Ecological Modelling, 45 (1989) 133–150
Elsevier Science Publishers B.V., Amsterdam – Printed in The Netherlands

BEEPOP: A HONEYBEE POPULATION DYNAMICS SIMULATION MODEL

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(Accepted 3 October 1988)

ABSTRACT

DeGrandi-Hoffman, G., Roth, S.A., Loper, G.L. and Erickson, E.H., Jr., 1989. BEEPOP: a honey bee population dynamics simulation model. *Ecol. Modelling*, 45: 133–150.

BEEPOP is a computer model that simulates honey bee colony population dynamics. Estimates of population size and composition (i.e., proportions of workers and drones) at time (t) are based upon initial colony population size, weather conditions, reproductive potential of the queen, and forager longevity. Results of a sensitivity analysis indicate that the queen's egg-laying potential has the greatest effect on colony population size. Yearly trends in population growth and age structure generated from simulations are also discussed.

INTRODUCTION

The population dynamics of a honeybee colony can be considered a feedback system of interdependent elements. Brood rearing and colony growth depend upon the queen's reproductive state (i.e., the number of eggs a queen can potentially lay per day) and, because larvae are reared by adults, the size of the worker population (Harbo, 1986). The amount of brood that is reared determines the colony's population size and hence future brood rearing. Additional factors such as the queen's age, ambient temperature, photoperiod, and colony resources also influence the reproductive potential of a hive (Ribbands, 1964; Kefuss, 1978).

The objective of this report is to describe a computer model (BEEPOP) that simulates the interactions of parameters that influence colony population dynamics. These include colony population size, weather, and the queen's reproductive state. The model was constructed using literature values for developmental rates of workers and drones, brood production cycles, average worker age before becoming a forager, average spermatozoa

0304-3800/89/$03.50

per drone, and spermatozoa holding capacity of a queen's spermatheca. Values for factors that vary among colonies or locations can be entered by the user during the interactive portion of the program. These include the number of spermatozoa obtained by the queen during mating, initial colony population size, queen egg laying potential, weather conditions, forager longevity, and the time of year to begin the simulation. Due to the interactive nature of the BEEPOP model, the influence of any one of these factors on colony population growth can be determined using sensitivity analysis. This procedure permits the influence that various factors exert on a model's final output to be defined by varying each parameter while holding all others constant. Results of a sensitivity analysis are included.

MODEL DESCRIPTION

The model is written in Fortran 77, and consists of two major components (Fig. 1). The first (EGGLAY) determines the number of eggs laid by the queen at any time (t). The percentage of eggs that will develop into workers (fertilized) and drones (unfertilized) is also assigned in this subroutine. The second major portion of the program (COLPOP) tracks the development of eggs to adult, and predicts the colony's adult population size at any time (t). BEEPOP updates egg, larvae, and adult populations daily, and reports colony population size (i.e., number of adult bees) after each worker brood cycle.

Simulations begin by prompting the user to answer questions concerning the colony (Table 1). Following the interactive portion of the program, the first calculations executed by BEEPOP estimate eggs laid per day (P_t) at time (t). The number of eggs a queen can potentially lay each day is estimated as a function of the total number of days the queen has been laying eggs using the equation:

$$P_t = E_{\max} + \left[-0.0027(d)^2 + 0.395(d)\right] \tag{1}$$

where $E_{\max}$ is the maximum number of eggs the queen can lay per day as entered by the user, and d the number of days the queen has been laying eggs (initialized to $d = 0$ at the beginning of a simulation). In the model, as a queen ages her egg-laying potential is reduced.

The actual number of eggs laid by a queen each day is a function of ambient temperature (expressed in degree days with a 0 °C base), photoperiod, and adult population size. Eggs laid per day (E_t) is estimated by the equation:

$$E_t = \mathrm{DD}\ L_t N_t P_t \tag{2}$$

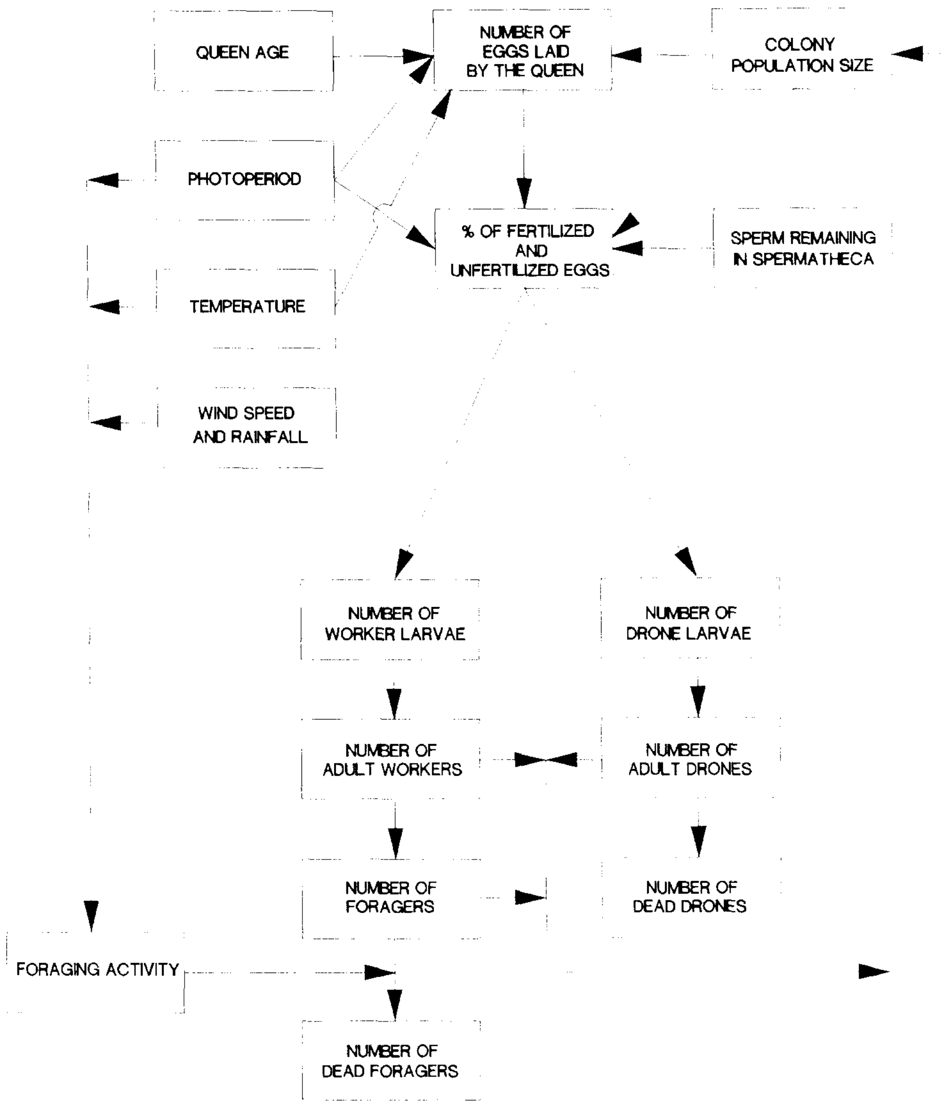

Fig. 1. Logical flow of the components in the BEEPOP model.

where

$$\mathrm{DD} = -0.0006(\mathrm{dd})^2 + 0.05(\mathrm{dd}) + 0.021$$

$$L_t = -0.00743(l_t)^3 + 0.312(l_t)^2 - 4.04(l_t) + 16.58$$

$$N_t = \left[\log((n_t \times 0.001) + 1)\right] \times 0.672$$

in which dd degree days, l_t hours of sunlight per day, n_t foraging population size, and P_t number of eggs that can potentially be laid at time (t) from (1).

TABLE 1

Parameters that can be entered by the user during the interactive portion of the BEEPOP program

(1) Initial colony population size
(2) Starting date of simulation
(3) Weather conditions
(4) Amount of sperm obtained by the queen during mating
(5) Potential number of eggs laid per day
(6) Number of days a bee can forage before it dies
(7) Number of brood cycles in the simulation

After the actual number of eggs laid per day is estimated (E_t), the proportion that will develop into either workers or drones is predicted. The proportion of eggs that will become drones is calculated as the sum of two response equations. The first estimates the proportion of unfertilized eggs as a function of the spermatozoa remaining in the queen's spermatheca. As the total number of eggs laid by the queen increases, the number of remaining spermatozoa decreases non-linearly, so that by the end of a queen's life she may become almost exclusively a drone-layer (Butler, 1975; Harbo, 1979). The amount of spermatozoa in a queen is dependent upon the number of drones she mated with during her mating flight(s). During the interactive portion of the program the user can specify the amount of spermatozoa entering the spermatheca. The maximum number of sperm that can be stored in a spermatheca is estimated to be 5.5 million (Mackensen and Roberts, 1948; Woyke, 1962; Rinderer et al., 1985).

The second response equation used to predict drone production is the product of egg fertilization responses to photoperiod and the foraging population size in the colony. The total proportion of eggs that are unfertilized each day (Z_t) is estimated by the equation:

$$Z_t = S_t + B_t \tag{3}$$

where

$$S_t = 1 - \left(-6.355 s_t^3 + 7.657 s_t^2 - 2.3 s_t + 1.002\right) \qquad \text{and} \qquad s_t > 0.60$$

$$B_t = L_t F_t$$

$$L_t = \left[\log(l_t \times 0.1)\right] \times 0.284$$

$$F_t = \left[\log(f_t \times 0.0006)\right] \times 0.797$$

in which s_t spermatozoa used at a time (t)/total spermatozoa in the spermatheca after mating, l_t hours of sunlight per day at time (t), and f_t foraging population size at time (t).

Daily drone production (V_t) is estimated by the equation:

$$V_t = E_t Z_t \tag{4}$$

in which E_t eggs laid at time (t) from (2), and Z_t proportion of eggs that are unfertilized from (3). The production of workers (W_t) is estimated daily by the equation:

$$W_t = E_t - V_t \tag{5}$$

in which V_t unfertilized eggs produced at time (t) from (4), and E_t eggs laid at time (t) from (2). Using these equations, drones can comprise no greater than 5% of the brood being reared under conditions where the amount of spermatozoa in the queen's spermatheca is not limiting (Jay, 1974).

After the number of fertilized and unfertilized eggs is estimated, eggs are aged to larvae and adults through discrete delays. Only 85% of the eggs become adults (Fukuda and Sakagami, 1968). The number of days before eggs develop into either adult workers or drones can be entered by the user. Default values for these parameters are 21 days for eggs to become adult workers and 24 days for adult drones (Jay, 1963). After workers become adults they become foragers in 21 days (Free, 1965). Adult workers are removed from the colony population after they have foraged for a number of days specified by the user in the interactive portion of the program. Honeybees forage on days when average temperatures exceed 12°C (Lundie, 1925), wind velocity < 34 km/h (Rashad, 1957), and rainfall is < 0.5 cm.

Construction of weather conditions

Two different sets of yearly weather scenarios were constructed simulating midwestern and desert southwestern U.S. conditions. Temperature, photoperiod, wind velocity, and rainfall are included. Under midwestern weather conditions temperatures range between 0 and 31°C, and photoperiod ranged from 9.1 (December) to 15.25 (June) hours of light per day. Under southwestern weather conditions, temperatures range between 0 and 39°C and photoperiod is between 10 (December) and 14.5 (June) hours of light.

These weather conditions were chosen because of the resulting differences in the yearly behavior of honey bee colonies. Under midwestern conditions, bees do not produce brood from autumn to mid-winter (late January), and can be confined in the hive (i.e., do not forage) from late October to early April (personal observation). Conversely, bees produce some brood and weather conditions are favorable for flight almost year around under desert southwestern conditions (personal observation). Consequently, colony population dynamics under each set of weather conditions differ.

RESULTS

Simulations were conducted where each parameter that can be entered by the user (Table 1) was examined for its influence on colony population dynamics. The following are the results of those simulations.

Influence of weather conditions and initial colony population size

Yearly colony population growth (beginning on 1 January) for midwestern and southwestern weather conditions is shown in Fig. 2. Simulations were run with queens that could potentially lay 3000 eggs per day, and foragers were removed from the colony population after 10 days of foraging. Adult drone life was estimated to be 59 days which is the average maximum under optimal colony conditions (Howell and Usinger, 1933).

The population growth rate under midwestern conditions was minimal until early May. Colony populations continued to grow until early September. Under southwestern conditions, colony populations declined in April, but then increased during each brood cycle until early October. Drone production began in early May and drone populations peaked in early September under midwestern conditions, while under southwestern conditions drones were initially produced in mid-June and populations peaked in early October.

Colonies with initial populations of 1500–10 000 bees under midwestern conditions peaked at 40 341 to 50 370 bees, respectively. The greatest increase in peak population size occurred when the initial population was increased from 1500 to 3000 bees. Under southwestern conditions, colonies that initially had 1500–10 000 bees peaked between 39 979 and 46 092 bees, respectively. Raising the initial population from 1500 to 3000 bees resulted in the greatest increase in peak population size (almost 3000 bees).

A second set of simulations was conducted with initial populations of 1500–7500 bees and starting dates of May, June or July. The simulations were run under midwestern and southwestern weather conditions, with the purpose of simulating the growth of colonies begun from swarms during those times of year.

Under midwestern conditions, populations of 1500–7500 adults peaked at 19 205 to 33 396 bees, respectively (Fig. 3). If the same size colonies were begun in June, the populations peaked at 13 170 to 22 300 bees. When colonies were started in July with 1500–7500 bees, populations peaked at 6501 to 13 906 bees, respectively. An increase of 6000 bees in May resulted in over 14 000 more bees at the peak population interval. In June the 6000-bee increase in initial population size resulted in a peak population of about 9100 more bees, but in July only 7300 more.

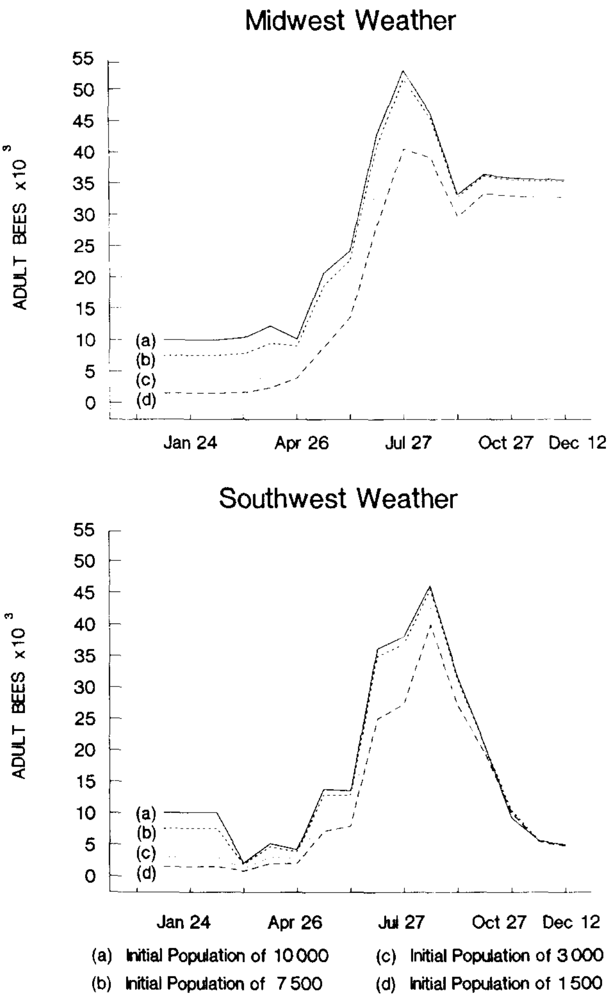

Fig. 2. Colony growth throughout the year as a function of weather conditions and initial population size.

Under southwestern conditions, colonies started in May with 1500–7500 bees had peak populations of 19 651 to 30 600, respectively. Colonies started in June with initial populations of 1500–7500 bees had population peaks of 15 522 to 26 269 bees. If colonies were started in July with 1500–7500 adults, their populations peaked at 7365 to 16 784 bees, respectively. A difference of 6000 bees in May resulted in an increase of almost 11 000 more bees at the peak population interval. In June the 6000-bee difference resulted in a peak population of 10 700 more bees, and in July 9400 more.

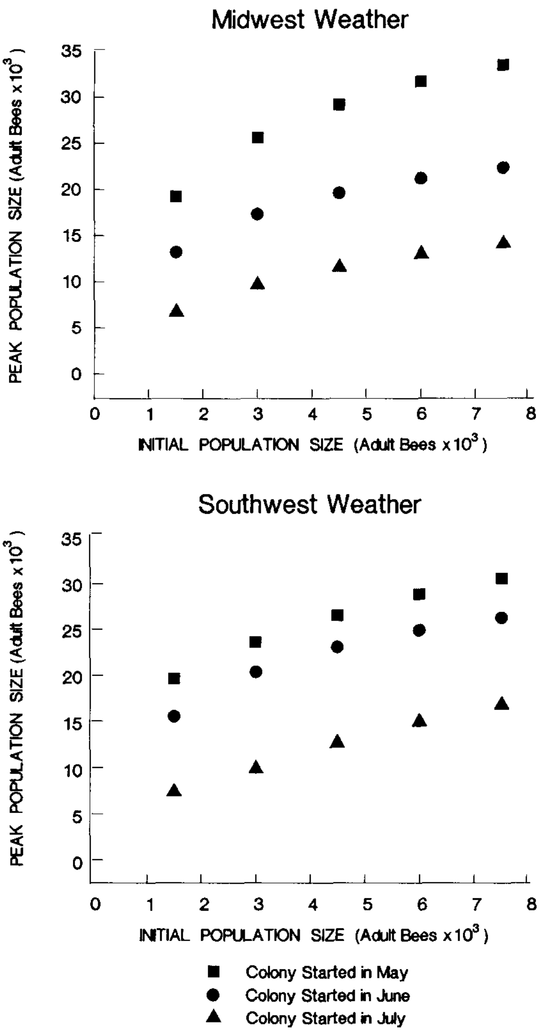

Fig. 3. Estimates of peak populations from simulations started in May, June or July with various initial population sizes.

Influence of the queen's egg-laying potential

Simulations were conducted under midwestern and southwestern weather conditions, with colonies that initially contained either 6000 or 10 000 workers on 1 January, and queens that could potentially lay 1000–3000 eggs per day.

The number of eggs actually laid each day varied as a function of weather, colony population size, and the number of eggs the queen had already laid in her lifetime. Egg laying rates reached their potential for only

TABLE 2

Influence of the queen's egg laying potential on population growth

Weather	Initial colony population size	Potential eggs laid per day	Peak population size
Midwestern	6000	1000	6801
		1500	15054
		2500	37303
		3000	50370
	10000	1000	7646
		1500	16372
		2500	39541
		3000	53030
Southwestern	6000	1000	3071
		1500	11779
		2500	32672
		3000	44995
	10000	1000	4681
		1500	12434
		2500	33764
		3000	46092

a short period of time in the spring. Under midwestern conditions, colonies with initial populations of 6000 bees had population peaks ranging between 6800 (egg-laying potential = 1000) and 50 370 (egg-laying potential = 3000) bees (Table 2). Under southwestern conditions, population peaks ranged between 3071 and 44 995 (egg laying potential = 1000 to 3000, respectively). Colonies initially containing 10 000 bees under midwestern conditions peaked between 7646 and 53 030, while under southwestern conditions they peaked between 4681 and 46 092 bees (egg laying potential = 1000 to 3000, respectively).

Colony growth and drone production as influenced by the number of spermatozoa obtained by a queen during mating

Simulations were conducted using queens that had 1.14, 2.28 and 4.56 million spermatozoa in their spermatheca (Q-1, Q-2, Q-3, respectively). For comparison, a simulation was also conducted with a queen who had a full complement of spermatozoa in her spermatheca (i.e., 5.5 million spermatozoa) (Q-F). Simulations were run for a 3-year period under midwestern and southwestern conditions beginning 1 January, with initial populations of 6000 bees, and queens with egg laying potentials of 3000 eggs per day.

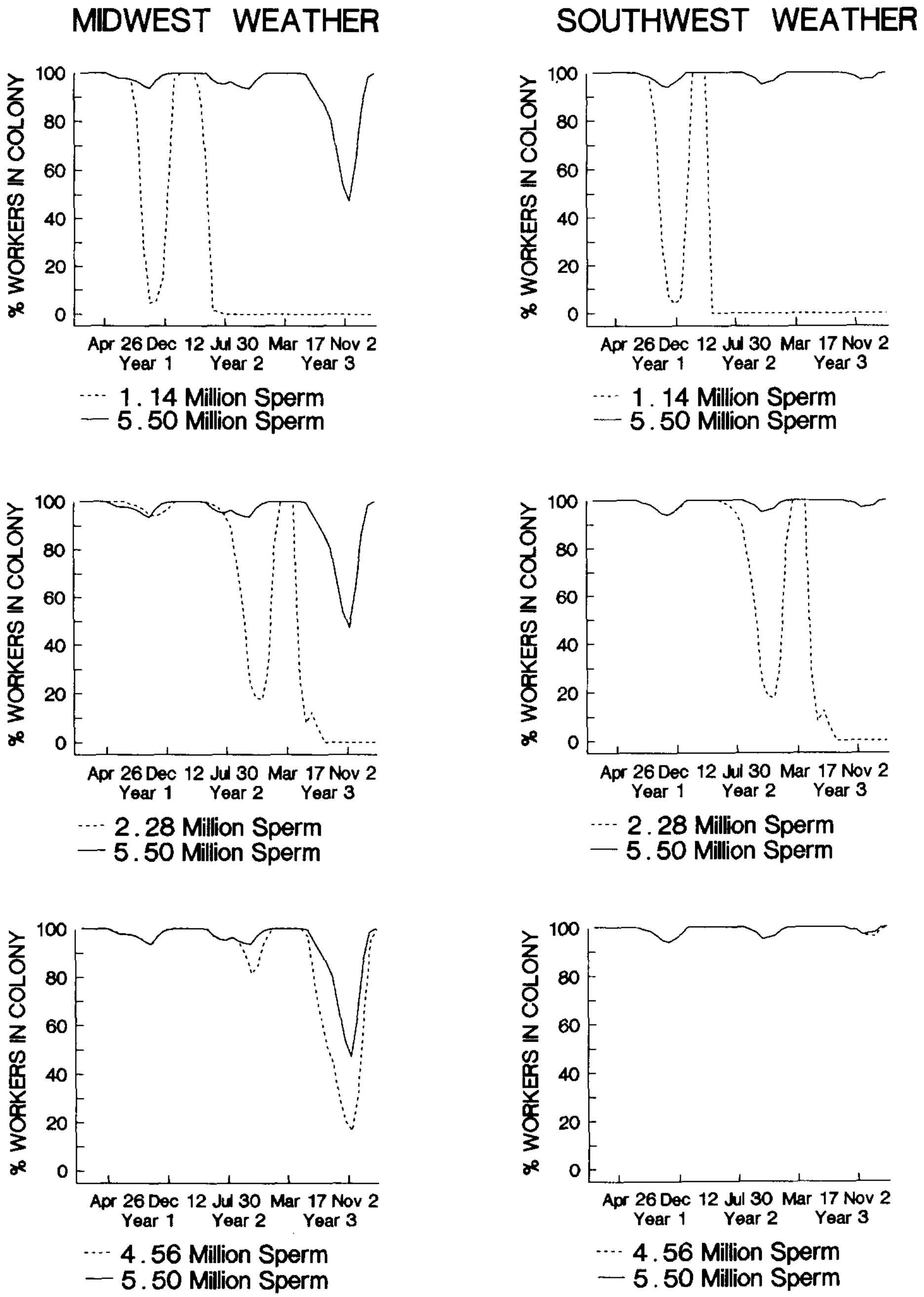

Fig. 4. Percentages of the colony that are workers during a three year period. Queen spermathecas contained 1.14, 2.28, 4.56 or 5.5 (completely mated) million spermatozoa.

Q-1 under midwestern conditions produced proportions of workers and drones equivalent to Q-F for the first eight brood cycles (i.e., until mid-summer of year-1) (Fig. 4). Afterwards, considerably more drones were produced by Q-1 and colony populations were reduced. By winter the drones had expired and the population was composed again entirely of workers. By mid-June in year-2 the queen became exclusively a drone layer, and the colony expired within two brood cycles (about 40 days). Similar results occurred under southwestern conditions except higher proportions of drones were produced after 10 brood periods (mid-August of year 1). Queens became drone layers during mid-March of year 2, and the colony died within three brood periods.

Under midwestern conditions Q-2 produced the same number and proportion of workers and drones as Q-F until September of year 1. Afterwards Q-2 began to produce more drones than Q-F and colony population size was smaller. Drones expired in the late fall and the colony was composed entirely of workers. By mid-June of year 3, Q-2 became exclusively a drone layer and the colony expired within three brood cycles.

Q-2 under southwestern conditions produced the same brood pattern as Q-F during year 1. By year 2 though, Q-2 produced drones earlier and in higher proportions compared with Q-F. Q-2 populations were smaller than Q-F during year 2. The Q-2 population reverted back to entirely workers in late fall as the drones expired. By mid-June of year 3, Q-2 became exclusively a drone layer, and the colony died within three brood periods.

Under midwestern conditions, Q-3 produced the same brood pattern as Q-F during year 1, but by the end of July of year 2 produced higher proportions of drones. Q-3 did not become exclusively a drone layer, but colony populations had higher percentages of drones compared with Q-F beginning in September of year 2 (brood-period 43). Colony populations were also lower by year 3 with Q-3.

Q-3 under southwestern conditions produced the same brood pattern as Q-F during the first 2 years of the simulation. By year 3, Q-3 produced a slightly higher proportion of drones, but did not become a drone layer.

Influence of varying the number of days a bee can forage

Simulations were run with initial colony populations (1 January) of 6000 and 10 000 bees, under midwestern and southwestern conditions. Bees could forage for 4, 6, 8, 10, or 12 days. Increases in peak population size with increased forager longevity were greater under southwestern compared with midwestern conditions, and with initial colony populations of 6000 versus 10 000 bees. Under midwestern conditions, colonies that initially contained 6000 bees had population peaks between 17 429 (4 foraging days) and 60 418

TABLE 3

Influence on population growth of varying the number of days a bee can forage before dying [a]

Weather	Initial colony population size	Foraging days	Peak population size	Percent increase [b] in population
Midwestern	6000	4	17429	–
		6	29782	70.9
		8	38803	30.3
		10	50370	29.8
		12	60418	19.9
	10000	4	18962	–
		6	31739	67.4
		8	41009	29.2
		10	53030	29.2
		12	63422	19.6
Southwestern	6000	4	7767	–
		6	18472	137.8
		8	35019	89.6
		10	44995	28.5
		12	52054	15.7
	10000	4	8604	–
		6	19470	126.3
		8	36151	85.7
		10	46092	27.5
		12	53993	17.1

[a] All simulations were conducted using queens with an egg laying potential of 3000 eggs per day.

[b] % increase in population size

$$= \frac{\{\text{Peak population size } (x+2 \text{ Foraging days}) - \text{Peak population size } (x \text{ Foraging days})\}}{\{\text{Peak population size } (x \text{ Foraging days})\}}$$

(12 foraging days) (Table 3). Under southwestern conditions, initial populations of 6000 adults peaked between 7767 (4 foraging days) and 52054 (12 foraging days). Colonies with initial populations of 10000 adults had population peaks between 18962 (4 foraging days) and 63422 (12 foraging days) under midwestern conditions, and 8604 (4 foraging days) and 53993 (12 foraging days) under southwestern conditions.

Estimating the colony's potential foraging population throughout the year

The BEEPOP model ages adult workers from their time of emergence, and reports the number of 'house bees' (i.e., bees that perform tasks in the hive and do not forage) and foragers in the population at the end of each

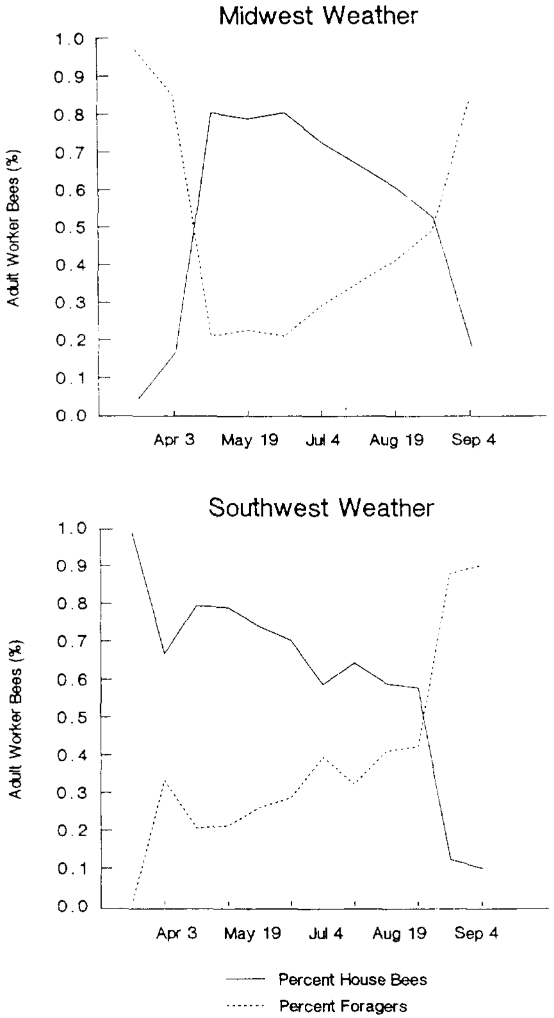

Fig. 5. Proportions of a colony population that are either foragers or house bees.

brood period. Adults that are 1–21 days old are assumed to be house bees, while those older than 21 days are assumed to be foragers (Free, 1965).

The percentage of the adult population that is house bees and foragers from April to October under midwestern conditions, and March to December for southwestern conditions (i.e., the months when foraging is most likely to occur) is shown in Fig. 5. Under midwestern conditions, foragers comprised the largest proportion of the adult population during April (approximately 97%). The foraging population declined by May and stabilized between late May and mid-July at 21–23%. The foraging population increased to 29–49% from August to September when brood rearing was on the decline, and reached 99% by the end of October. Under southwestern conditions, the adult population was comprised almost entirely of bees of foraging age in March. These bees died by the beginning of April shifting the adult population age structure to primarily younger bees (i.e., < 21 days old) at this time. By the end of April the foraging population increased to 33% of the adult population. The foraging population stabilized at 20–28% from May to August, and then increased from 33–90% from late August to early December when brood rearing rates were reduced.

DISCUSSION

There have been several models developed to describe honeybee colony population dynamics. Models have been constructed to predict brood production throughout the year based upon algorithms describing the increasing and decreasing rates of egg laying (McLellan et al., 1980; Rowland and McLellan, 1982). Harris (1985) developed a model that predicts adult populations based upon field estimates of sealed brood or daily egg laying rates, survival rates of immatures and adults, developmental rates of eggs, larvae, and pupae, and the initial size of the adult population. BEEPOP incorporates information from previous models while adding a new dimension of flexibility in user input (Table 1). BEEPOP also includes features not present in other models such as estimates of drone populations, division of the worker population into house bees and foragers, and the effects on population growth of components such as weather and the amount of spermatozoa acquired by queens during mating. At this point the model has to be considered a research tool that will undoubtedly be modified as additional information becomes available.

BEEPOP simulations demonstrate yearly trends in population growth and age structure of a colony. All parameters tested in the sensitivity analysis including weather, initial colony population size, egg laying potential of the queen, spermatozoa obtained by the queen during mating, and forager longevity affected population growth. Of these parameters, the queen's egg-laying potential had the most dramatic effect on colony population dynamics. This agrees with results from the honeybee population dynamics model developed by McLellan et al. (1980).

BEEPOP simulates different brood rearing cycles for midwestern and southwestern conditions and demonstrates how the cycles are dependent both on temperature and geographic location. Under midwestern conditions, brood rearing ceases in late fall and early winter. At this time temperatures are at or below freezing, but perhaps more importantly, daylength is < 10 h. Brood rearing resumes in late January or early February. Although temperatures may not yet be above freezing, more than 10 h of daylight occur at this time. Conversely, daylength is nearly equal to or greater than 10 h throughout the year in the southwest, and day time temperatures regularly above freezing, so although brood rearing may decrease in the late fall and winter, it never completely stops.

When brood rearing rates decline, populations are comprised primarily of older workers. In the spring when foraging weather occurs, a decline in the population can occur (spring dwindling) because the foraging population is composed of older bees with shorter life expectancies (Cale et al., 1975). The decline in the adult population temporarily decreases egg laying until brood in the pupal stage emerges. BEEPOP simulates spring dwindling which is especially pronounced under southwestern weather conditions where foraging weather occurs almost daily in February and March. In simulations using southwestern weather, populations are sharply reduced in the early spring and must build from this low point. As a result, peak populations were always higher under midwestern conditions where spring dwindling limited population growth but did not actually reduce it.

The life expectancy of a worker bee is dependent upon the time of year when it emerges (Ribbands, 1964; Sakagami and Fukuda, 1968; see refs. in Michener, 1974). Bees emerging in autumn live longer than those emerging in the spring or summer. The differences in life expectancy have been at least partially attributed to foraging activity at the time of emergence. In the model, worker longevity is dependent upon foraging activity, making the lifespan of a worker contingent upon the date of emergence. Adults emerging in the fall have a considerably longer lifespan than those emerging in spring or summer, particularly under midwestern conditions where autumn bees do not accumulate a sufficient number of foraging days to expire until the following spring. Autumn bees comprise a major portion of the adult population in the spring.

Population growth is affected by initial population size. Simulations with a 1 January start indicated that colonies with larger populations in the winter maintained larger populations throughout the entire year. These results concur with studies conducted by Nolan (1925).

Time of year when colonies reach particular population sizes also influences peak population levels. Simulations estimating population growth after hiving various size swarms at different times of year demonstrated that the largest populations result if swarms are hived in May, followed by June and July. This pattern occurs in the field as well. Swarms captured in May or early June are the most valuable to beekeepers because they have a good chance of building into populous colonies. Swarms captured in July rarely developed into colonies with large populations, because the time of year when the greatest potential brood rearing can occur has passed.

A colony's ability to rear brood at rates that result in population peaks of

> 50 000 bees is dependent not only upon population size in the late winter and spring, but on the queen's egg laying potential. No other factor in the sensitivity analysis was as influential on colony growth. The potential egg laying rate amplifies the interdependency between colony population size and the rate of colony growth. Low egg-laying potentials limit population growth, but the effects are compounded by the limited colony populations they produce. Reduced colony populations further limit egg-laying rates because the number of eggs laid per day is partially dependent upon colony population size.

Populations are affected not only by the queen's egg-laying rate, but by the amount of spermatozoa obtained during mating. In simulations, incompletely mated queens eventually laid more drones resulting in colonies with lower populations compared with fully mated queens. This is because the number of eggs laid per day is partially a function of the adult worker population size. The effects of reduced amounts of spermatozoa in the queen were realized in fewer brood cycles under midwestern conditions because colony populations were larger resulting in more brood rearing, and a greater spermatozoa utilization rate.

Harbo (1979) hypothesized that honeybee queens release a constant volume of spermathecal fluid for each fertilized egg. The fluid is replaced, thus continually reducing the concentration of spermatozoa in the spermatheca. Initially, each aliquot of fluid contains sufficient spermatozoa to fertilize an egg, but as egg laying continues the probability of releasing spermatozoa decreases. The dilution rate in the spermatheca is dependent upon the number of spermatozoa acquired during mating. BEEPOP simulates Harbo's hypothesis. Incompletely mated queens produce brood patterns that are identical to fully mated queens for at least part of their lives. This simulates the initial aliquots of spermathecal fluid which contain sufficient spermatozoa for fertilization. Eventually, more drones are produced, simulating the dilution of spermatozoa with spermathecal fluid, and the reduced probabilities of sufficient spermatozoa for fertilization. Queens with fewer spermatozoa produce increasing numbers of drones sooner than those with higher initial spermatozoa, thus simulating that the dilution rate is dependent upon the initial spermatozoa concentration.

In nature, colonies usually replace their queens before they become exclusively drone layers. The final brood cycles in simulations with queens having low initial spermatozoa would rarely occur in an actual situation. The ability of workers to recognize a failing queen and replace her is a highly advantageous behavioral mechanisms, because it ensures the survival of a colony otherwise destined to expire.

Bees potentially can fly an average of 800 km during their lifetime (Neukirch, 1982). If nectar sources are far from the hive, bees should forage for fewer days before dying. Simulations were run to indirectly test the effects of distance from a nectar source on colony population size by varying forager longevity. Simulations indicate that colony population size is affected by forager longevity, particularly under southwestern conditions. This is partially because increased forager longevity reduces spring dwindling which is especially pronounced under southwestern conditions. These simulations suggest the importance of placing colonies close to nectar sources particularly in the spring when populations are building.

The size of a colony's foraging population has been a subject of interest particularly to pollination biologists, because it at least partially influences pollination rates. BEEPOP simulations indicate that the percentage of adult bees that reach foraging age is not constant, but is dependent upon colony size and age structure. Jay (1974) reported that in late June proportionately fewer bees forage than in late August when adult numbers are high and brood numbers are low. BEEPOP simulations corroborate this. During the summer, 20–26% of the adult population consists of foraging age bees, whereas foragers comprise higher percentages of the adult population from late summer to early spring, when brood rearing rates are low and the colony is composed of mostly older bees.

Simulations to determine changes in the foraging population throughout the year provide information concerning the dynamics of age structure in the colony. High percentages of foragers indicate times when older bees predominate in a colony. During the summer (May–early August), the foraging population comprises a fairly constant percentage of the adult population suggesting a stable age distribution. The stability is disrupted after mid-August though, as brood rearing wanes, older bees predominate, and the percentage of foragers increases. This trend continues until spring when brood rearing rates increase, foraging resumes, older bees die, and the population is composed of primarily younger bees.

There are many factors that influence colony population dynamics that are not included in the BEEPOP model. For example, the availability of nectar and pollen, hive space, pests, pathogens, and pesticides in hives can reduce both brood and adult populations. However, we constructed the BEEPOP program so that modules can be added to simulate additional factors that influence population growth. The development of such modules will enable BEEPOP to help us further our understanding of interactions between colony population dynamics and various biotic and abiotic factors.

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