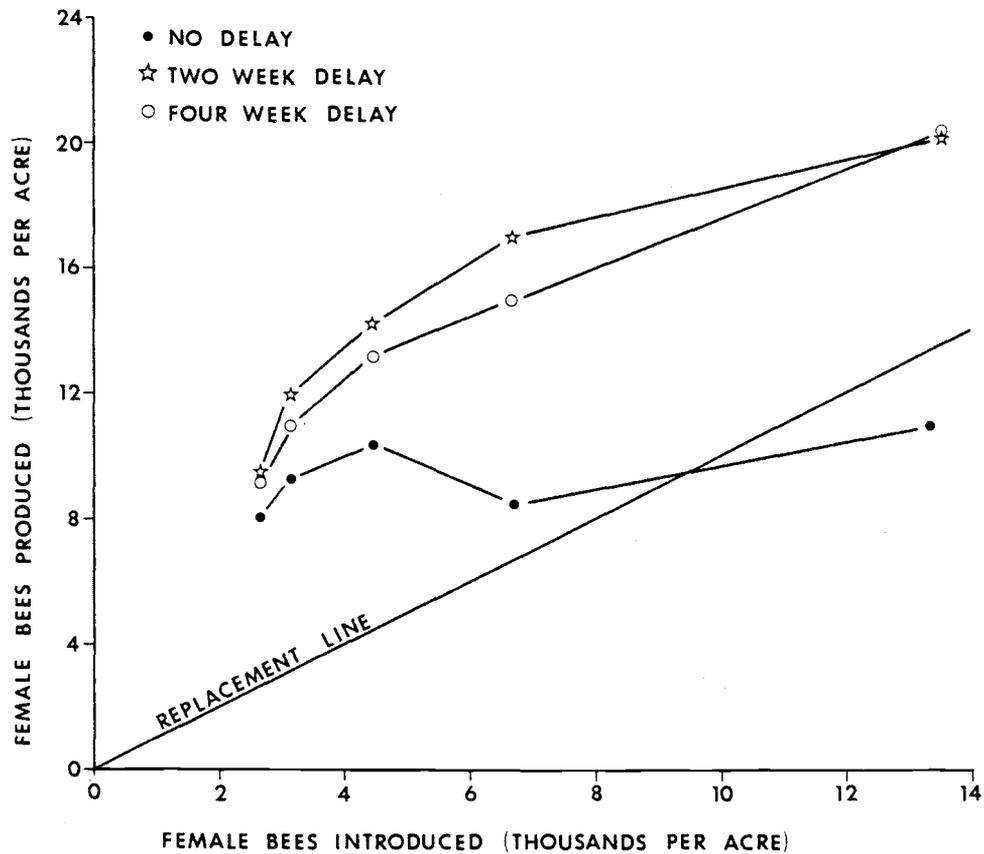


Figure 9. Gross female bee production under several levels of female introduction and under several levels of delay of emergence and flowering.

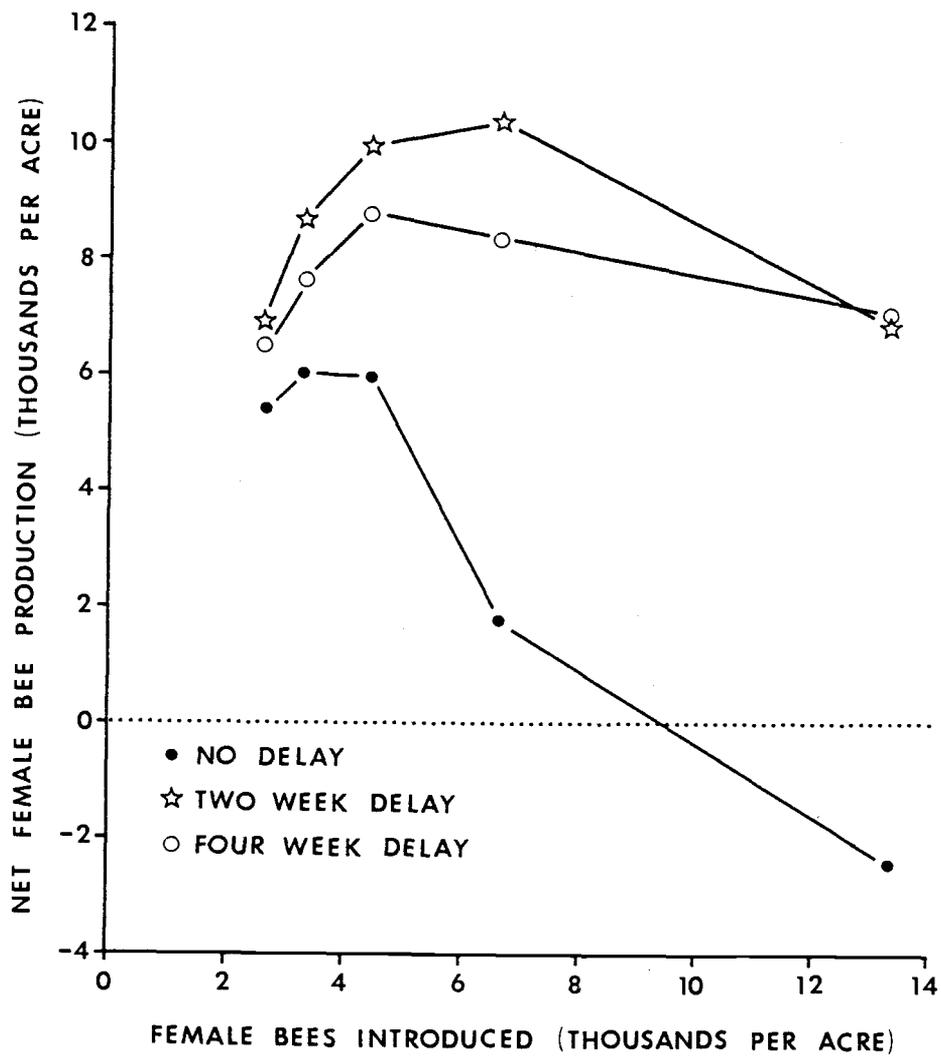


Figure 10. Net female bee production under several levels of female introduction and under several levels of delay of emergence and flowering.

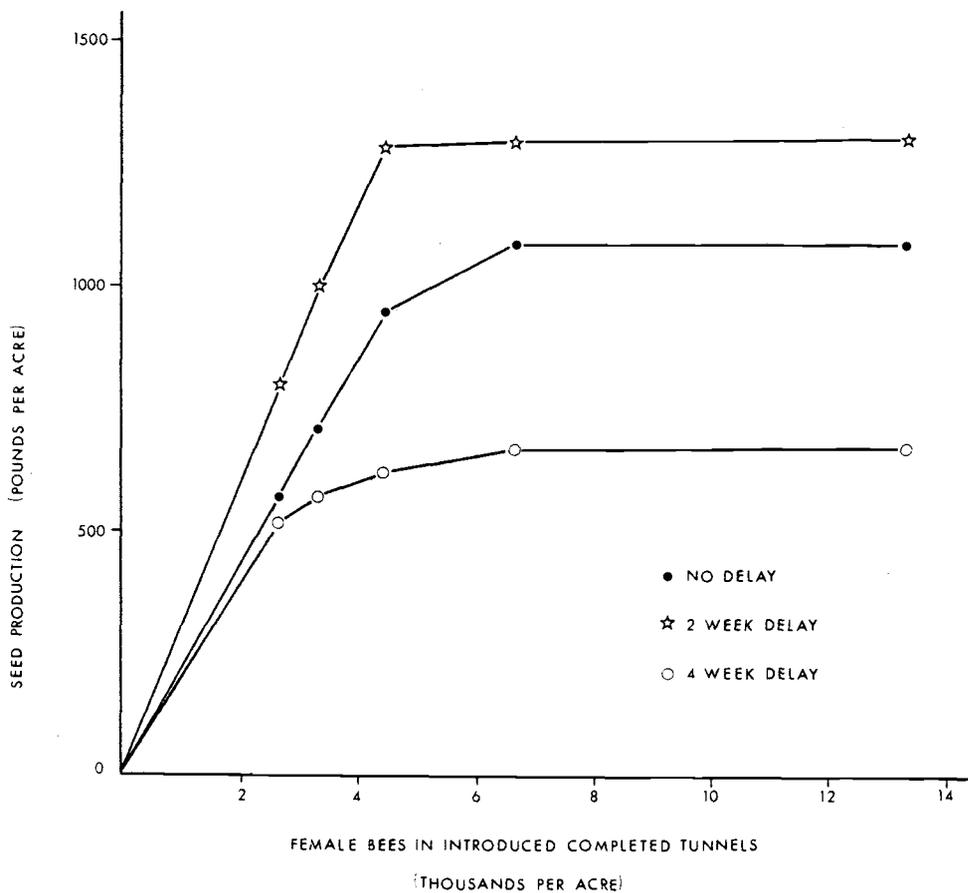


Figure 11. Seed production under several levels of female introduction and under several levels of delay of emergence and flowering.

The choice of the best tactic is determined by the total revenue from bee and seed productions and the associated costs of production. Increased management costs associated with increased bee populations are considered here to be insignificant in relation to resulting increased seed revenues. A strategy is sought in which large seed productions are obtained and the bee population increase is adequate to provide for destructive sampling for population assessment and to provide a buffer against unexpected losses. The introduction of large numbers of females under the standard timing for emergence and flowering causes the population to fall below the replacement line, and is thus an undesirable strategy.

Total revenues from seed and net bee productions obtained under the various tactics are presented in Table 5. Female bees are assumed to be worth \$0.015 apiece and seed is assumed to be worth \$1.25 per pound. Total revenue rapidly increases as the level of bee introduction increases to 4430 females, but changes relatively little with further increases in the bee introduction level. While the two week delay substantially increases the total revenue in relation to that obtained with the standard management timing, the four week delay results in substantial decreases, especially with the large female introductions.

Table 5. Total revenue (per acre) from seed production and net bee production under several levels of female introduction and under several levels of delay of emergence and flowering. Standard timing (no delay) is June 22. Assumed prices are \$1.25 per pound of alfalfa seed and \$0.015 per female bee.

NUMBER OF INTRODUCED FEMALE BEES	WEEKS DELAY IN EMERGENCE AND FLOWERING		
	0	2	4
13320	1355 <sup>a</sup> - 36 <sup>b</sup> = 1319 <sup>c</sup>	1615 + 103 = 1718	835 + 106 = 941
6660	1355 + 27 = 1382	1618 + 155 = 1733	833 + 125 = 958
4430	1181 + 89 = 1270	1603 + 149 = 1752	775 + 132 = 907
3330	894 + 91 = 985	1245 + 130 = 1375	713 + 114 = 827
2664	715 + 81 = 796	996 + 104 = 1100	643 + 98 = 741

<sup>a</sup>revenue from seed production (dollars)

<sup>b</sup>revenue from net bee production (dollars)

<sup>c</sup>total revenue from bee and seed productions

The results of this study are of interest for several reasons. First, the typical management strategy emphasizes early alfalfa flowering and bee emergence, typically starting about June 22. However, this probably results in a very large percentage of nondiapause bees produced by first generation bees nesting early in the season. The resulting second generation bees emerge too late to contribute to seed set and they forage at a time when the flower production is very low. This may place the grower in a dilemma: prolong the flowering period, so that the bees may replace themselves, and risk loss of the seed crop from late season rains and shatter of the early-set seed; or do not prolong the flowering, harvest on schedule, and lose the second generation of bees.

Increased production of nondiapause second generation bees which fail to replace themselves during the season accounts for the lower bee production with the standard management timing than with the two delays. With the standard timing, the flower demand of the second generation bees exceeds the flower supply at some time during the season, even at the lowest level of female bee introduction (2664 bees). Increasing the level of female introduction results in increased pollination intensities during the first bloom period, causing a reduction in flower production during the second bloom period. The low level of flower production during this period results

in the failure of the second generation to replace itself.

Under the standard timing, the extreme drop in the female bee production between the 4430 bee and 6660 bee introduction levels is due to the lack of flower production during the second bloom period at the higher population level. All of the flowers produced during the first bloom period are pollinated, causing a termination of flowering at the end of this period. Since population replacement must occur during this period, unless the first generation has produced diapause bees, this termination of flowering substantially reduces the annual bee production.

With the delays in emergence and flowering, a reduced second period bloom also results from a large introduction of females. However, the impact on the annual bee production is much less. The replacement of the bee population occurs mainly from the first generation nesting, since more diapause second generation bees are produced when emergence is delayed. Since the first generation is nesting primarily during the first bloom period, a reduced second period bloom does not significantly reduce the annual bee production.

Although the model does not explicitly account for adult starvation due to a lack of flowers, the model terminates egg-laying when flowers are not available.

Once flowering is terminated due to intense pollination, it is assumed not to resume at a later point in the bee flight period. Even though adult females are assumed to survive in the absence of flowers, they are producing no eggs. Thus, the bee (and seed) production behaviors revealed in the study of activity delay and level of bee introduction are not affected by the absence of adult starvation, which probably occurs under these conditions.

A two week delay in flowering and bee emergence results in a superior thermal environment for the foraging activities of first generation bees. Figure 12 shows a typical trajectory of first generation foraging females with the two week delay and the trajectory of weekly day-degrees over the same time period. The foraging female trajectory is well synchronized with the day-degree trajectory, with the peaks of both occurring after the assumed onset of diapause-inducing conditions, July 13. The first generation cell production is potentially greater with the two week delay than with no delay or the four week delay since the thermal environment is more favorable for bee flight.

With no delay or the four week delay in bee foraging and alfalfa flowering, the trajectory of first generation foraging females is not well synchronized with the day-degree trajectory. With the four week delay, females are foraging in a less desirable thermal environment and

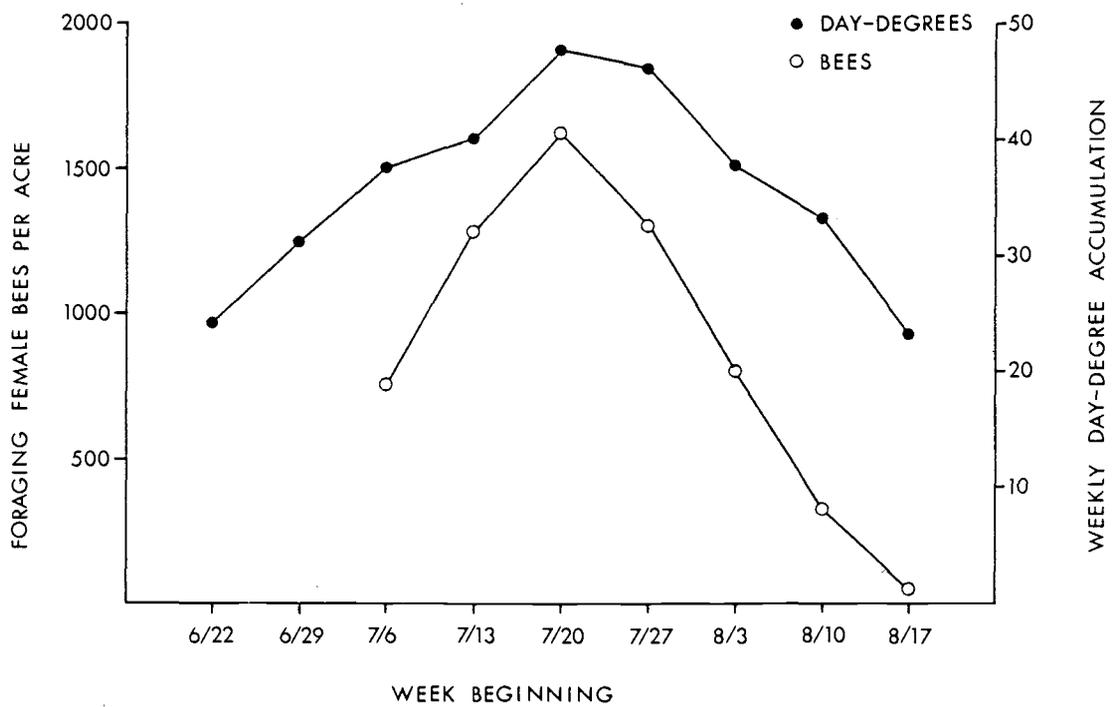


Figure 12. Trajectories of day-degrees and first generation female bees under the two week delay in emergence and flowering.

producing fewer cells. With the standard tactic (no delay), the effect of the coincidence of the trajectories of first generation bees and day-degrees is not so easily characterized, since the population replacement occurs mainly during the second generation. However, it is apparent that both generations are faced with less than optimal thermal conditions under the standard tactic.

All of the flowers produced during the first bloom period are pollinated when 6660 females are introduced, regardless of level of delay. (This implies the pollination of all flowers produced during the season, since there is no production of second period flowers when all first period flowers are pollinated.) In spite of this, female bee production increases when the introduction is increased to 13320 females, apparently a counterintuitive result. Actually, total bee production is decreasing, while the proportion of female bees produced is increasing, resulting in a net increase in females. Increased production of inactive tunnels is the cause of this behavior. With twice the nesting females, the production of inactive tunnels is approximately doubled (although with a tunnel shortage, these would probably be nested in). While the average number of cells in these inactive tunnels is reduced by the increased competition for flowers, the average number of female cells is insignificantly affected since they

are the first constructed in the tunnel and since there are so few per tunnel (Table 3).

As previously illustrated in Figure 11, seed production reaches a maximum at the 6660 bee introduction level for all delay tactics because of the total utilization of available flowers. These maximum seed productions all occur as a result of intense pollination during the first bloom period, halting bloom during the second period. Although the numbers of flowers pollinated during the first bloom period are the same, the times between pollination and the fixed harvest date vary with the three activity delay levels, leading to differences in the realized seed productions. Under standard management, with no delay in emergence and flowering, much of the flower pollination occurs early in the season, resulting in reduced seed production due to increased pod shatter and predation. With a four week delay in emergence and flowering, much of the flower pollination occurs late in the season, resulting in reduced seed production because of insufficient time for seed maturation. A two week delay in emergence and flowering results in most flower pollination at a time when an adequate developmental period remains. The two week delay also results in reduced pod shatter and predation due to a reduced period between pollination and harvest.

These results are strongly dependent on the specified seed production function, which is qualitatively valid but may be quantitatively out of adjustment. The same may then be said of the assumed behavior. In particular, an earlier (one week) harvest would reduce the shatter losses and increase production under the standard management, and a later (two weeks) harvest would increase production under the four week delay. The nominal harvest time appears optimal under the two week delay.

Even if the harvest times are adjusted to maximize production under all the delay tactics, the above qualitative behaviors (Figure 11) are not significantly changed. Under the four week delay tactic, the increased seed production resulting from the two week harvest delay would probably be lost due to late season rains. Under the standard tactic, the increased production resulting from the one week advance in harvest seems feasible. However, the production would still be less than that under the two week delay, except at the 6660 and 13320 bee introduction levels, where the productions would be equal.

The annual seed production behaviors are also strongly dependent on the flowering mechanism. The nature of the flowering mechanism is not precisely known, and it is apparent that an alternative mechanism could

result in different seed production behaviors. For example, the mechanism could allow termination of flowering under intense pollination at any time during the bloom period, rather than only at the start of the sixth week of bloom. The maximum seed production would probably then be obtained only with small to intermediate size bee introductions. Larger introductions would cause intense pollination and termination of flowering early in the bloom period, resulting in lower annual seed productions. Similar reductions in annual female bee production would also be expected with the larger bee introductions. If a mechanism of this type is operating, the timing of emergence and flowering and the level of bee introduction become more critical.

The rate at which seed production approaches its maximum value varies over a wider range of bee abundances for the four week delay in emergence and flowering than for the zero and two week delays (Figure 11). The rate of increase in seed production slowly drops with increasing bee abundances up to 6660 bees, while the rates for the other two levels of delay vary little during the approach to the maximum. This appears to be due to a lack of coincidence of the flower supply and demand trajectories. The thermal conditions during the last week of flower pollination resulting in at least some production of harvestable, mature seed (August 3 to

August 9) are less favorable for bee flight, reducing the flower demand during that week. However, in the case of the four week delay, the flower supply peaks during this week, and many flowers remain unpollinated, even when the flower demand exceeds the supply during the preceding weeks of the seed production period. Thus, even though the trajectory of foraging bees closely parallels the flower supply trajectory, the flower demand trajectory does not. After it has reached a certain level, increasing the demand trajectory by introducing more bees increases the number of flowers pollinated and, consequently, the seed production only during the single week where the flower supply is not yet exhausted. The flower demand already exceeded the supply during the previous weeks, and a further increase in the number of bees foraging these weeks does not increase seed production.

Where the flower demand trajectory more closely parallels the supply trajectory (as with the two week delay) but does not exceed it, increasing the demand trajectory increases the number of flowers pollinated during most or all weeks of the potential seed production period. Thus, the rate of increase of seed production is nearly constant up to the maximum seed production level. At the point where this maximum is reached there is an almost synchronous switch from excess flowers to a

shortage of flowers during all weeks of the seed production period.

The model for bee foraging assumes that all flowers are equally accessible to the bees. Thus, foraging success is not dependent on flower availability until the total supply is exhausted. A more realistic assumption might prescribe a foraging success rate relative to the total flower availability. When the flower demand is high relative to the supply, but not exceeding the supply, bees would likely be foraging farther from the domicile and forced to search out unpollinated flowers deeper in the alfalfa foliage. These bees would have a reduced foraging success rate, with a greater reduction when the remaining unpollinated flowers become scarcer. In Figure 11, this effect would tend to reduce the seed production to a greater extent as a lower maximum seed production was approached. However, the relations between the curves would likely remain approximately the same. The reduced foraging success rate would also decrease the egg-laying rate and alter the female population dynamics.

## A-2. The Synchrony of Bee Flight and Alfalfa Flowering

The proper timing of bee foraging with regard to alfalfa flowering is of great importance in leafcutter bee management. The objective is to obtain a time trajectory of flower demand which best parallels that of the flower supply. Model runs were made to investigate the effect of different levels of asynchrony between the times of first emergence and first flowering, representing cases where bees are introduced at various times relative to the onset of flowering.

Two tactics from the study of activity delay and level of bee introduction were selected as the nominal situations for the bee flight-flowering synchrony study. The first uses the standard time for flowering and bee flight with the 4430 bee introduction level. The second uses the two week delay in alfalfa flowering and bee flight with the same (4430) bee introduction level. For each case, the onset of first generation bee emergence is set at one or two weeks before the onset of flowering and one or two weeks after. This results in eight runs to examine synchrony. A nominal introduction of 9310 open tunnels with seven cell capacities was used in each run.

Table 6 summarizes the results of these model runs. Situations where emergence precedes flowering will be considered first. Increasing the gap between the times

Table 6. Bee and seed productions under standard timing and two week delay of emergence and flowering and under various levels of asynchrony between first emergence and flowering.

<u>WEEKS BETWEEN FIRST EMERGENCE AND FLOWERING</u>	<u>PRODUCTION WITH STANDARD TIME OF FLOWERING</u>		<u>PRODUCTION WITH TWO WEEK DELAY IN FLOWERING</u>	
	<u>BEES<sup>a</sup></u>	<u>SEED<sup>b</sup></u>	<u>BEES<sup>a</sup></u>	<u>SEED<sup>b</sup></u>
+2	74%	313	120%	787
+1	104%	624	177%	1023
0	135%	943	224%	1282
-1	148%	923	173%	930
-2	159%	822	112%	544

<sup>a</sup>percent annual increase in the female population

<sup>b</sup>seed production in pounds per acre

of initial emergence and flowering to two weeks results in a reduction of nearly one-half of the annual rate of increase in the female bee population for both the standard time of flowering and the two week delay. While seed production is reduced by only about 40% with the two week delay in flowering, it is reduced by nearly 70% with the standard management time. These results suggest that management errors resulting in too early emergence cause the greatest production losses when the standard time for the onset of flowering is used.

The model assumes that adult starvation does not occur, even when emergence precedes flowering. To avoid starvation of newly emerged bees in this situation, they must be held below the activity threshold temperature. An alternative and equivalent assumption would be that flower availability was adequate to prevent adult starvation but inadequate for cell production, and no seed production resulted from pollination during the interval between emergence and flowering. Relaxing this assumption would result in greater losses than predicted here, but the general relations should hold.

In the situation where emergence lags behind flowering, a lag from zero to two weeks results in relatively small changes in bee and seed productions with the standard flowering time. However, with the two week delay in flowering both the seed production and the

annual rate of increase in the female population are reduced by approximately 50%. These results suggest that management errors leading to late emergence result in substantial production losses when flowering is delayed but not when the standard time for flowering is used. In general, under a one week lack of synchrony, the delay tactic is uniformly better than the standard tactic, but greater asynchrony in the direction of late emergence is best offset by the standard tactic.

#### A-3. The Number and Distribution Over Potential Capacities of Introduced Open Tunnels

Another tactic of interest in the management of the leafcutter bee is the introduction of open tunnels in various numbers and distributions of potential capacities. Open tunnels of various capacities left after emergence and accumulation of nesting debris can be reintroduced, or unused (or cleaned-out) tunnels with the maximum capacities can be provided.

As previously discussed, the nature of the nesting tunnels is important in the bee population dynamics for several reasons. First, the sex ratio of eggs laid in tunnels varies with the depth of the tunnels, with a greater percentage of fertilized (female) eggs in deeper tunnels. Second, more of the female's time is spent

capping tunnels and selecting new ones when nesting takes place in short tunnels. Lastly, the total available nesting space may become limited or may be composed of less preferred shallow tunnels, making both the number and distribution of tunnel depths important.

Model runs were made to investigate the system response to the number and distribution of depth of introduced open tunnels, relative to introduction of a nominal set of completed tunnels. The nominal set contained 3500 completed tunnels distributed uniformly over realized capacities of one to seven cells, corresponding to the 3330 female bee introduction level of the previous studies. With this nominal set of completed tunnels, open tunnels varying in number and distribution of potential capacities were introduced.

Two distributions of open tunnels were investigated. The first distribution prescribes that all introduced open tunnels have seven cell capacities, representing a situation where all new (or reclaimed) materials are provided for nesting. The second distribution has the introduced open tunnels evenly distributed over potential capacities of from one to seven cells, to represent situations where previously used nesting materials are reintroduced. Runs were made for each distribution with 3500, 5250, 8170, 14000, and 31500 open tunnels.

Figure 13 shows the effect of this management tactic on the annual rate of change in the female bee population size. The general trend is for a sharp rise in the bee production with increasing levels of open tunnel introduction at the low end of the range, changing to a more moderate increase over the intermediate and high levels of introduction. The use of the seven cell capacity tunnels results in a greater increase than that obtained with the even distribution over capacities, for all levels of open tunnel introduction.

Figure 14 provides an alternate illustration of these responses. Here, the open tunnel introduction is represented in terms of the total cell space rather than the number of tunnels. The behavior of the annual rate of change in the female population is quite similar under both distributions. The two curves rise at a similar rate, but approach two different asymptotes. The asymptotes appear to be set by the sex ratio of the bee production, as influenced by the distributions.

A lack of open tunnel space, resulting in female bees without nesting tunnels at some time during the season, occurred in situations represented by the three points in the lower left corner of Figure 14. Providing more open tunnels results in a sharp initial rise in the annual rate of increase.

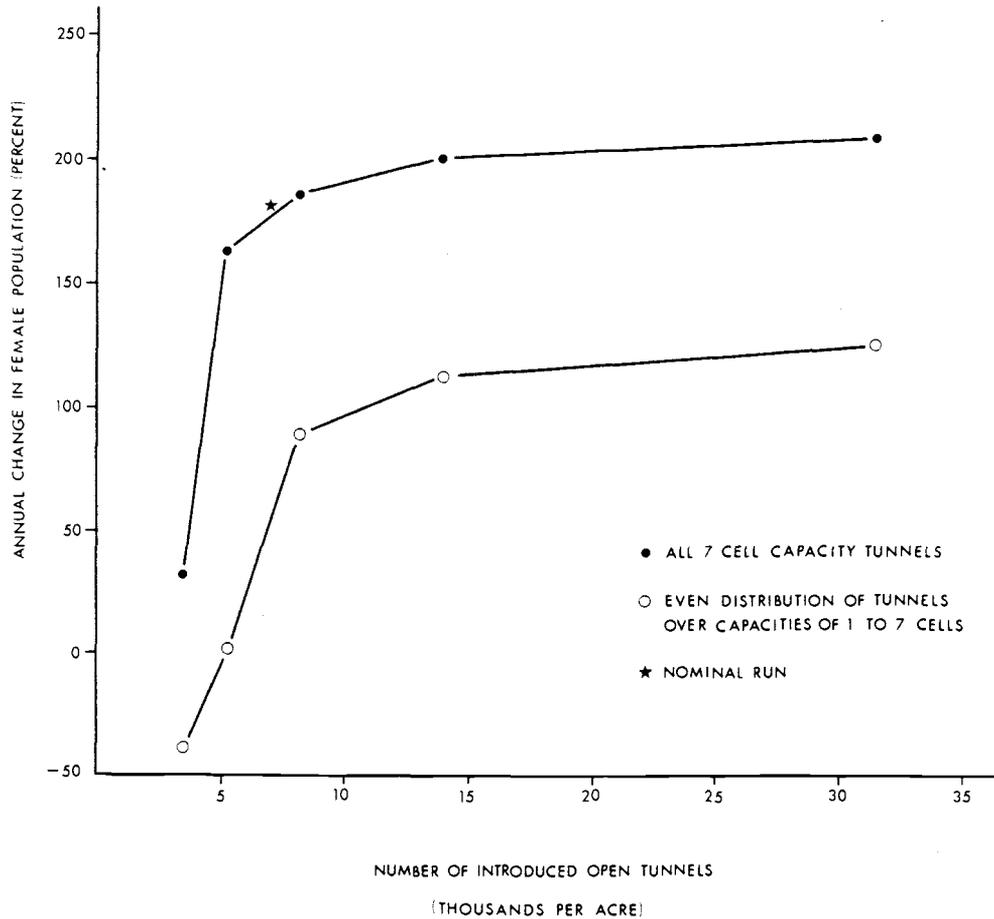


Figure 13. Annual change in the female population number under varying level of open tunnel introduction for two distributions of open tunnel capacity.

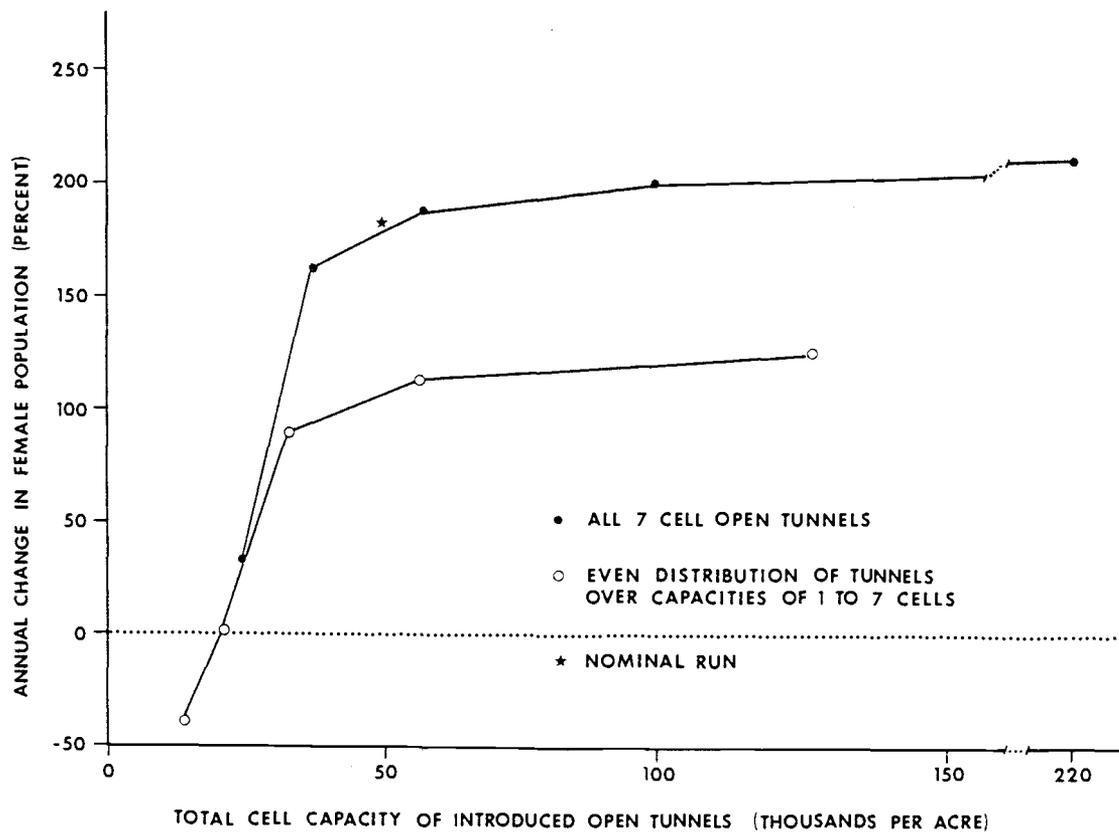


Figure 14. Annual change in female population number under varying level of total cell space in open tunnels for two distributions of open tunnel capacity.

When the open tunnel supply is not exhausted, further increases in the open tunnel introduction result in a more gradual rise in the annual rate of increase. This rise seems mainly due to the greater abundance of the preferred deeper tunnels throughout the season. An increased percentage of fertilized eggs and more efficient nesting result from egg-laying in these deeper tunnels.

Another effect of increased abundance of open tunnels is the reduced reoccupation of inactive tunnels. Reoccupation and nesting in these inactive tunnels does not significantly contribute to the female production.

#### B. Sensitivity Analyses

Several model runs were made to determine the sensitivity of the two annual resolution model outputs, diapause female bee production and seed production, to changes in certain parameter values. The information from these analyses is useful in identifying parameters to which the model outputs are sensitive, which may then require more precise estimation. These parameters may also indicate tactics for manipulation of the sensitive behaviors.

Sensitivities were determined by increasing and decreasing each parameter by certain percentages of its

nominal run value, as presented in the model parameterization section. The relative change of value of an output variable resulting from a change in a parameter value indicates the sensitivity of the output to the parameter. A small change indicates insensitivity, while a large change indicates sensitivity.

Figure 15 shows the sensitivity of diapause female bee production to certain parameters; production is insensitive to the first three parameters in the legend. The second entry in the legend requires some explanation. The array of values describing the minimum immature survival rate at which emergence would occur was the same as that used to describe the minimum immature survival rate at which a tunnel would be plugged with debris and cadavers following emergence. This array was changed proportionally, reflecting a multiplicative change in the parameters,  $a$ , of Figures 5 and 6.

Female bee production is slightly more sensitive to the day-degrees sufficient for the maximum cell production than to the other three parameters in Figure 15. Note also the nonlinear response to this parameter. With the higher day-degree threshold, bee production is reduced relative to the nominal. However, bee production is also reduced with the lower day-degree threshold. The bees pollinate more of the flowers in the first bloom period, causing a reduction in flower

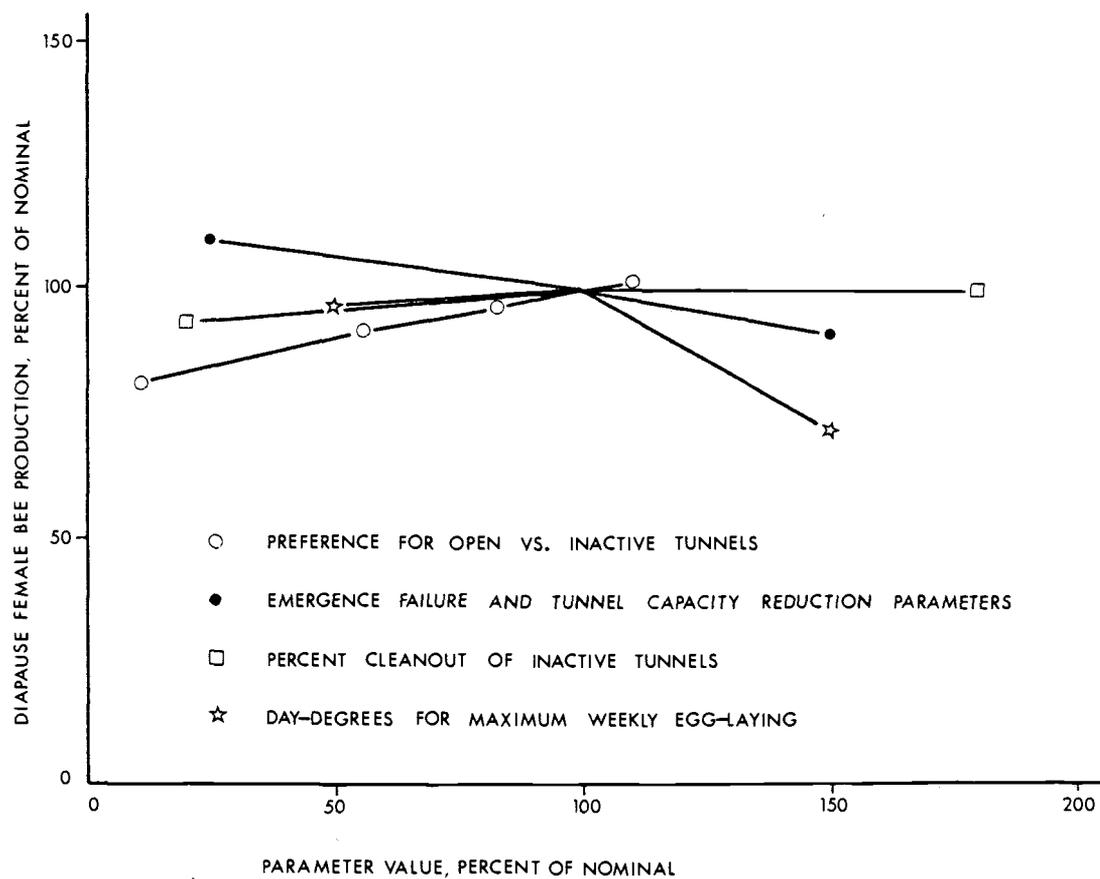


Figure 15. Sensitivity of diapause female bee production to various parameters.

production during the second bloom period. This results in greater competition for flowers and in a lower bee production than obtained under the nominal threshold.

Figure 16 presents the sensitivity of diapause female bee production to parameters associated with bee survival. Bee production is similarly sensitive to all survival rates. Sensitivity is greater to background survival than to chalkbrood survival because background mortality is cumulative over the developmental period while chalkbrood mortality is not. The average adult lifespan is represented here as a single value to characterize the entire adult survivorship schedule, composed of the proportions of an original cohort surviving after one, two, three, and four weeks of adult life.

Figure 17 shows the sensitivity of seed production to the same parameters. Seed production sensitivity to all the parameters is similar to that of bee production. One noticeable difference occurs with reduction in the day-degree threshold, which causes an increase in seed production.

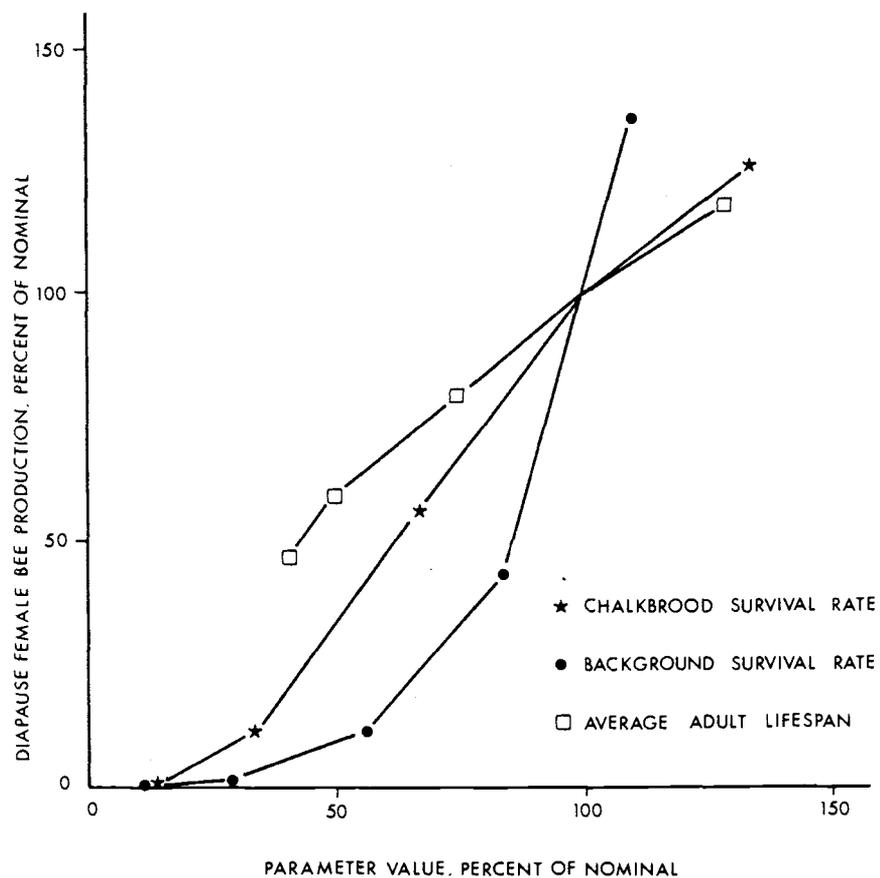


Figure 16. Sensitivity of diapause female bee production to parameters associated with bee survival.

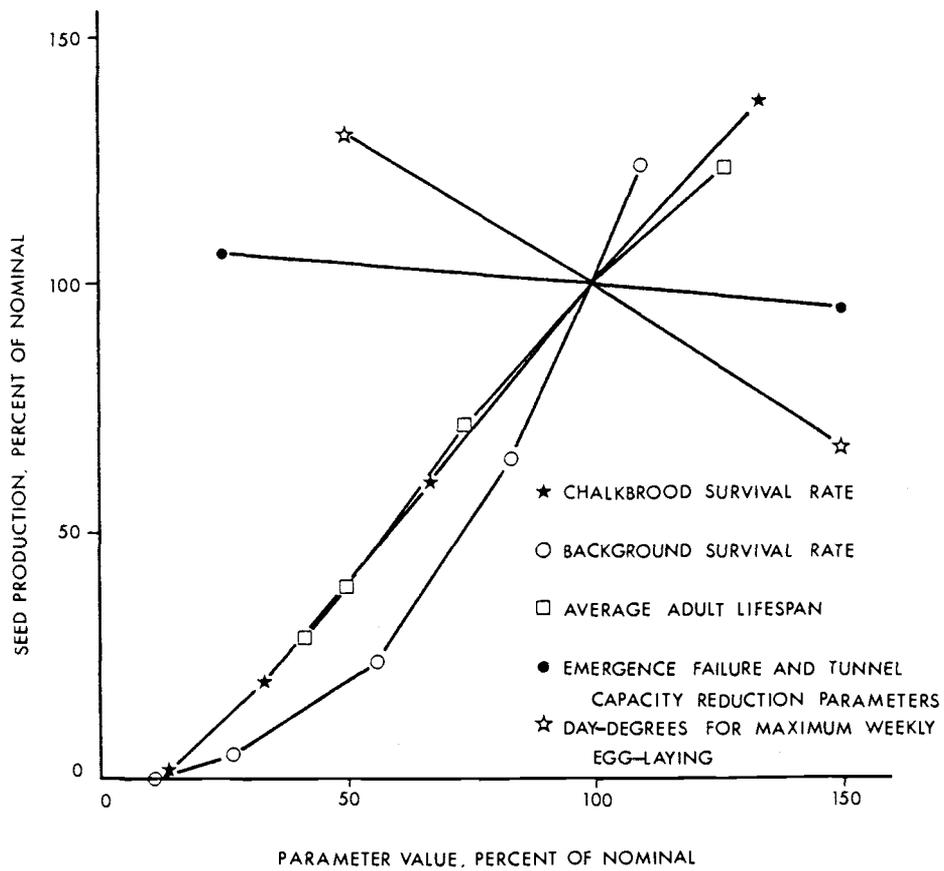


Figure 17. Sensitivity of seed production to various parameters.

The insensitivities of diapause female bee production and seed production to the capacity preference schedule for selection of open tunnels are shown in Table 7. The nominal array represents increasing preference with increasing tunnel capacity, with slightly less preference for the new seven cell capacity tunnels than the used six cell capacity tunnels. The first perturbation eliminates response to tunnel capacity. The second perturbation represents an exaggerated selection for tunnel capacity of the same nature as that represented by the nominal. Changing from one of these arrays to another has little effect on the diapause female bee production. Seed production is totally insensitive to these tunnel capacity preference coefficients, given the other model conditions.

It is noted that the sensitivities of bee and seed productions would probably change if the nominal run conditions were different. If, in the nominal run, the flower supply was exceeded by the flower demand, an increase in the bee survival rates would not increase seed production to the extent noted here. If, in the nominal run, the open tunnel introduction was smaller, the bee production would be more sensitive to the preference coefficients for open versus inactive tunnels than noted here.

Table 7. Sensitivities of diapause female bee and seed productions to capacity preference coefficients for open tunnels. Nominal preference coefficients are 0.10, 0.11, 0.13, 0.15, 0.17, 0.19, and 0.15 for capacities of one to seven cells, respectively.

PREFERENCE COEFFICIENTS <sup>a</sup>	PERCENT OF NOMINAL PRODUCTION	
	DIAPAUSE FEMALE BEES	SEED
.14, .14, .14, .14, .15, .15, .14	99%	100%
.03, .07, .12, .16, .21, .25, .16	102%	100%

<sup>a</sup>female bee preference coefficients for capacities of one to seven cells in open tunnels

## VI. Summary and Conclusions

The alfalfa leafcutter bee-seed production system model was developed to identify the general behaviors of the system under imposition of various management tactics and to identify the mechanisms associated with these behaviors. Existing knowledge about the natural history of the system provided the basis for the development of a structured system conceptualization, from which a computer simulation model was formulated. Analyses of the model revealed the following behaviors:

- 1) Gross female production increases when the initial emergence and flowering are delayed beyond the standard management time (Figure 9). The increase is greatest with a two week delay and is almost as large with the four week delay. This increase is associated with increased production of diapause second generation bees when emergence and flowering are delayed. With the delay, the population replaces itself at a time when flowers are abundant and conditions are favorable for bee flight.

Seed production is increased by a two week delay of emergence and flowering, but is greatly reduced by a four week delay (Figure 11). A key model mechanism in this behavior is the relation of

the time of pollination to the probability of production and retention of mature, harvestable seed at a particular harvest date. This relation is based on reports of increased shatter of pods produced early in the season (Smith and Melton 1967) and of production of immature seed from late season pollination (Stephen, personal communication).

Key model mechanisms in the population behaviors involve the timing of diapause, the effect of temperature on bee flight, and the production of flowers. Although these model mechanisms were felt to reflect the current understanding of these processes, all are somewhat subjective (see model parameterization section). These mechanisms are judged to be adequate to generate the qualitative behaviors of the system, but inadequate for precise prediction. For example, it is not known what will be the exact response to a two week delay or to a four week delay, but it is strongly indicated that a moderate delay will give enhanced production, and that production under a greater delay will regress.

2) With increasing female introductions, the gross female production behaves similarly for both delay tactics, but quite differently for the standard (Figure 9). The key model mechanisms in the above behaviors involve the reduction of flowering late in

the season due to intense pollination early in the season and the reduction of female productivity due to competition for flowers. Although the nature of the bloom reduction under different timing and intensity of pollination has not been characterized, the flowering mechanism used in the model seems to adequately represent the current understanding. The mechanism for reduced bee productivity due to competition for flowers is based on fairly extensive research. The assumption of spatial homogeneity, however, results in predicted bee and seed productions which are likely higher than would be observed. This effect will be greatest when competition for flowers becomes great.

With increasing female introduction, seed production increases rapidly to a maximum, and then levels off (Figure 11). The mechanisms involved in this behavior are those affecting the bee pollination activity (see above).

3) The effects on bee and seed productions of asynchrony in first emergence and flowering depend on the timing of the onset of flowering (Table 6). When the standard flowering time is used, early emergence (two weeks before flowering) results in greater production losses than does late emergence. When the flowering is delayed by two weeks, late

emergence (two weeks after flowering) results in greater production losses than early emergence. In general, under a one week lack of synchrony, the flowering delay tactic is uniformly better than the standard tactic, but greater asynchrony in the direction of late emergence is best offset by the standard tactic.

4) The introduction of open tunnels with small capacities (rather than large) greatly reduces the rate of population increase. The population increase is also greatly reduced when the overall capacity of the introduced open tunnels is insufficient for the population's cell production. These behaviors indicate the importance of providing deep open tunnels in sufficient number to accommodate the cell production. The primary mechanisms associated with these behaviors involve the effect of tunnel capacity on sex ratio and the loss of cell production due to insufficient nesting space. These mechanisms are based on information from several studies (Gerber and Klostermeyer 1972, Stephen and Osgood 1965b) and are thought to be appropriate representations.

The orientation throughout this study was on the development of a model realistic enough, in terms of the mechanistic structures, to be of use in the

identification of the behaviors of the system under the imposition of several management tactics. As some of the necessary mechanisms were not understood in great enough detail, it was recognized that the development of a model capable of highly accurate quantitative predictions was infeasible. In this orientation to modeling, the model is not considered as an end product, but as a conceptual and integrative tool in the ongoing study of the system. The model provides a context for organization of thought and sets the stage for future research into the dynamics of this system.

Specifically, the identification of key mechanisms for the behaviors of interest leads to examination of the adequacy of current knowledge of those mechanisms and to the identification of needed research. Additionally, identification of weak or inadequate structures in the model leads to specification of needed research.

In particular, several aspects of the knowledge base that have apparent needs are identified:

- 1) the flower trajectory and the nature of bloom reduction under intense pollination;
- 2) the contribution of pollination in the successive weeks to harvestable seed at different dates;

3) the timing of diapause and the extent of concurrent production of both diapause and nondiapause bees;

4) the relation of female emergence failure and residual tunnel capacity to immature survival rates and tunnel depth; and

5) preferences of female bees for tunnels of different types.

Additionally, several model structures should be modified to improve the representation of the following:

1) heterogeneity in spatial distributions of available flowers and foraging bees;

2) concurrent production of diapause and nondiapause bees;

3) pollination, as conceptualized rather than as currently coded (to account for the reduction due to time spent in tunnel selection and capping);

4) the generation of the residual tunnel capacity following emergence; and

5) mortality of adult females under flower shortages.

The model could play a key role in the identification of areas of research and investigation. The above processes can be evaluated by including appropriate mechanisms in the existing model. For example, by including a mechanism for concurrent

production of diapause and nondiapause bees, the importance of concurrent production can be evaluated prior to data collection. If concurrent production strongly affects system behavior, further investigation is necessary.

In addition, a more extensive behavioral study of the existing model would be illuminating. The model has provided valuable insights into the management process, and a great potential in research and management remains.

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