A Population Model and Its Application to

The Study of Honey Bee Colonies

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James Lloyd Harris

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Acknowledgements

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

LIST OF ILLUSTRATIONS (cont'd)

LIST OF ILLUSTRATIONS (cont'd)

Figure

LIST OF ILLUSTRATIONS (cont'd)

Abstract

A model of honey bee population dynamics was formulated.
Estimates of the number of eggs, larvae, pupae, and adults of various
age classes were determined from sealed brood, using life tables, and
the survival of worker bees marked at emergence with fluorescent
paint.   The model was tested and found to estimate 100.02% of the
adult bees, 99.63% of the pupae, 104.76% of the larvae, and 87.31% of
the eggs presents in a colony.

The model was then used to study the development of colonies
initiated from 0.9 kg packages of bees. During the initial phase of
development, the ratio of nurse bees (bees less than eighteen days of
age) to total brood was approximately 2:1.   This ratio declined as
the forager population (bees greater than eighteen days of age)
increased and large quantities of nectar were gathered.   Colonies in
1975 and 1976 attained maximum adult populations of 45-60,000 bees,
one hundred and eight days after hiving.

Requeening colonies with (B) mated queens, (C) queen cells and
(D) supersedure queens the last week of July was observed to alter
normal brood rearing patterns and the age structure and numerical
size of the adult populations.   Colonies which received new queens
tended to continue rearing brood in the fall after colonies which
retained their original queens had ceased.

Colonies were observed to contain brood in early December when
they were placed into winter quarters.   Brood rearing continued
during confinement although it decreased towards spring.   The low

level of brood rearing which occurred during the winter resulted in the replacement of those bees which had died during the winter and the maintenance of adult population at levels only slightly smaller than when they were placed into winter quarters.

Upon removal from winter quarters adult populations decreased for forty-eight days. Adult populations then increased rapidly until late June-early July. Adult populations tended to level off in all colonies during July and August except those which had been requeened with mated queens in July of the previous year, these colonies increased until the experiment was terminated in mid August. Requeened colonies tended to have larger adult populations throughout the summer than were observed in colonies which had retained the original package queens.

CHAPTER 1

Introduction

The honey bee, <u>Apis mellifera</u> <u>L.</u> is one of the few insects which
has been exploited by man. Its colonies are used in almost every
climatic zone, to pollinate agricultural crops and to produce honey.
The aim of every beekeeper is to manage his colonies so they will
have large populations of worker bees to coincide with major nectar
flows or when they will be required to pollinate a specific crop. To
accomplish this end, a beekeeper must be able to predict how his
colonies will respond to weather conditions, nectar flows, and
particular management systems.

Evaluation of various environmental factors and colony
management, upon colony growth has been largely neglected because of
methods for estimating colony populations are largely subjective in
nature (Jeffree 1955; Nelson and Jay 1972) or difficult to implement
(Moeller 1961).

The object of this thesis was to develop a population model
which would be relatively easy to implement, and more objective than
methods which are currently being used to estimate honey bee
populations and to provide information on the number of eggs, larvae,
pupae, and adults of various age classes in a colony throughout a
season. The model was used to study: (1) the normal development of
colonies started from package bees, (2) the effect of fall requeening

upon colony development, (3) the development of colonies while confined to winter quarters and (4) the development of colonies after their removal from winter quarters.

It is hoped that this model will become the foundation for all future studies of honey bee populations.

CHAPTER 2

A Rapid Method for Colour-marking Single
Honey Bees with Fluorescent Paint

2.1 Summary

A technique is described for marking up to 1800 individual honey bees per hour with various coloured fluorescent paint.

2.2 Introduction

The identification of specific bees within a honey bee colony requires that they be marked in some way. Marking methods used by biologists, including apiculturalists, have been discussed by Southwood (1966) and Smith (1972), but many use materials that do not fulfill all the basic requirements for marking honey bees, i.e. (1) they should not affect the lifespan or behaviour of the bees, (2) they should be quick and easy to apply, (3) marked bees should be easily distinguished from unmarked ones, and (4) the identifying mark should be permanent.

2.3 Materials and Methods

The following procedure combines and modifies the methods described by McDonald and Levin (1965) and Spangler (1974), and allows bees to be marked quickly in one of six different colours.

The paint used to mark honey bees was a suspension of fluorescent ink[1] in quick drying lacquer.[2] It was a mixture of 8 parts clear lacquer, 2 parts white lacquer, and 3 parts ink (other fluorescent dyes and pigments may be substituted), and could be thinned with clear lacquer or enamel (dope) thinner. It was possible to prepare six fluorescent colours distinguishable in daylight or UV light: pink, orange, yellow, blue, green, light purple. Green ink was insoluble in white lacquer and so could be suspended in clear lacquer only. Since the green ink fluoresced in visible yellow light, green was made by mixing the primary colours yellow and blue. Light purple was obtained from a mixture of red and blue. Small quantities of base paint material were added where necessary to intensify the contrast between colours.

The mixture was applied to the bee using a 1-ml or 3-ml disposable hypodermic syringe. A 21 gauge needle was specially modified by grinding away half of its bevelled point. The syringe was then filled with paint, and the needle affixed to it.

Worker bees were marked while on the comb. The syringe was held with the end of the plunger resting in the palm of the hand (Fig. 1). Pressure applied to the piston controlled the release of a small drop of paint which was lightly applied to the anterior dorsal

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[1]Fluorescent Speedball Waterproof Ink, Hunt Manufacturing Co., Statesville, NC 28677, U.S.A.

[2]Aero Gloss Dope, Pactra-Canada, Hasbro Industries, Longueuil, Quebec, Canada.

portion of the bee's thorax (Fig. 2). Paint penetrated the hair and dried quickly, so preventing other bees from smearing it. Worker bees could also be marked while foraging, without restriction or handling.

Queens were held immobile to prevent possible smearing of the paint on application. They were then slowly released using the method described by Benecke (1968), to prevent workers in the hive balling and killing them.

2.4 Results and Discussion

We found it advantageous to use inexpensive disposal syringes, as the paint solvent gradually attacked the fabric of the syringe.

After loading, a syringe was usually used within 4-5 h; however, if the needle was kept open with a fine insect pin, it could be stored in a cool place for several days.

The method made it possible to distinguish six different groups of bees (or a greater number if the bees were marked with more than one colour), and had the following advantages.

(1) A minimum of equipment was required, and the method can be used in the field.

(2) Up to 1800 bees per hour could be marked.

(3) As many as 90-100 newly emerged bees could be located on the comb and marked in 5 minutes.

(4) Fluorescent marked bees were easily visible in daylight, and also at low light intensities if illuminated with UV light.

Fig. 2.1 Position of hand held syringe during

marking procedure

Fig. 2.2 Application of fluorescent paint to unrestrained

worker bee on the comb
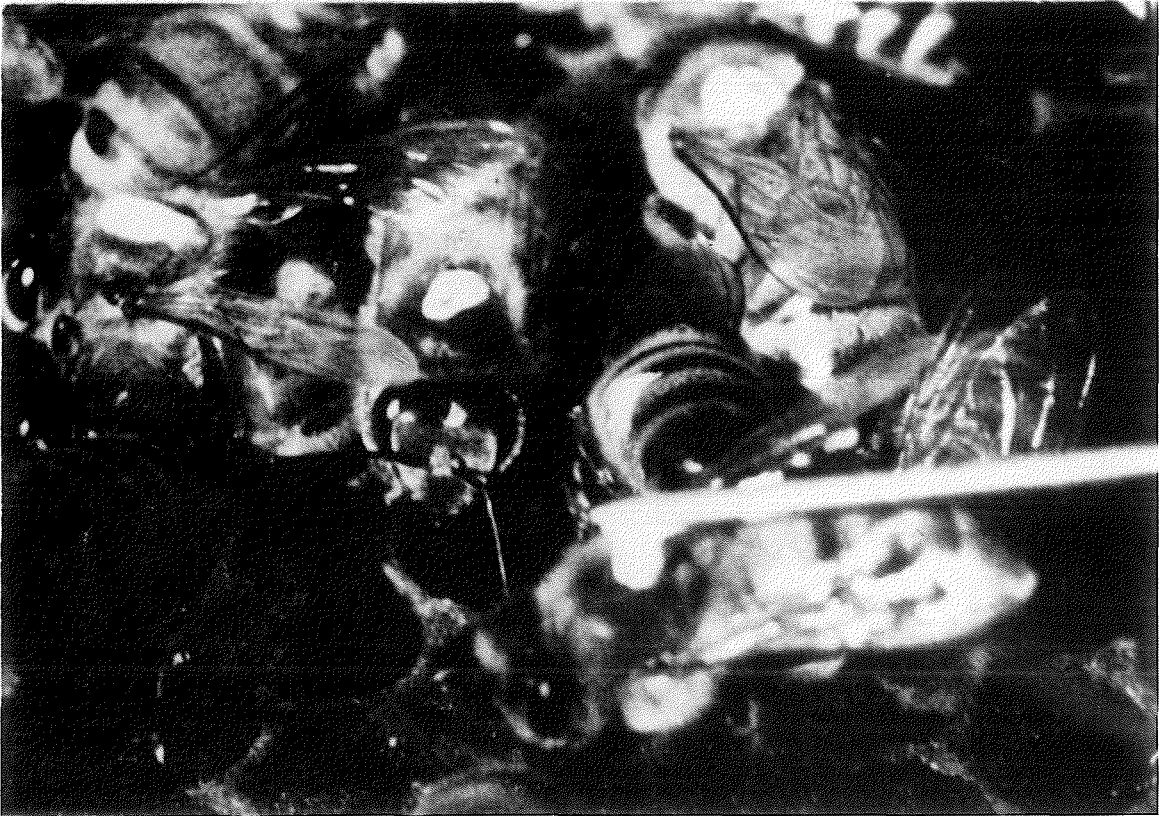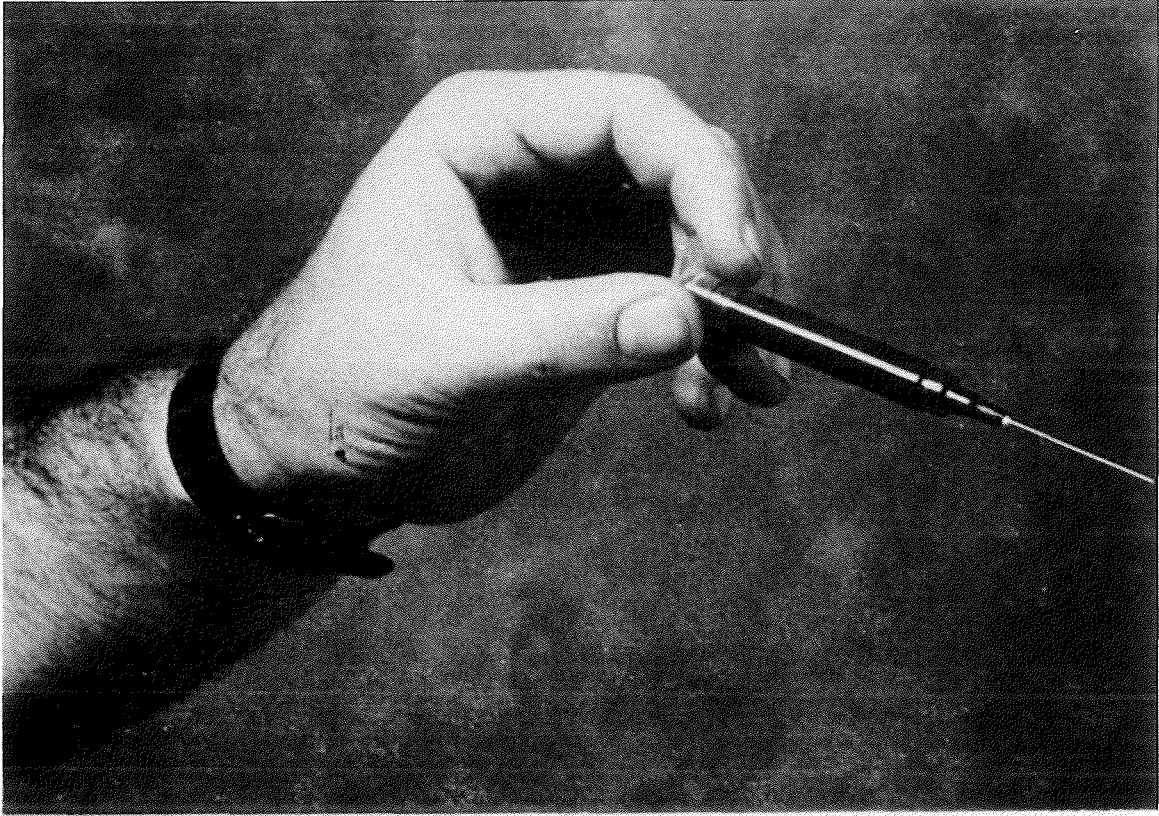
(5) Marked bees were generally not rejected by other workers when returned to the hive.

(6) The amount of paint applied to each bee could be precisely controlled.

(7) Handling of the bee produced no apparent detrimental effects or changes in its behaviour or lifespan: marked bees were observed feeding larvae, guarding the hive, and foraging normally. Recovery of marked bees was possible for as long as 72 days after marking during the summer and for up to 200 days during the winter.

(8) The needle need not be dipped into the paint bottle before every application.

(9) Large numbers of individual honey bees (or other insects) could be marked and identified.

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CHAPTER 3

A Model of Honey Bee Colony Population Dynamics: I. The Model

3.1 Summary

ˋ A model is proposed for the estimation of single honey bee colony populations. Eggs, larvae, pupae and adults were estimated from the survival of sealed brood areas measured or estimated at regular twelve day intervals.

3.2 Introduction

The honey bee, <u>Apis mellifera</u> L., is a social insect living in colonies which may contain from several hundred to over eighty thousand adult bees in addition to eggs, larvae and pupae, or sealed brood. An average colony will contain predominantly worker bees, a lesser number of males or drones and a single mated queen. The queen is normally the sole reproductive female within the colony. However, she is physically incapable of caring for her offspring or foraging. These duties are the responsibility of the worker caste. Division of labour amongst worker bees depends partially upon the age of the individual bee and partially on the colony's needs (Michener 1974). In general, duties relating to the brood are performed by worker bees until they are two or three weeks of age (Lindauer 1952), while foraging begins at approximately eighteen days of age (Sakagami 1953, Ribbands 1952). Drone bees serve primarily as mates for the virgin

queen during her nuptial flights.

Because this insect is the basis for a multi-million dollar honey and pollination industry, changes in colony populations during any given season are important to certain types of agriculture. If colonies are to be managed so they survive winter with large populations or produce large populations to coincide with major summer nectar flows, it is necessary to find a tool by which colony dynamics can be studied. A model of colony dynamics is required if fluctuations in colony populations are to be explained or the effect of environmental variables evaluated. Attempts at modeling the dynamics of colony populations were begun by Ebert (1922). He divided the colony into three subgroups: (1) juveniles, (2) hive bees and (3) foragers based on total brood and estimate of the forager population and total colony population. Ebert's model was subsequently refined by Nolan (1932) and Bodenheimer (1937) based on the consecutive division of labour hypotheses proposed by Rosch (1925). Bodenheimer's approach, which was essentially the same as Nolan's, has been criticized by Uchida and Sakagami (1955; cited by Fukuda 1971) because of errors produced during (1) measurement of brood, (2) calculations, notably the appearance of negative estimates and (3) oversimplification of the duration and mortality of each stage. Fukuda (1971) subsequently made recommendations to rectify some of the inadequacies of Bodenheimer's model. Many of those recommendations are incorporated in the model of honey bee population dynamics described in this paper. The model described is used to estimate total colony population every twelfth day by incorporating estimates

of birth and death. Eggs, larvae and pupae are estimated from sealed brood. Adult populations are estimated from the initial adult population's survival and the survival of adult bees as they emerge from the pupal stage.

3.3.0 Model Framework

Total honey bee colony populations at any time can be represented by two additive components:

$$Pt = A + B$$

where

Pt = total population at time, t

A = total population of adults at time, t

B = total population of immatures at time, t

The adult population A, is composed of bees which were present in the colony at time Ts and those adult bees emerging from sealed brood after time Ts. Because the two groups of adult bees are estimated by different procedures it is more convenient to consider the adult population at time Ts as the initial adult population Pi, and to consider adult bees entering the adult population from sealed brood (along with the immatures) as Pd, the descendants of the initial adult population, Pi: Therefore:

$$Pt = Pi + Pd$$

where

  Pt = total population at time, t

  Pi = initial adult population surviving at time, t

  Pd = descendants of Pi surviving at time, t

3.3.1 Initial adult population, Pi

All adult bees in a colony will belong to the subpopulation Pi at some starting point ts. However, Pi is not a constant. It decreases in response to factors causing honey bee mortality such as adverse weather, disease and predation. As the adult bees succumb to these mortality factors Pi becomes a smaller part of the total population. Therefore:

$$Pi_{ti} = Pi_{ts} - Pm_{ti} \qquad (2)$$

where

  Pi_{ti} = initial adult population surviving at time, ti

  Pi_{ts} = initial adult population surviving at time, ts

  Pm_{ti} = cumulative mortality up to time, ti.

Evaluation of Pi_{ti} requires an initial estimate of Pi at time, ts and an estimate of its survival from which estimates of cumulative mortality and mortality rates can be calculated.

3.3.2 Descendant population, Pd

The descendants of Pi are considered to be all the immature stages in a colony plus the adult bees which emerge from sealed brood. Pd like Pi is not constant. It decreases in response to mortality factors, but unlike Pi it also increases as factors become favorable for reproduction. The descendant population at time t_i can be expressed as:

$$Pd_{ti} = I_{ti} + A_{ti} \qquad (3)$$

where

Pd_{ti} = total descendant population at time, ti

I_{ti} = total immatures present at time, ti

A_{ti} = total adults surviving after emergence from the pupal stage

The immature section of this subpopulation may be expressed as:

$$I_{ti} = E_{ti} + L_{ti} + P_{ti} \qquad (4)$$

where

E_{ti} = total eggs at time, ti

L_{ti} = total larvae at time, ti

P_{ti} = total pupae at time, ti.

Two successive pupal estimates taken twelve days apart are required to estimate I_{ti}. The first measurement is used to estimate P_{ti}. The second measurement of pupae at ti+dtp is used to estimate eggs and larvae present at time ti. A separation of twelve days between pupal estimates is required to prevent measuring the same pupae twice (Nolan 1925, Sakagami and Fukuda 1968).

Estimates of eggs, larvae, and pupae at some time, ti are derived using the following equations:

$$E_{ti} = \frac{(P_{ti} + dtp) \cdot dt_e \cdot mf_{e+\ell}}{dtp} \qquad (5)$$

$$L_{ti} = \frac{(P_{ti} + dtp) \cdot dt_\ell \cdot mf_\ell}{dtp} \qquad (6)$$

where

$P_{ti + dtp}$ is the number of pupae at time, ti + dtp

P_{ti} is the number of pupae at time, ti

E_{ti} is the number of eggs at time, ti

dt_e is the average developmental time of the egg stage, i.e. 3 days,

$mf_{e+\ell}$ is 1/probability of an egg surviving to become a pupae, i.e. 1.16,

L_{ti} is the number of larvae at time ti

dt_ℓ is the average developmental time of the larval stage, i.e. 5 days,

mf_ℓ is 1/probability of a larvae to surviving to become a pupa, i.e. 1.06,

dt_p is the developmental time of the pupal stage, i.e. 12 days.

(The preceding developmental times and mortality correction factors were based on the work of Sakagami and Fukuda (1968).)

The logic for equation (5) can be better explained by

rearranging the equation to the following form:

$$\frac{E_{ti}}{dt_e} \cdot \frac{1}{mf_{e+\ell}} = \frac{P_{ti} + dtp}{dtp} \qquad (7)$$

The right-hand side of equation (7) represents the pupae at time, ti + dtp divided by the developmental time for pupae. This ratio represents the rate at which larvae enter the pupal stage. This is also the same as the number of eggs deposited by the queen dtp time units ago after correction for mortality occuring during the egg and larval stages. The left hand side of the equation contains two terms. The first term, E_{ti}/dt_e is an estimate of the total number of eggs layed by the queen per day while the second term $1/mf_{e+\ell}$ accounts for the mortality occurring during the egg and larval stages. A similar argument holds for equation (6). Note that equations (5) and (6) imply that the ratio of eggs:larvae will be a constant, although the daily egg laying rates and mortality rates may fluctuate during the egg and larval stages. A constant ratio, though not too unrealistic was unavoidable if eggs and larvae are to be estimated from pupal counts alone. If counts of eggs and/or larvae had been obtained, it would be possible to formulate a model without the above restriction of assuming temporal constancy of both rates and developmental times regardless of environmental factors, population density or other effects.

Adults are constantly emerging from their cells. As the pupal

stage lasts an average twelve days, the adult portion of the descendant population can be partitioned every twelfth day into discrete sub-populations, $A_1 \ldots \ldots A_n$. The initial value of A_j is given by:

$$A_{jti} = (P_{ti} - dtp) \cdot sf_p \qquad (8)$$

where sf_p is the survival rate through the pupal stage, i.e. 0.99 (Sakagami and Fukuda 1968). Subsequent survival of A_{jti} is given by:

$$A_{jti + dt} = A_{jti} - ma \qquad (9)$$

where ma is the adult mortality occurring between time ti and ti + dt, where dt is an arbitrary time increment (dt>o) in days. Total colony population at any time is found by summing the corresponding temporal estimates of the initial population, eggs, larvae, pupae and adults so that:

$$Pt_{ti} = (Pi_{to} - Pm_{ti}) + \frac{(P_{ti} + dtp) \cdot dt_e \cdot mf_{e+\ell}}{dt_p} \qquad (10)$$

$$+ \frac{(P_{ti} + dtp) \cdot dt_e \cdot mf\ell)}{dtp} + P_{ti} + (A_{jti} - ma)$$

3.3.3 Application of the Model

Honey bee colonies in western Canada are often started from 0.9 kg. of worker bees and a mated queen shipped in screened packages from the southern and southwestern United States (L'Arrivee and Geiger 1965). Therefore this type of colony was selected to test the

preceding model. The package bees were placed into a standard hive body well supplied with honey and pollen in late April. A group of one hundred and twenty worker bees was marked (Harris 1979) to assess mortality of Pi throughout the season.

Pupae were measured every twelfth day after hiving by super-imposing a grid, 25.4 x 25.4 mm squares, over the pupae (see Nolan 1925, Moeller 1961). This method underestimated pupal area by a factor of 1.11 and hence all estimates were corrected using this figure.

Survival of individual bees after emergence from their cells was determined from a group of newly emerged bees marked to coincide with the measurement of pupae. Because the sealed brood stage lasts twelve days, emerging adults have a similar age range. Consequently, attrition should be determined either by: (1) applying marked bee attrition rates on a daily basis or (2) by determining an average attrition rate for each sub-population of emerging adults. The latter procedure was employed. Marked bee survival was estimated to coincide with brood measurements every twelfth day after hiving. The twelve day cycle for survival estimates, however, need not be rigidly adhered to. An alternative sequence may be implemented to estimate marked bee survival if it is found to be more convenient.

In calculating the survival of the marked adults it should be remembered that not all marked bees can be successfully introduced into a colony because (1) some marks may not adhere properly, (2) some marking process may cause physical or behavioural changes, or

(3) some marked bees may be rejected by the colony. Therefore, an additional estimate of marked bees successfully introduced to colonies should be obtained. The number of bees located in a colony twelve days after marking was arbitrarily defined as one hundred percent of those successfully introduced into a colony.

Occasionally, marked bees will appear to increase in numbers between successive estimates. This is indicative of either (1) movement of colour-marked bees between colonies or (2) an error in locating marked bees. The former is not likely to be significant if colonies are arranged in non-repetitive patterns (Jay 1969). The latter can almost be entirely eliminated if care is taken when locating colour-marked bees. In an effort to minimize problems associated with counting marked bees, all estimates of marked bees were made in the early morning as worker bees do not normally begin leaving the colony until between 8:30 am. and 10:30 am. (C.S.T.) (Lundie 1925). Hence, efficiency of counting marked adults is seen to be of little concern.

3.4.0 Results and Discussion

Application of the model allowed the number of eggs, larvae, pupae and adults present in a colony during a season to be calculated at regular twelve day intervals (Figs. 3.1 and 3.2). Egg, larval and pupal estimates (Fig. 3.1) showed similar trends when pupal estimates were shifted in time to compensate for the twelve day time lag associated with development. Larval and pupal estimates, being a

Fig. 3.1 Seasonal changes in the number of eggs, larvae

and pupae in a honey bee colony
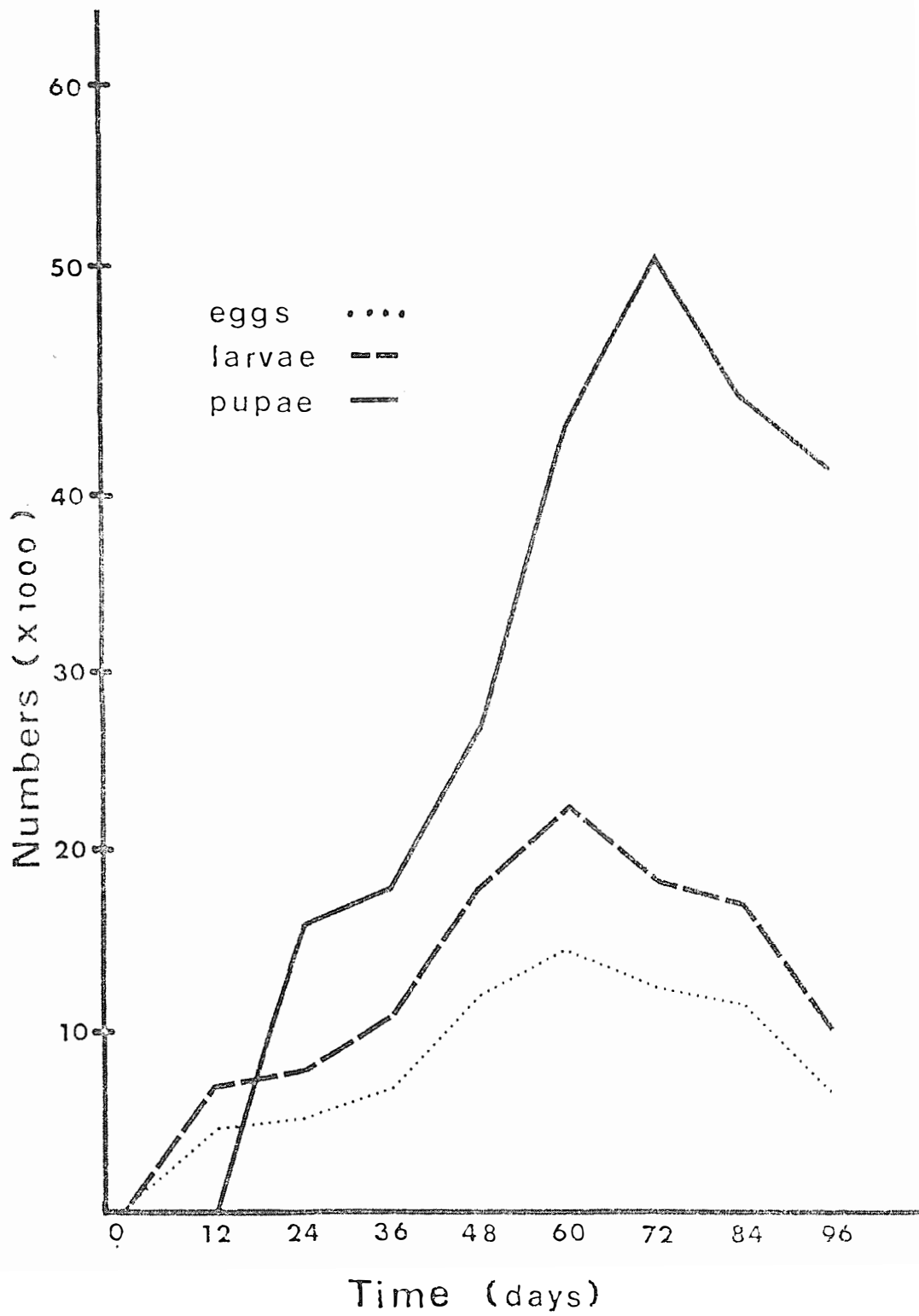
Fig. 3.2 Seasonal changes in adult honey bee population

initiated from 0.9 kg of bees, as affected by

the emergence of their descendants

initial population – Pi
descendant population – A$_{1-6}$
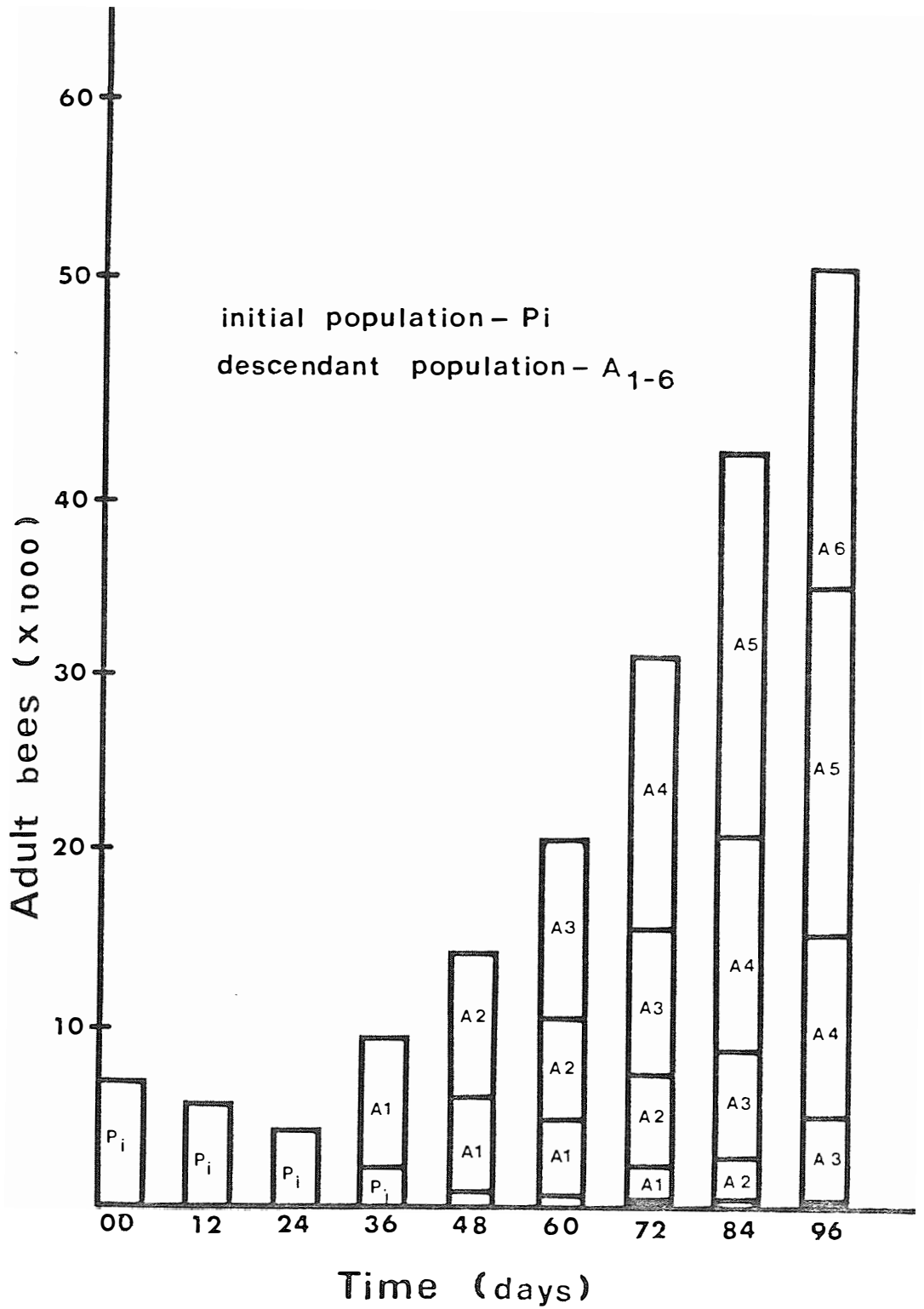
function of the eggs layed, were sensitive to small changes in daily oviposition rates. The total adult population (Fig. 3.2) decreased until day 24. It subsequently increased after day 24 with the emergence of new adult bees. The initial population, Pi, became extinct between day 72 and day 84. After day 84, all adult bees contributing to the adult population were from Pd.

The model implemented many of the suggestions made by Nolan (1932), Bodenheimer (1937) and Fukuda (1971). In addition, brood estimates were coupled with adult mortality values observed in a colony. The model can be used to estimate the number of eggs, larvae, pupae, and adult bees within a colony, independent of environmental factors being studied. Coupling life tables with measured sealed brood as recommended by Fukuda (1971) for worker bees (Sakagami and Fukuda 1968) or drone bees (Fukuda and Ohtani 1977) does not provide the same flexibility, although it may prove to be satisfactory in many situations.

In general, investigations about genetics and the influence of various environmental components including disease, nutritional supplements upon colony development have been hindered by the lack of objective methods to monitor colony populations. It is anticipated that studying the impact of environmental components upon colony development can be considered using the preceding model. In fact, the influence of a particular component upon colony development can be predicted by this model, if model input is provided to estimate the possible effect upon colony birth rates and death rates.

Previously, it was virtually impossible to speculate with confidence, the impact of various age groups upon colony development, as adult bees are morphologically identical. However, with the aid of this model, it will be possible to make inferences as to the influence of various adult age groups (or immatures) upon colony activities such as brood rearing and foraging. The model also enables one to construct an age distribution for a colony.

Although the model framework was designed for honey bee populations, the procedure may have merit in applications to other social insect populations, if the appropriate species developmental times can be incorporated.

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CHAPTER 4

A Model of Honey Bee Population Dynamics:II. A Test of the Model

4.1 Summary

The model of honey bee population dynamics was tested on twenty colonies initiated from package bees and twenty-four overwintered colonies. Average estimates of adults, pupae, larvae, and eggs were 100.02%, 99.63%, 104.76%, and 87.31% respectively, of those predicted by the model.

4.2 Introduction

A model for estimating honey bee populations was proposed in Chapter 2. The model partitioned the population into eggs, larvae, pupae, and adults of various age groupings. Estimates were based on the survival of sealed brood measured or calculated at regular twelve day intervals. Theoretically, the procedure should predict populations independent of colony size. The model's value as a tool, however, can only be determined by comparing the theoretical estimates with those obtained under field conditions. If the model is able to mimic or predict field situations under a wide range of conditions, then it is probably a realistic model. The model's usefulness will depend on whether or not the information generated from the model has any practical value in understanding colony management practices, colony social structure or the interaction of

colony members.

A preliminary test of the model seemed to indicate that the model may be useful in observing changes in a number of the adult and immature honey bees in a colony over time (Chapter 2). When the model was applied to a colony initiated from a 0.9 kg. package of worker bees it appeared to predict the colony's growth for the first ninety-six days after hiving.

The present study was undertaken to determine the model's reliability in predicting colony populations under a variety of conditions.

4.3 Methods and Materials

The model, as described in Chapter 2, was applied to twenty-four overwintered colonies and twenty colonies initiated from 0.9 kg. packages of bees. Colonies were killed at various times throughout the summer and their adult population determined by counting the adult bees. The adult populations of four colonies were manipulated by addition of brood, removal of brood, removal of the queen, and by inducing swarming, to determine if these treatments would adversely influence adult population estimates. Eggs, larvae, and pupae were counted in seven colonies and the observed values compared with those predicted by the model.

4.4.0 Results and Discussion

The results are presented in Fig. 4.1 a-d and Table 4.1

4.4.1 Adult Population

The model was used to estimate adult populations which ranged from 4.3×10^3 to 7.6×10^4. The adult populations observed were 100.02% of those predicted using the model (see chapter 3). Of the forty-four colonies estimated, nineteen (43.18%) were overestimated and twenty-five (56.82%) were underestimated. Unlike the method presented by Jeffree (1951) to estimate honey bee populations, there was no need to perform a square root transformation on the data prior to fitting the linear least squares regression line (R=0.97), since the model estimated small, medium and large populations equally well.

Manipulation of colony populations by addition or removal of brood, the removal of the queen, or by swarming did not appear to seriously affect adult population estimates (see Table 4.1).

Errors, associated with prediction of adult populations, may be attributed to: (1) the method used to estimate the initial population, (2) differences in the survival rates for drones and worker bees, (3) locating marked bees and the methods used to measure brood.

P_i, the initial adult population of a colony will probably be estimated to within ten to twenty percent of its true value by most methods currently used to estimate adult populations (see Merrill 1920, 1921; Ebert 1922; Jeffree 1951; Cherednikov 1964; Simpson 1969; Nelson and Jay 1972). As P_i becomes a smaller proportion of the total adult population (due to mortality factors), error from this source will be eliminated in time. During the spring and summer, the initial adult population, P_i, will become extinct after approximately

seventy-two days.

Drones were treated by this model as if they were similar to worker bees with respect to development times and survival. The error introduced because of this assumption is likely to be minimal as (1) drones are seldom more than 5% of the total adult population (Allen 1965; Jay 1974), (2) drone survival under normal conditions is similar to that of worker bees (see Free and Spencer-Booth 1959; Fukuda and Sekiguchi 1966; Fukuda and Ohtani 1977), and (3) the developmental time for drones exceeds that of worker bees by only three days (Butler 1975). Drones may be estimated separately with only minor changes in sampling procedures should it be required.

The inability to locate marked bees can seriously affect adult population estimates, especially when bees become densely clustered on combs because of inadequate space or low temperatures experienced by the colony during early spring and late fall. However, an accurate count of the marked bees can be obtained if it is taken before the bees begin foraging and care is taken in locating them. Locating marked bees can be facilitated if less than one hundred marked bees of each colour are introduced into a colony every twelve days, colonies are provided with adequate space and/or hives are insulated in cool weather.

Inaccurate measurement of sealed brood can also seriously affect adult estimates. For example, should the sealed brood area of twenty combs be overestimated by six square inches per comb, the corresponding subpopulation of worker bees, A_j, emerging from this sealed brood would be overestimated and would result in the total

adult population being overestimated by two thousand nine hundred and seventy adult bees. This source of error could be minimized if sealed brood were determined with an electronic device (i.e. image analyser) from photographs.

Table 4.1 The influence of manipulating colony populations on population estimates.

colony #	treatment	estimated population	actual population
1	add brood	33228	29764
2	remove brood	30128	28248
3	remove queen	18320	15923
4	induce swarming	46425	46687

4.1.2 Immatures

The immature segment of the population was also estimated from sealed brood by employing appropriate mortality correction factors and developmental times for eggs, larvae, and pupae. Since the immatures were estimated from sealed brood measurements, inaccurate sealed brood measurements will produce erroneous estimates of the immatures present in a colony. Errors may also arise from incorrect estimates of the mortality which will occur between the various stages of development. In addition, a correction factor of 1.11 was used to compensate for an ineffective brood measuring technique. The correction factor will probably need to be changed depending on the method used to measure sealed brood (see Fresnaye and Lensky 1961; Al-Tikity et. al. 1971) and the ability of the person measuring the brood area.

The model's capacity to accurately estimate immatures was evaluated by counting cells of eggs, larvae, and pupae and comparing those with estimates generated from sealed brood measurements. The observed values for eggs (Fig. 4.1a), larvae (Fig. 4.1b), and pupae

Fig. 4.1a Regression of estimated adult population on actual

adult populations in honey bee colonies

Fig. 4.1b Regression of estimated pupae on actual pupae in

honey bee colonies

Fig. 4.1c Regression of estiamted larvae on actual larvae in

honey bee colonies

Fig. 4.1d Regression of estimated eggs on actual eggs in

honey bee colonies

Fig. 4.1a

ESTIMATED ADULT POPULATION X1000

R = .97
Y = .90X + 3446.13

ADULT POPULATION X1000

Fig. 4.1b

ESTIMATED PUPAE X1000

R = .90
Y = 1.19X + -1632.01

PUPAE X1000

Fig. 4.1d

ESTIMATED EGGS X1000

R = .37
Y = .32X + 1957.69

EGGS X1000

Fig. 4.1c

ESTIMATED LARVAE X1000

R = .67
Y = .51X + 1792.74

LARVAE X1000
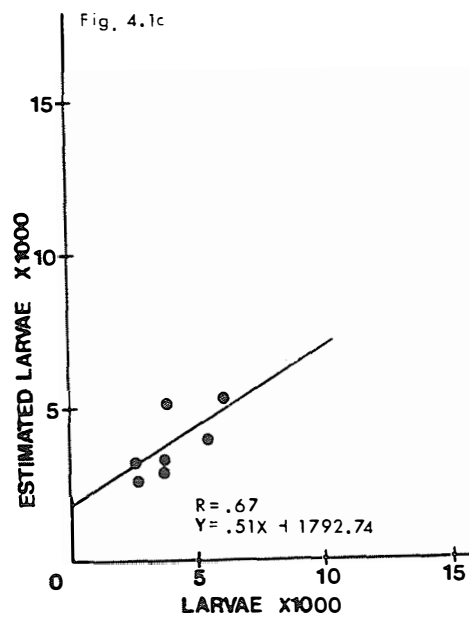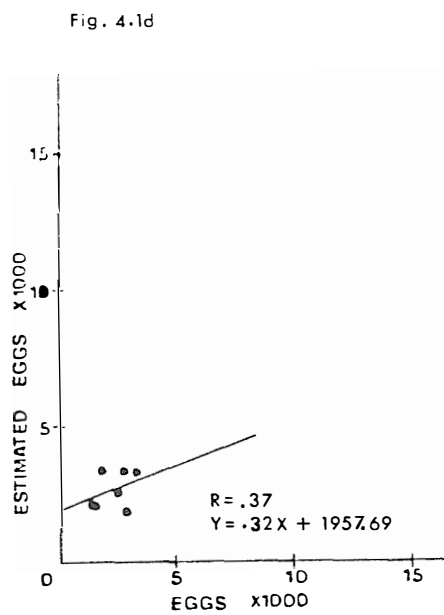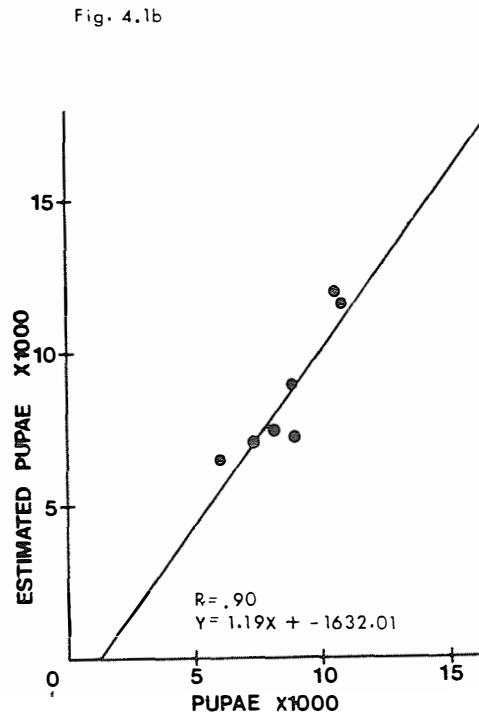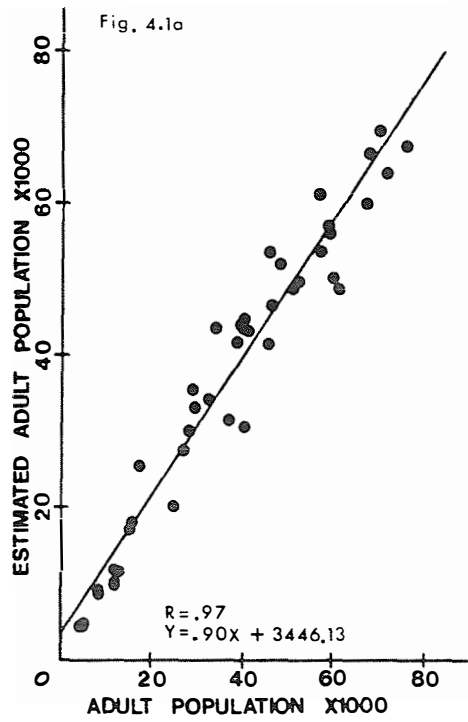
(Figure 4.1c) were respectively 87.31% (R=.35), 104.76% (R=.67), and 99.63 (R=.90) of the values predicted by the model.

Under most conditions the model can be used to predict the total population of immatures in an average colony. However, the model may produce erroneous egg and larval estimates should conditions change suddenly because of the lack of available cells into which the queen can lay eggs or by cannibalization of eggs and larvae by worker bees.

4.5 Conclusions

The model as presented provides a tool which is capable of estimating eggs, larvae, pupae, and adults in a honey bee colony. In addition it partitions the adult population into age classes and provides a vehicle for studying the interaction of the various groups within the colony.

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CHAPTER 5

Development of Honey Bee Colonies: **I.Initiated from Package Bees**

5.1 Summary

The development of honey bee colonies populations started from 0.9 kg of worker bees was recorded for two years. Colony age structure was determined and the relationships between nurse bees, foragers and brood production considered.

5.2 Introduction

The beekeeping industry of the north central United States and the Canadian prairies is largely dependent upon package bees for establishment of colonies each year. However, little information is available concerning how these colonies develop. Studies to date have been primarily concerned with population growth, or brood rearing in relation to: (1) the initial number of worker bees in the colony, (2) hiving dates and (3) honey produced per colony (Merrill 1924a, Mitchener 1931; Nolan 1932; Braun 1936; Kelty 1948; L'Arrivee and Geiger 1966; Geiger 1967; Pankiw 1968; Smirl and Jay 1972a; and Nelson and Jay 1972). The following relationships have been observed in previous studies: (1) sealed brood to adult bee ratios decline as total population increases (Farrar 1931; Jay 1974), (2) honey production and total adult populations are positively correlated (Farrar 1937; Moeller 1961), (3) brood rearing is negatively

correlated to nectar collection (Merrill 1924a, 1924b), (4) adverse weather conditions contribute to decreased brood rearing and foraging activities (Hambleton 1925, Lundie 1925, Nolan 1925, Smirl and Jay 1972a) and (5) oviposition rates are dependent upon the interaction of the queen and worker bees (Merrill 1925a, 1925b). Although recognized by beekeepers and apiculturists, the relationship between brood rearing, worker bee populations and honey production has received less attention than they merit.

This study traces the seasonal changes in brood and adult populations in colonies initiated from package colonies and outlines some of the developmental factors which are operating throughout the year.

5.3 Methods and Materials

Colonies were hived from packages containing .9 kg of worker bees (ca. 7000 worker bees) and a mated queen of a yellow strain on 24 April, 1975 and 22 April, 1976. In both years, colonies were located in commercial apiaries in south-central Manitoba. Queens were placed in their respective colonies still within their shipping cages and released after three days. To minimize drifting between colonies (see Free and Spencer-Booth 1961; Jay 1966), hives were arranged in a circular pattern placed one meter from adjacent colonies with their entrances facing away from the circle and hived on the same evening they were received. Each year, one colony was placed on a beam scale and weighed during the nectar flow between 20

20 June to 31 August (see Mitchener 1949, Smirl and Jay 1972b).
Extra hive bodies were placed above those already present as
required. Honey was removed from colonies the last week of July,
ninety-six days after hiving (day 96) and again the last week of
August (day 120) in both years. Colonies were fed sugar syrup on day
132 and received insulated inner covers on day 204 in 1976 only.

Total colony populations were derived from the method outlined
in Chapter 3. During November and December, adult population
estimates were based on average summer mortality and extrapolation of
winter mortality when bees became densely clustered.

5.4.0 Results and Discussion

The methods used in this study allowed for consideration of
colony age structure and the relationships existing between different
age groupings. They also allowed for observations of seasonal change
in sealed brood production and adult populations.

5.4.1 Colony Age Structure

Changes in colony age structure throughout the season are pre-
sented in Figs. 5.1 and 5.2 commencing at hiving and continuing every
twelfth day thereafter. The initial package population was composed
of adult worker bees and a mated queen. The age distribution was
unknown, but was considered to be similar to that of rapidly growing
overwintered colonies (Table 5.1). The exact age structure

Table 5.1. Theoretical age structure and survival of the 7000 adult
worker bees, used to initiate honey bee colonies.

			Days after hiving				
Age class	0	12	24	36	48	60	72
72 – 83	0	0	0	0	0	0	13
60 – 71	4	4	9	57	36	92	
48 – 59	32	68	242	244	585		
36 – 47	221	785	832	498			
24 – 35	1406	1531	2336				
12 – 23	2093	2973					
0 – 11	3244						
Total	7000	5361	3418	799	621	92	13

Fig. 5.1 Changes in the age structure of honey bee colonies

   initiated from (0.9 kg) packages of bees at twelve day

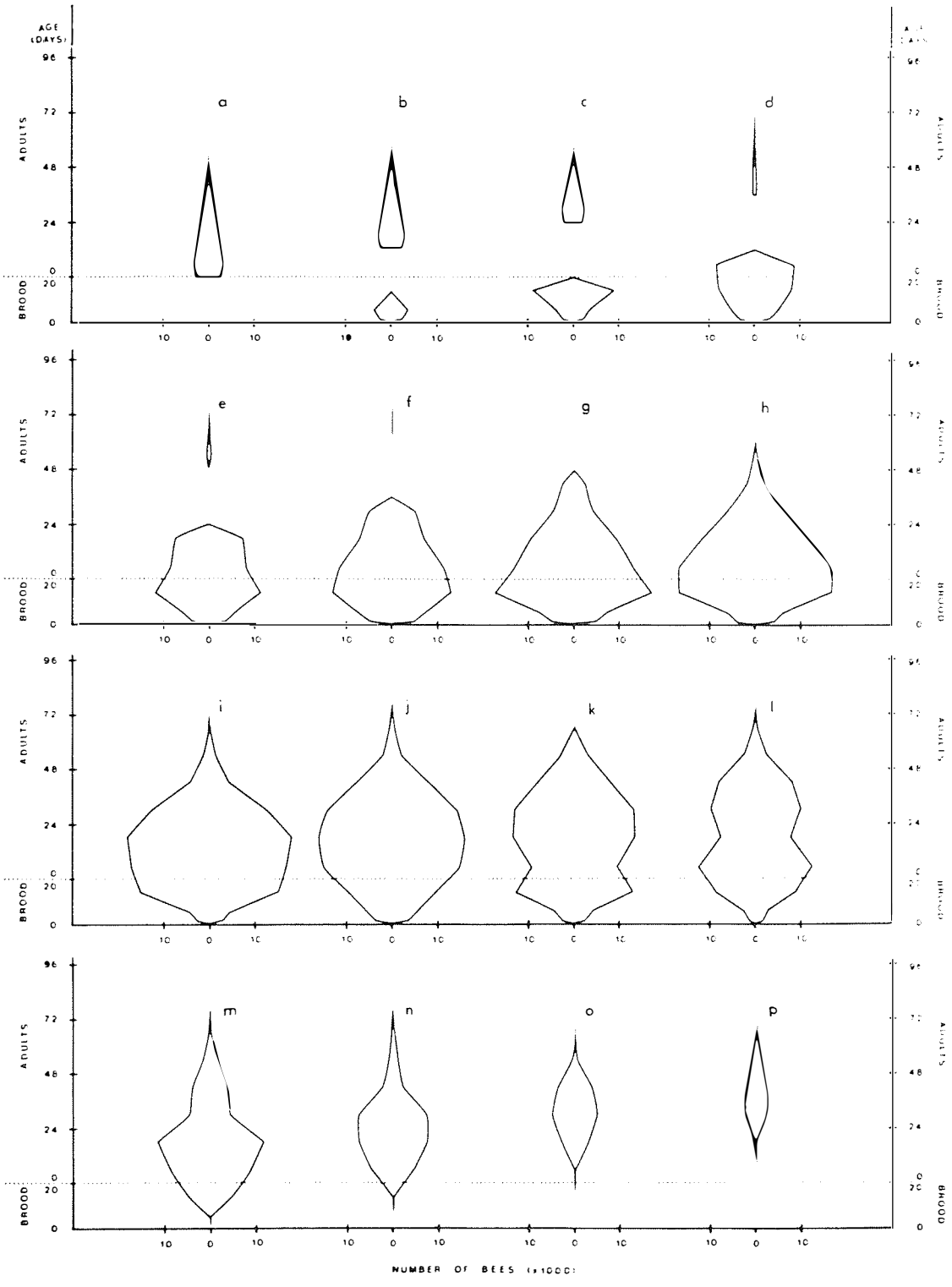   intervals (a-p) after hiving in 1975.

Fig. 5.2   Changes in the age structure of honey bee

colonies initiated from (0.9 kg) packages of

bees at twelve day intervals (a-t) after hiving

in 1976.
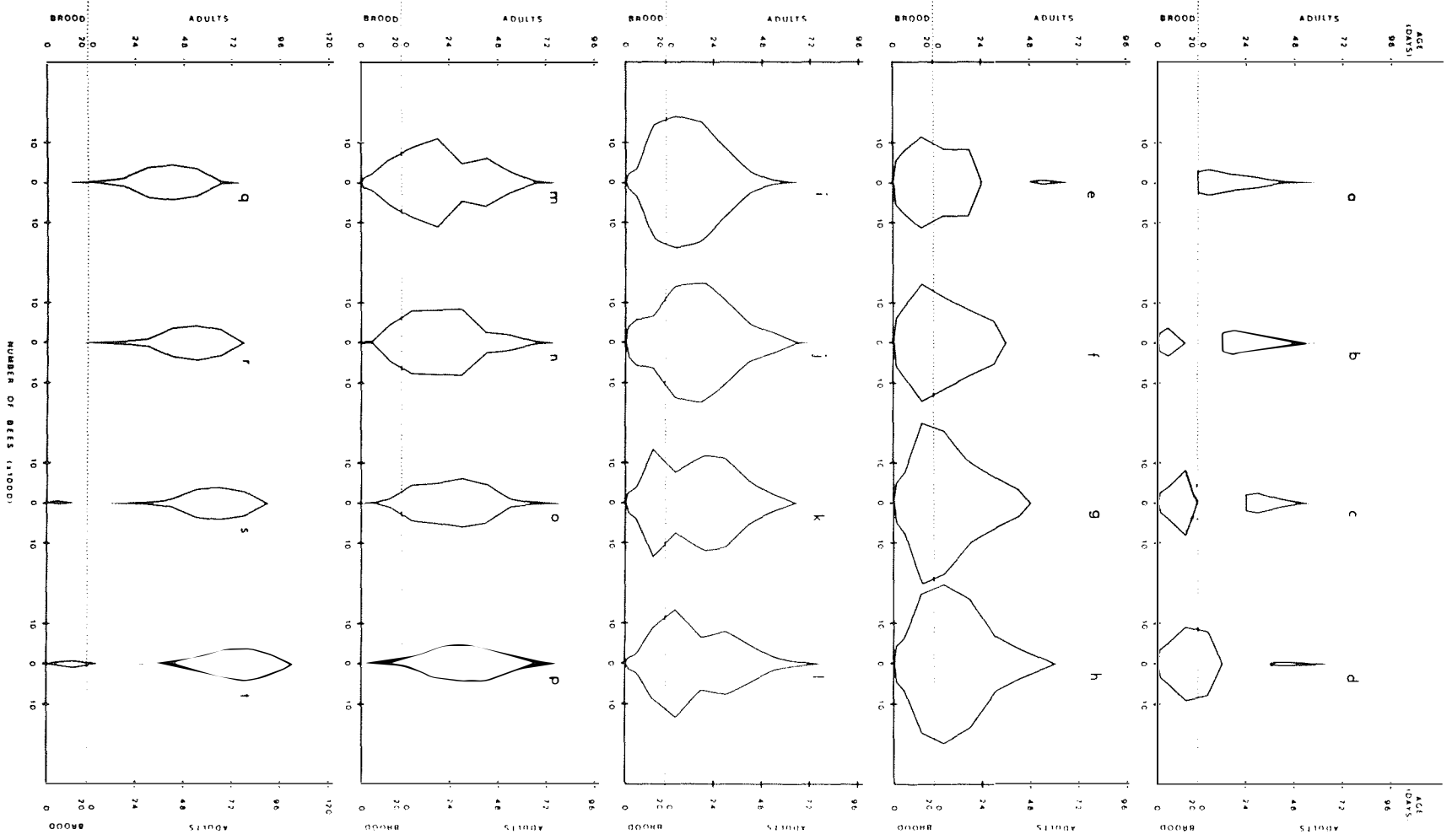
of the package bees, however, was certainly to have been influenced by environmental conditions and management systems employed at its place of origin.

During the first twenty-four days of colony development, the adult population decreased as the amount of sealed brood increased (Fig. 5.1, 5.2). This resulted in the highest brood to adult ratio observed each year (see Jay 1974). The high ratio was probably indicative of a birth rate significantly greater than the adult death rate. The ratio of brood to adults decreased with the emergence of adult bees after day 24.

More important to brood production than the total number of bees was the proportion of the adult population actively engaged in caring for brood or foraging. Since the boundary between these two groups is a function of colony needs and physical conditions as well as age (Rosch 1925, 1930; Lindauer 1952; Ribbands 1952; Hassanein 1953), the division of the adult population into nurse bees and foragers is somewhat arbitrary. Rosch (1925), Ribbands (1952) and Sakagami (1953) considered the average first day of foraging to be 19.5, 20.1 and 18.3 days of age respectively. In this study, adult bees equal to or greater than nineteen days of age were considered to be foragers, while adult bees less than nineteen days of age were arbitrarily considered to be nurse bees.

Production of large quantities of brood in the initial stages of colony development appeared to be restricted by a combination of small numbers of worker bees and cool external hive temperatures. The amount of brood produced by colonies in both years between day 36

and day 60 was related with average daily temperatures, number of nurse bees and foragers (Table 5.2). The highest nurse bee to total brood ratio was observed twelve days after the package bees were hived (Fig. 5.3). The ratio at that time, was almost twice that observed between day 36 and day 60 (Fig. 5.3). This would seem to indicate that bees which would normally be considered foragers are probably functioning as nurse bees since bees not relieved of brood rearing duties by younger recruits tend to care for brood longer than normal (Himmer 1930). The brood to nurse bee ratios were relatively steady between day 36 and day 60 (Fig. 5.3). From this, it may be construed that approximately two nurse bees (see above) are required for every immature reared by the colony. Hence, it would seem that the colony's potential to rear brood was under utilized after day 60 as the brood to nurse bee ratio was considerably less than 2. This may indicate that after day 60, the queen's ability to produce eggs may become a limiting factor for colony growth. Perhaps the high nurse bee:brood ratio may have been maintained for an additional thirty or forty days if adequate space had been provided for brood rearing. Had a second queen been present in colonies after day 48 the brood/adult ratio may have increased. The utilization of excess nurse bees may be what allows two queen colonies to develop faster than single queen colonies. If this is so, then differential development of two-queen colonies should not become apparent until at least sixty days after installation of the package bees.

After day 60, the amount of brood produced declined as the forager population increased during the nectar flow, when large

Fig. 5.3 The ratio of total brood to nurse bees in
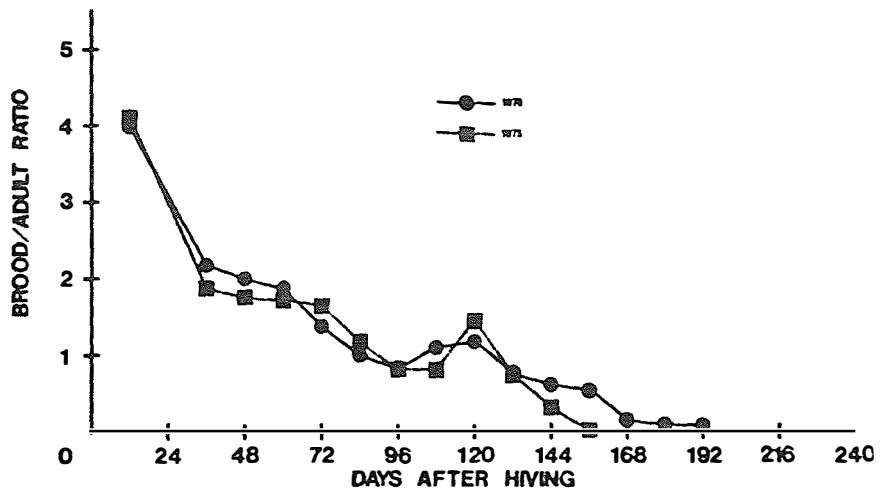
honey bee colonies in 1975 and 1976

Table 5.2. Seasonal relationships between adult populations, temperature, honeyflow and brood in 1975 and 1976.

Date		Days after hiving	Mean daily temp. for period ending	Cells of brood			Number of adult bees		Kg of honey collected
				Eggs	Larvae	Pupae	<19 days of age	>19 days of age	
1975									
05 May	1975	122	7.13	2586	3539	0	1487	3875	–
17 May	1975	24	13.24	2401	3657	8919	0	3419	–
29 May	1975	36	13.68	3341	5089	8281	8830	799	–
10 June	1975	48	12.47	4595	6998	12293	12632	4627	–
22 June	1975	60	16.97	4977	7579	13137	14894	8518	–
04 July	1975	72	21.48	4864	7408	17161	17800	11385	48
16 July	1975	84	20.81	4162	6339	16772	22871	13958	84
28 July	1975	96	21.07	2220	3380	14353	24136	19050	90
09 Aug.	1975	108	20.57	3916	5964	7654	21737	23266	95
21 Aug.	1975	120	14.83	2612	3978	13503	13617	24161	12
02 Sept.	1975	132	16.15	1373	2091	9008	16673	18659	-04
14 Sept.	1975	144	10.83	23	34	4734	14727	15768	-05
26 Sept.	1975	156	11.48	0	0	78	8526	11148	-05
08 Oct.	1975	168	12.16	0	0	0	1632	11072	–
22 Oct.	1975	180	7.79	0	0	0	35	6403	–
1976									
03 May	1976	12	5.34	2371	3611	0	1487	3875	–
15 May	1976	24	10.41	2664	4057	8175	0	3419	–
27 May	1976	36	13.39	3359	5116	9186	8093	790	–
08 June	1976	48	21.78	5232	7969	11583	12353	4585	–
20 June	1976	60	16.37	5793	8822	14774	15620	9783	–
02 July	1976	72	17.79	5017	7641	19975	22951	15268	64
14 July	1976	84	20.88	4382	6675	17299	27731	20367	93
26 July	1976	96	19.41	2767	4214	15113	26204	27304	61
07 Aug.	1976	108	17.84	3692	5623	9540	17021	48025	88
19 Aug.	1976	120	20.42	2549	3883	12732	16167	31704	26
31 Sept.	1976	132	16.76	1638	2495	8791	16508	21108	-01
12 Sept.	1976	144	18.24	1325	2019	5650	14312	19108	-03
24 Sept.	1976	156	11.51	293	446	4568	9584	17021	–
06 Oct.	1976	168	9.44	80	29	1010	7033	14744	–
18 Oct.	1976	180	4.43	19	0	228	3078	10973	–
30 Oct.	1976	192	-1.50	0	0	67	770	12429	–
11 Nov.	1976	204	-2.35	0	0	0	199	12165	–
23 Nov.	1976	216	-3.00	184	279	0	32	11774	–
05 Dec.	1976	228	-16.35	184	279	633	0	11261	–

quantities of nectar were being collected (Table 5.2). Declining brood at this time suggests that there was competition for space in which to store honey or to rear brood. This suggestion was further supported by the fact that when full combs of honey were removed and replaced with empty ones, additional brood was reared in the combs placed immediately above the brood area between day 108 and day 120. It is not known whether the extra nurse bees forage at a younger age as suggested by Sekiguchi and Sakagami (1966) or continue doing their normal age related duties (see Ribbands 1953).

Swarm cell preparation in 1975 and 1976 was evident between day 72 and day 96. The decrease in brood production associated with nectar collection by the forager population may be a primary cause of swarming, if the pheromones which inhibit the preparation of queen cells are a function of the amount of brood in a colony and/or the egg laying activities of the queen cells. Pain et al. (1972) observed a decrease in pheromone production by queens after June in France. It is not known if this was associated with changes in brood production or the preparation of queen cells. Morland (1930, 1935) observed that the swarming impulse was strong whenever a surplus of nurse bees grew very rapidly following a sudden fall in the queen's egg laying activity. Bodenheimer (1937) concurred. He felt that it was not the ratio of nurse bees to brood which induced swarming but only its rapid decline. If competition for space was the apparent cause of declining brood and swarm cell preparation, it may prove useful to place empty combs within the brood area in late June and/or early July. This seems reasonable as worker bees were observed

tearing down sealed queen cells following the insertion of empty combs into the brood area.

Declining adult to brood ratios after day 120 were associated with cool and overcast weather and/or a general lack of nectar and pollen in both years.

In 1975 and 1976 the largest forager population was obtained on day 120. Unfortunately, the nectar flow, at this time of year, was almost negligible. If maximum forager populations were to occur in early or mid July and were to remain at a high level, it might be possible to increase average colony honey yields by as much as fifty to one hundred kilograms. Any management technique which increases brood production is almost certain to increase the forager population, and hence the amount of nectar collected. Initiation of colonies with 1.4 or 1.8 kg of bees, altering hiving dates, using multiple queen colonies or using overwintered colonies may be a solution to obtaining larger forager populations sooner, to more closely coincide with peak honeyflows in Manitoba.

With the total colony population declining rapidly after the end of August, very few adult bees present in colonies at the end of August survived until December. Since honeyflows are minimal in September it may prove beneficial to physically reduce colony populations, (in particular the foragers), immediately after the main honeyflow. If this were done, the colony would not have to deplete valuable winter stores to provide for a large population which will not survive the winter. A reduced adult population at this time may

result in a reduction in the stores consumed, earlier brood rearing, and increase the probability of colony survival.

Colony age structure throughout the season was predominantly influenced by changes in brood production. Colony age structure increased or decreased in relation to the amount of brood produced. Changes in age structure relating to changes in worker bee survival were not evident until fall. As winter approached worker bees lived longer as indicated by the appearance of bees over eighty-four days of age. This is likely due to reduced foraging activities.

5.4.2 Adult Population

Adult population trends were similar in 1975 (Figure 5.4a) and 1976 (Fig. 5.4b). Colonies began with approximately 7000 worker bees, decreased to a minimum on day 24 and then increased until a maximum adult population of 40-60,000 bees was reached between day 96 and day 108. A steady decline in the size of the adult population followed after day 108. Colonies contained $1.3 \pm 0.3 \times 10^3$ bees (10 October 1975) as compared to $2.2 \pm 0.1 \times 10^3$ bees (7 October 1976) on day 168.

The original package bee population declined rapidly after hiving (Fig. 5.4). Survival of the package bee population was longer than previously predicted by Farrar (1968). Very few bees remained in the colony from the package population seventy-two days after their installation in both years.

Maximum adult populations occurred towards the latter part of the honeyflow. Had brood production not decreased in late July as previously mentioned, colony populations may have stabilized or

Fig. 5.4a Seasonal trends in adult populations of

honey bee colonies started from 0.9 kg of

worker bees in 1975

Fig. 5.4b Seasonal trends in adult populations of

honey bee colonies started from 0.9 kg of

worker bees in 1976
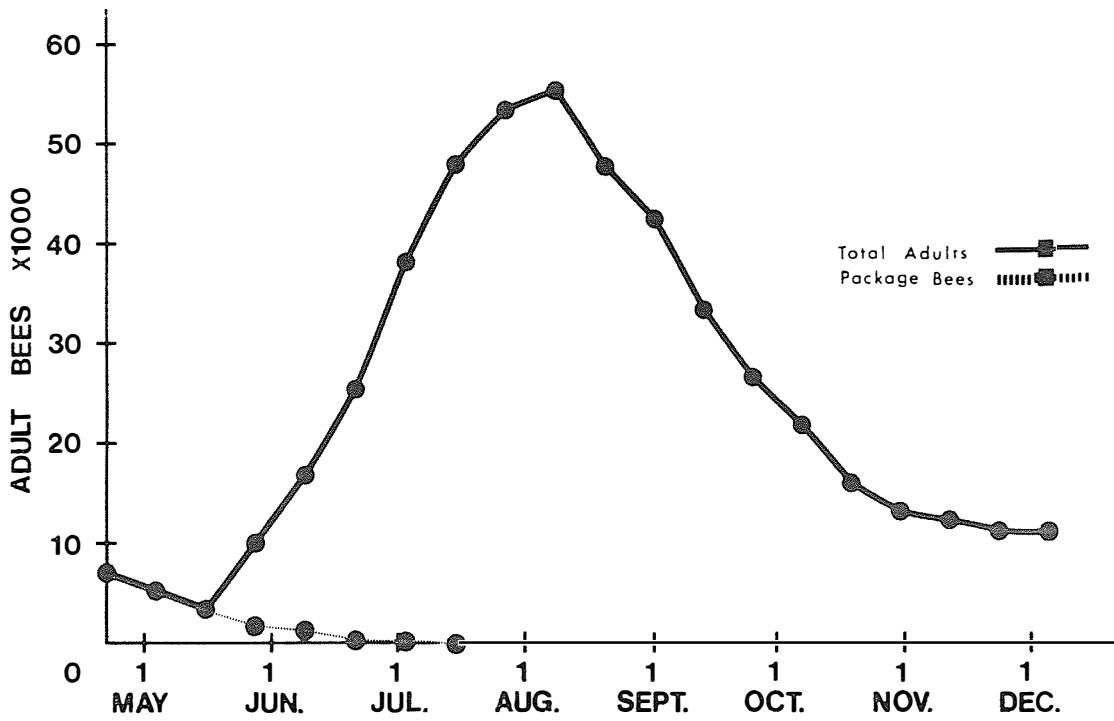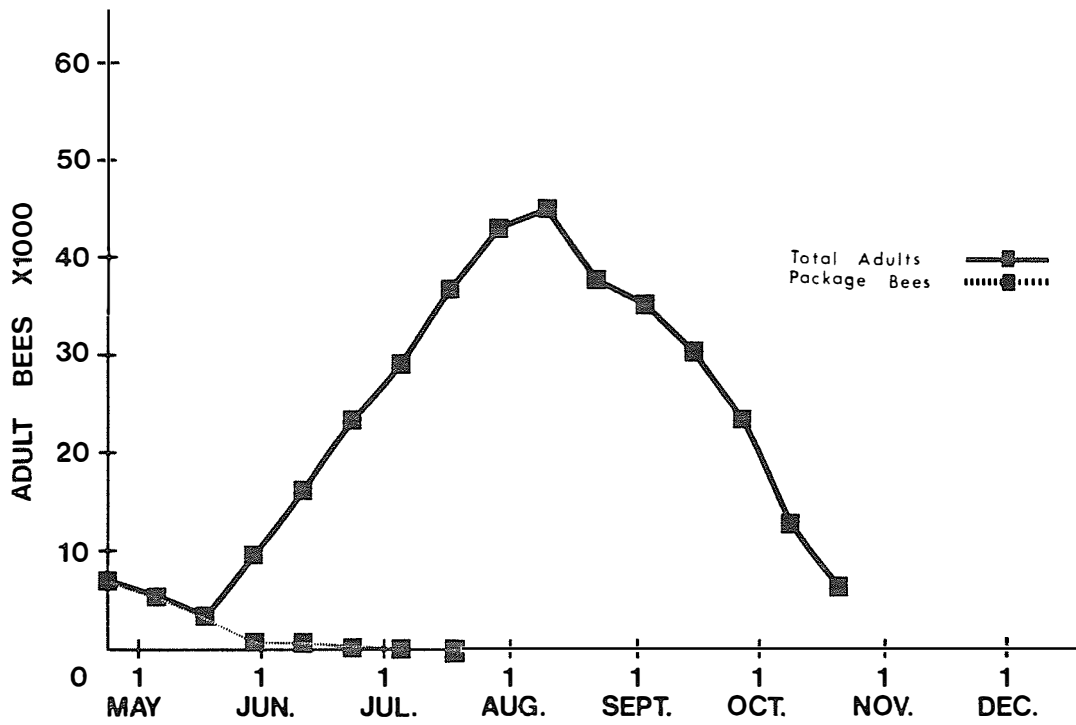
continued to increase until the beginning of September. The occurrence of maximum populations in late August is contrary to the popular opinion held by many beekeepers that colony populations initiated from package bees peak in early July. However, the results of this study concur with those of Smirl and Jay (1972a) and Nelson and Jay (1972). It appears that under conditions found in Manitoba at least one hundred and eight to one hundred and twenty days are required for colonies initiated from 0.9 kg packages of worker bees to reach maximum populations.

Maximum populations were $1.0-1.5 \times 10^3$ bees smaller in 1975 than in 1976. The differences may have been related to environmental conditions or management practices, for example supering was often delayed by two or three days to accommodate data collection in 1975.

Fall populations were numerically similar to those reported in Europe by Jeffree (1955, 1956) and Free and Racey (1969). However, they were considerably smaller than those recommended for overwintering in North America by Farrar (1952) and Furgala (1975). Differences in opinion as to the fall populations of adult bees may stem from estimates taken at different times during the season as colony populations declined rapidly with the end of the honeyflow (Fig. 5.4a,b).

5.4.3 Sealed Brood

Sealed brood produced by colonies was similar in 1975 and 1976 (Fig. 5.5a,b). Average sealed brood production, twenty-four days after hiving, was 8476±503 in 1975 and 1976. Little change in

Fig. 5.5a Seasonal trends in brood rearing by honey bee
colonies started from 0.9 kg of package bees
in 1975.

Fig. 5.5b Seasonal trends in brood rearing by honey bee
colonies started from 0.9 kg of package bees
in 1976.
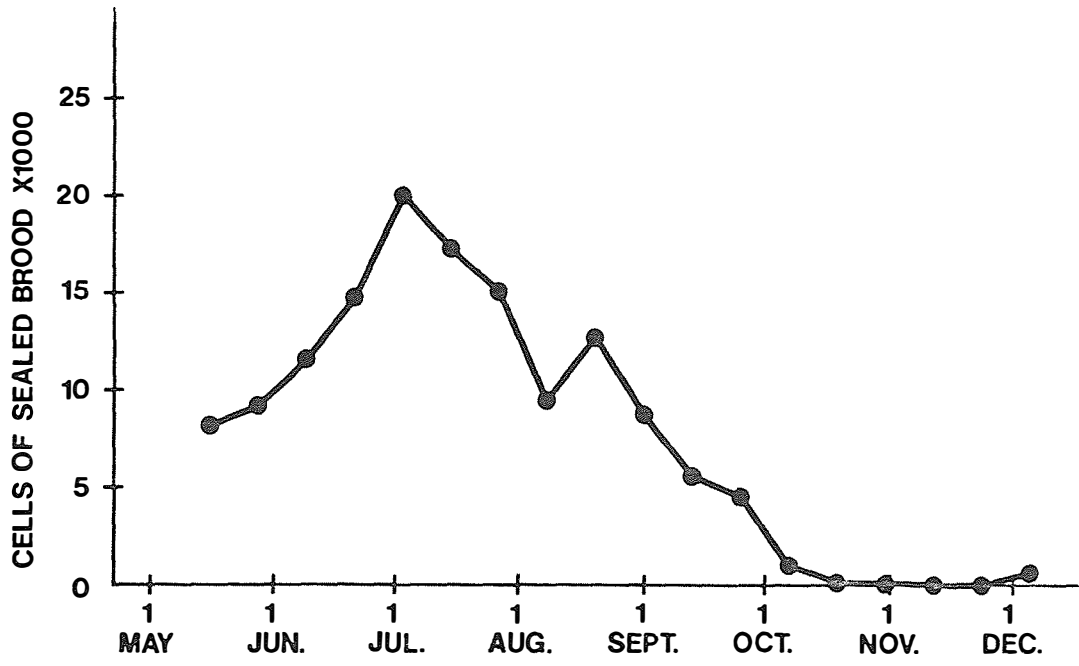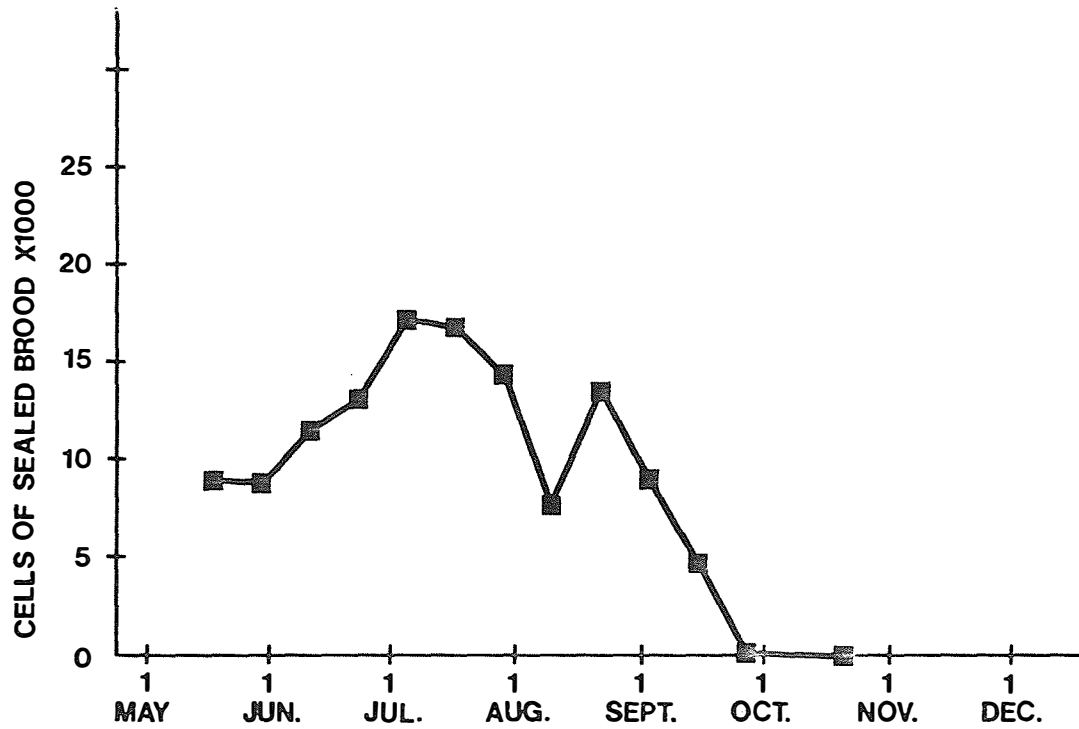
the amount of sealed brood occurred at day 36, followed by a sharp increase between day 48 and day 72. A decline in sealed brood production occurred between day 72 and day 108, followed by an increase between day 108 and day 120. A steady decline occurred between day 120 and the cessation of brood rearing. Brood rearing decreased slightly between day 144 and day 156 in 1976. The amount of brood reared may have decreased to even lower levels (as it did in 1975), had sugar syrup not been fed to colonies on day 132. Ribbands (1950) observed a similar stimulation of brood rearing after he fed sugar syrup to his colonies. The practice of feeding sugar syrup to colonies being prepared for overwintering may have a beneficial effect apart from increasing colony stores, it may alter normal fall brood rearing patterns.

Resumption of brood rearing, between day 216 and day 228 in 1976 may have been stimulated by the combined insulating effect of an early snowfall and a 25.4 mm thick sheet of expanded polystyrene beads above the inner cover. However, since Avitabile (1978) also observed brood present in overwintered colonies as early as mid November, it may be that normal brood rearing during the winter is initiated much earlier than first believed by Farrar (1952).

5.5.0 Conclusions

The development of honey bee colonies is affected by factors which influence a colony's birth and death rates. It appears that these factors may vary in their importance to colony growth

throughout the season. In the initial phase of colony development, growth is limited by the size of the adult population, (particularly the number of bees capable of caring for brood) and external temperatures. The size of the nurse bee population determines the maximum number of eggs, larvae, and pupae which can be cared for, while the external air temperature influences the area over which the bees are able to maintain favorable brood rearing temperatures. As the colony grows in size, colony growth appears to become less related to the size of the worker bee population and more related to the number of eggs the queen can deposit into brood cells. During the honeyflow, colony growth may once again be influenced by the adult population. If there is inadequate space to provide for incoming nectar, the workers will place it in cells which the queen requires for her eggs. This will reduce the number of progeny produced; there are also indications that it may even result in swarming. Finally, in the fall, as food becomes less abundant and temperatures decrease, there is a tendency for the queen, (which has been in the colony for a season), to restrict her egg laying activities. It is unknown, at this time, how much of this reduction can be attributed to external temperatures, the availability of food, and/or the age of the queen.

Further study is required if the factors influencing colony growth are to be isolated and their importance to colony growth determined.

5.6.0 References

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CHAPTER 6

Development of Honey Bee Colonies   **II. Effect of Requeening on Honey**

Fall Populations

6.1 Summary

The influence of requeening honey bee colonies in late July
with mated queens, mature queen cells and queens reared from emerging
queen cells, was examined.   The different requeening procedures
affected fall brood rearing, adult population size and colony age
structure.

6.2 Introduction

Providing colonies with large fall populations of young bees has
been considered to be an essential part of preparing colonies for
winter in temperate climates.   Bliss (1936) considered that the
introduction of young queens into colonies during the fall was the
easiest method of obtaining these populations.   The new queens would
continue to rear brood late into the fall when older queens
apparently cease brood rearing (Free and Racey 1968; Moeller 1977).

Requeening colonies can be accomplished by a number of different
procedures.   Requeening colonies with mated queens has been the
accepted method used by most beekeepers to requeen their colonies.
However, in recent years, requeening with mature queen cells has been
viewed as a more economical alternative method of requeening
colonies.   Since acceptance of the new queen by the colony will be

influenced by how long the colony was queenless (Baribeau 1976), it is not totally surprising that the introduction of queen cells into queen right colonies has produced varied results. Peer (1977) reported acceptance greater than 80 percent, while Jay (personal communication) and Boch and Avitabile (1979) obtained less than 40 percent acceptance. Occasionally, a beekeeper will remove the queen and allow the colony to rear a replacement queen if eggs or young larvae are present in a colony. A parallel situation may occur if colonies become queenless when bees are removed from honey combs while honey is being harvested or when requeening with mated queens and queen cells are unsuccessful.

The present study was undertaken to investigate changes in colony age structure, brood rearing activities and total adult population resulting from "fall" requeening of colonies.

6.3 Methods and Materials

Colonies were initiated from 0.9 kg packages of worker bees (ca. 7000 worker bees) and a mated queen of a yellow strain on 25 April, 1975 and 22 April, 1976. In both years, the colonies were kept in commercial apiaries in south-central Manitoba. Colonies were divided into four groups (A, B, C and D). Each group contained six colonies. Colonies which became queenless or swarmed were deleted from the experiment. To minimize drifting between colonies (see Free 1958; Jay 1966), the hives were arranged in a circular pattern one meter apart with their entrances facing away from the circle.

During the spring and summer, all colonies received similar

management. Extra hive bodies were placed above those already present as required, and honey was removed during the last week of July (ninety-six days after hiving) and again during the last week of August (day 120). In 1976 sugar syrup was fed on day 132 and insulated covers were placed on colonies on day 204.

The last week of July (day 96) colonies in groups B, C and D were made queenless. Colonies in group B were requeened with mated queens. Colonies in group C were requeened with mature queen cells and colonies in group D were allowed to rear a replacement queen. Colonies in group A retained an original package queen.

Total colony population estimates were made at twelve day intervals after hiving using the method outlined in Chapter 3. Sealed brood area was determined by superimposing a grid divided into 25.4 x 25.4 mm squares over the brood area and estimating the comb area occupied (Nolan 1925; Moeller 1961). Adult bees were marked with paint (see Chapter 2) to estimate adult bee mortality. The age structure of the package colony was estimated by the procedure discussed in Chapter 5. The above procedure for estimating colony populations was satisfactory until late fall when bees become densely clustered. During that period adult population estimates were based upon average summer mortalities and extrapolation of winter mortalities.
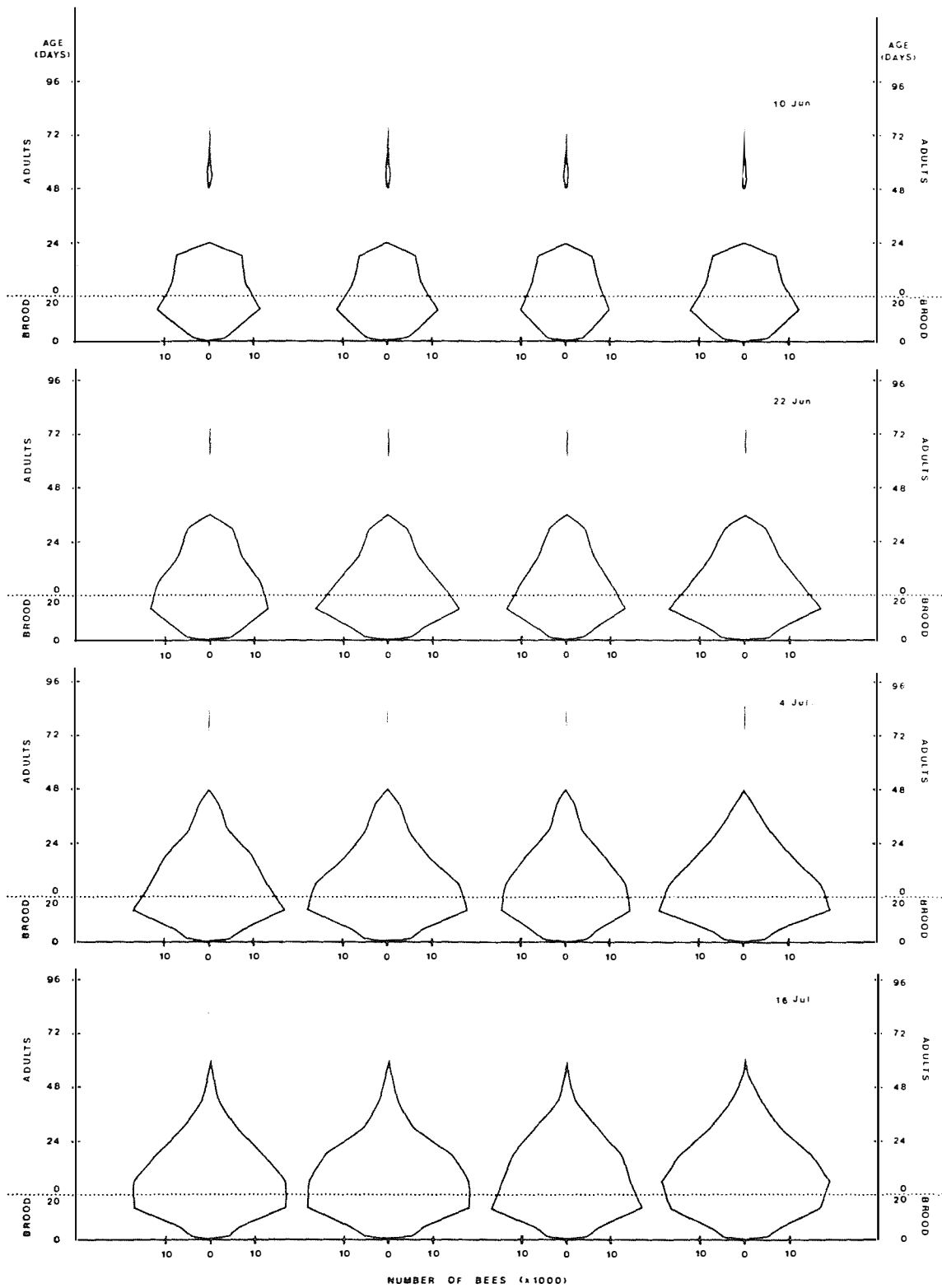
6.4 Results and Discussion

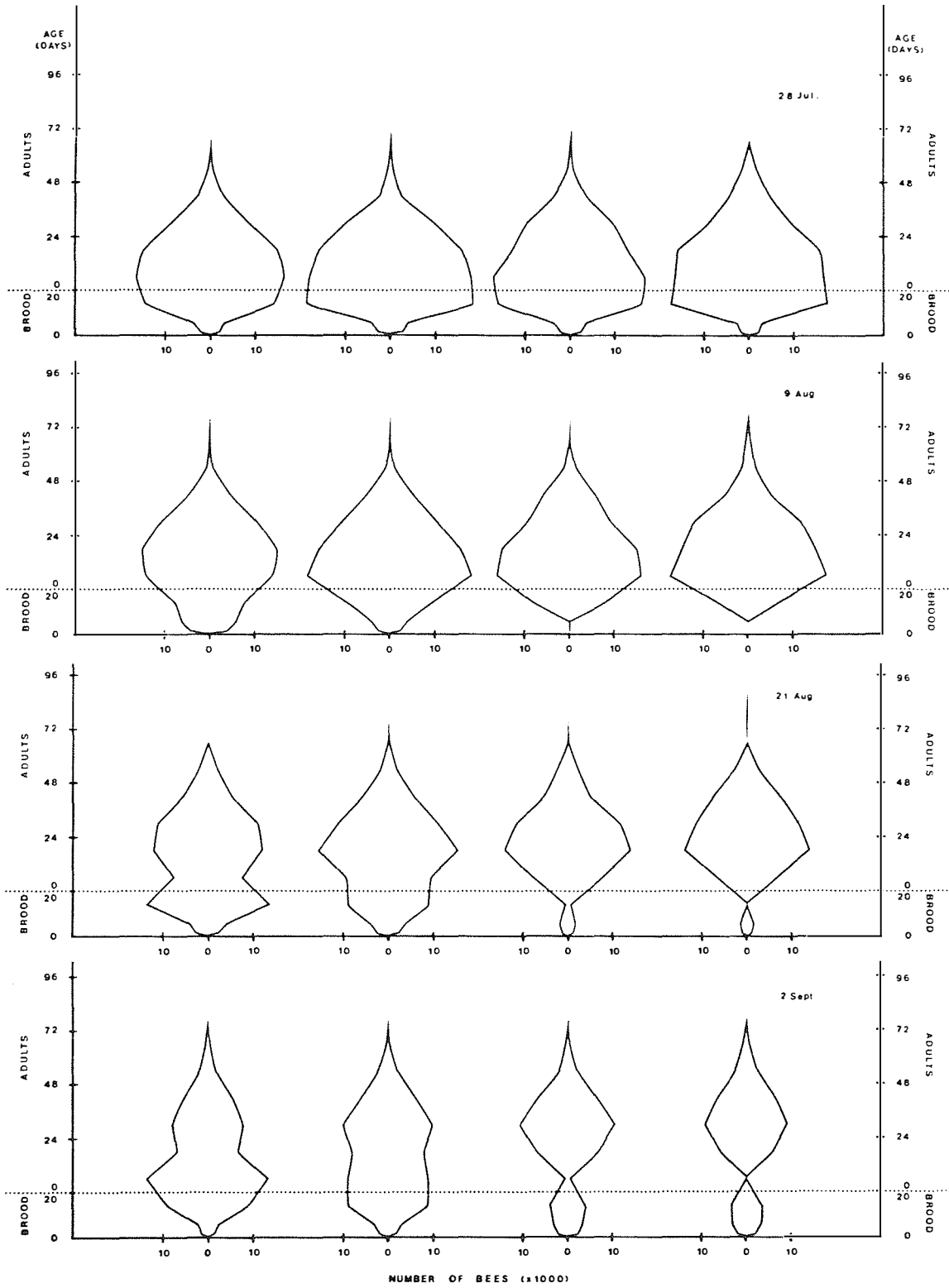### 6.4.1 Colony age distribution

Changes in colony age distribution during the 1975 and 1976

Fig. 6.1   Seasonal changes in the age distribution of

worker bees in honey bee colonies (A,

control) and the effect of requeening

colonies on 28 July 1975 with mated queens

(B), queen cells (C) and supersedure queens
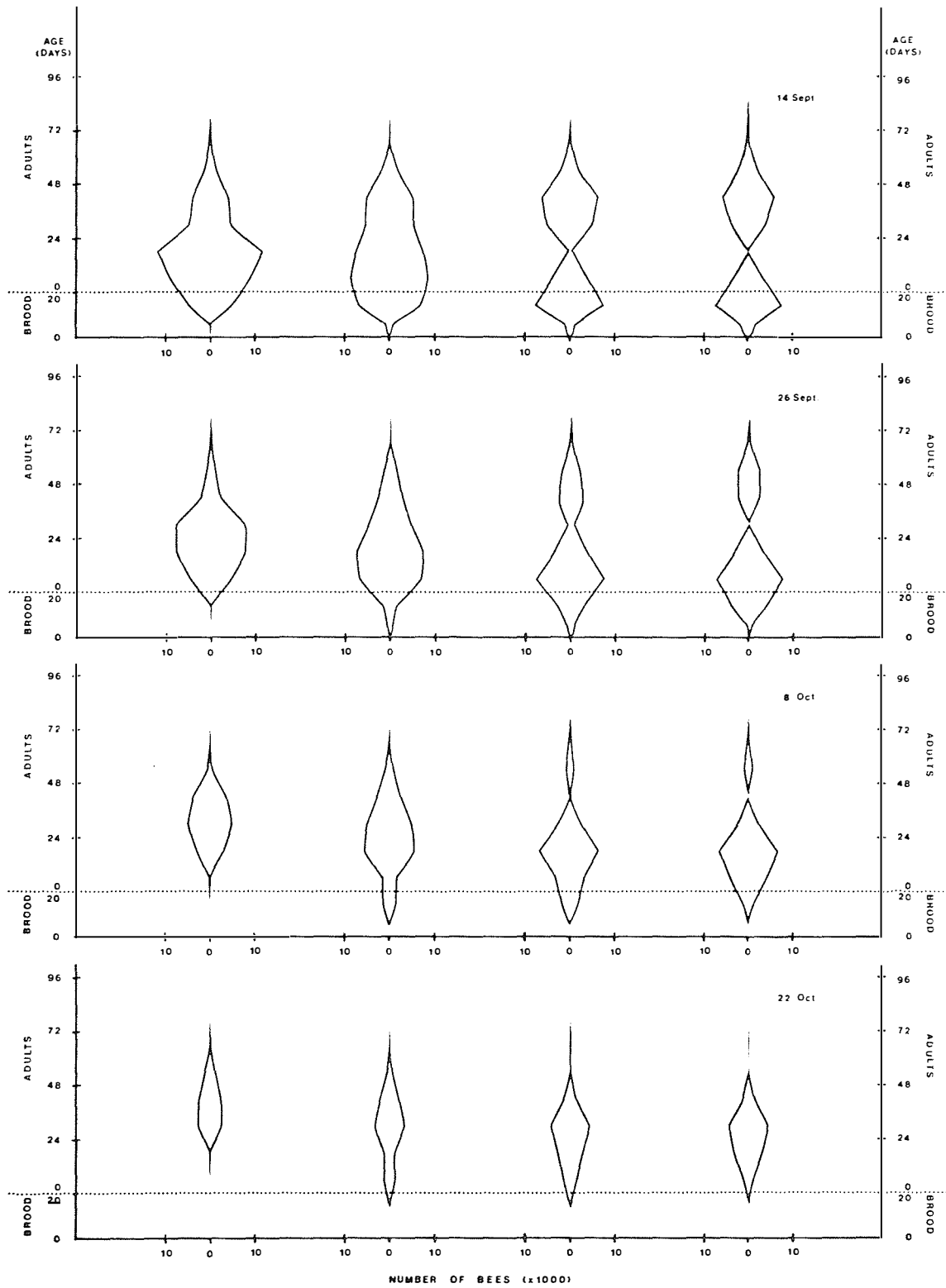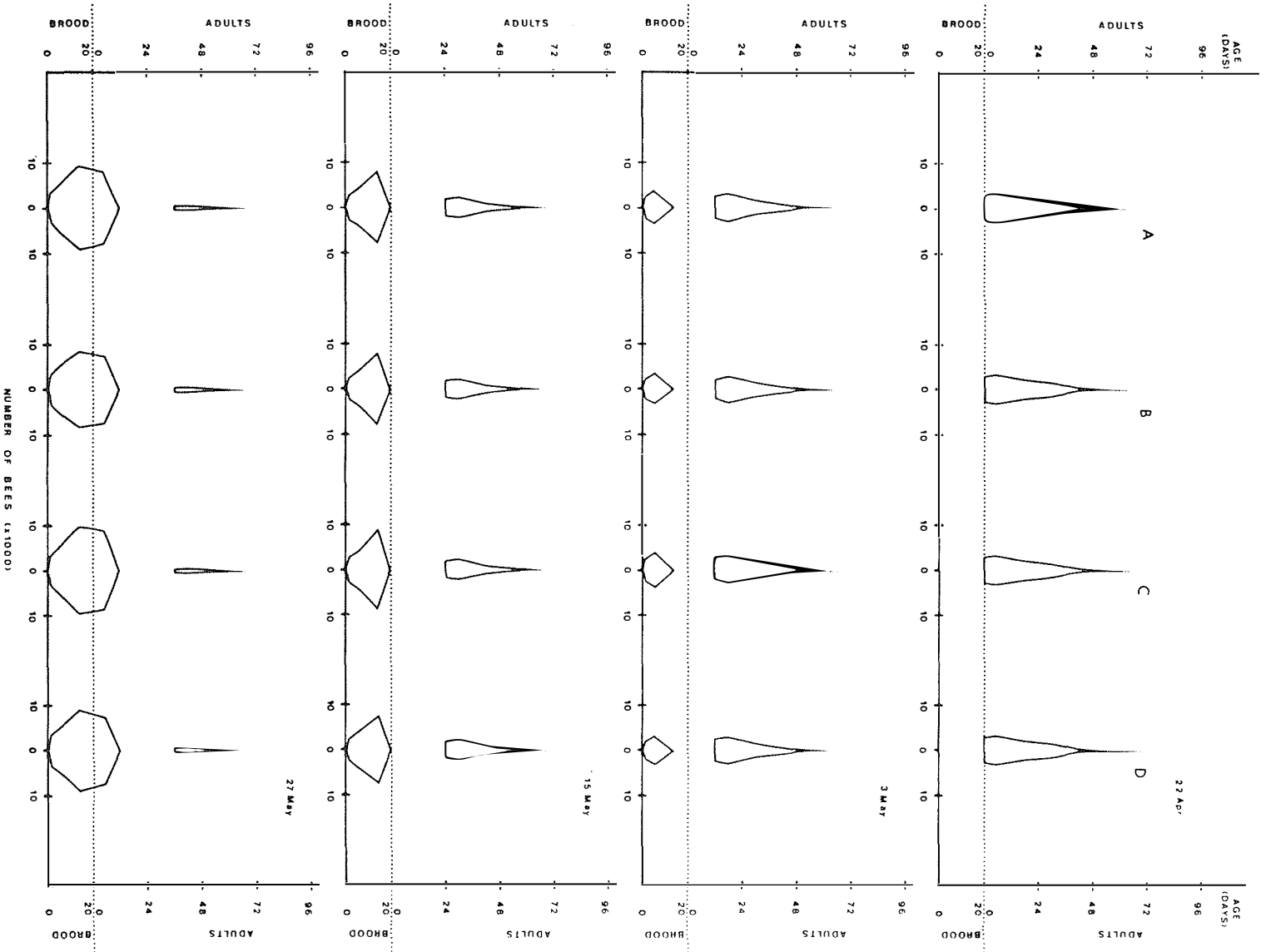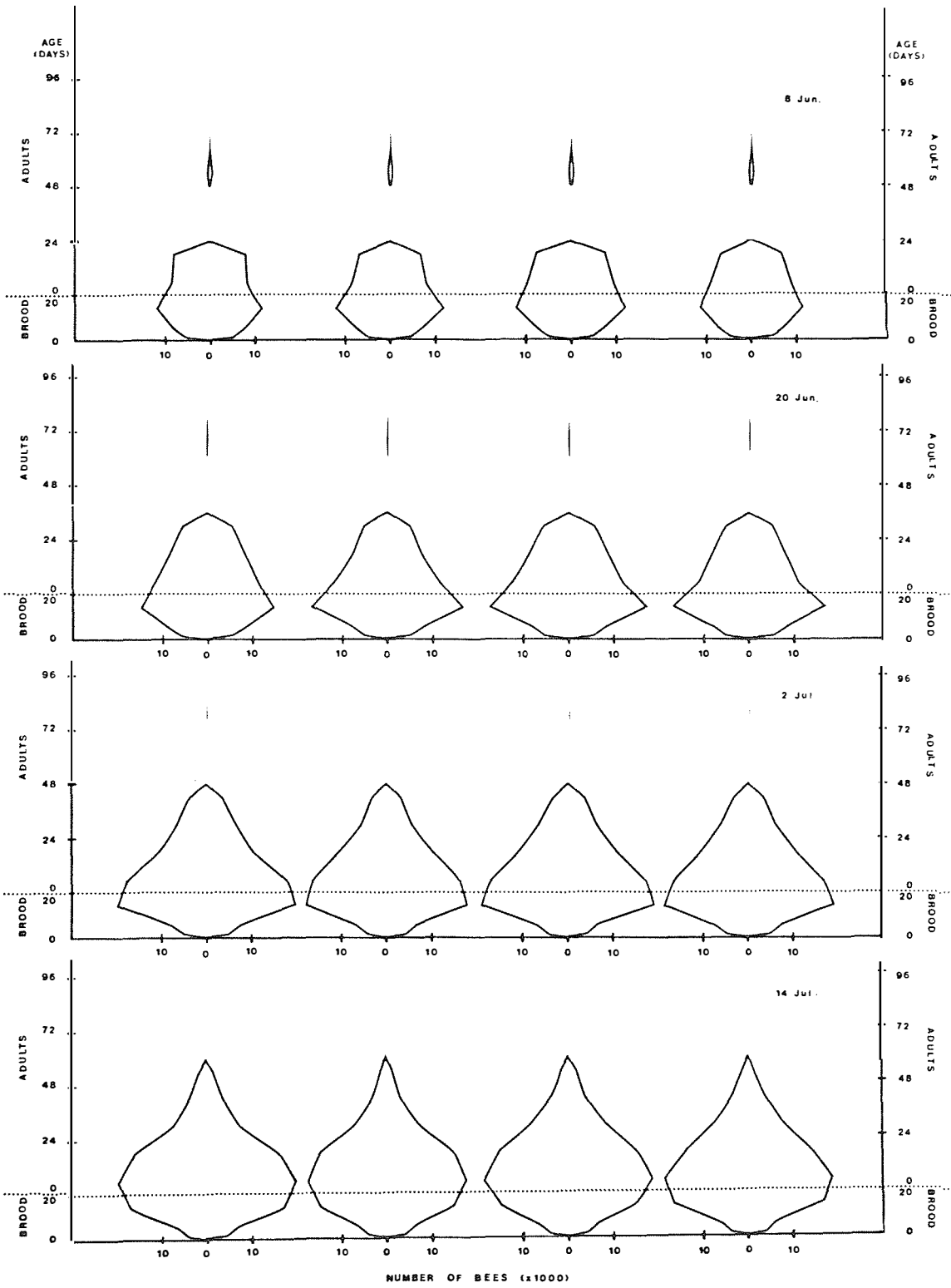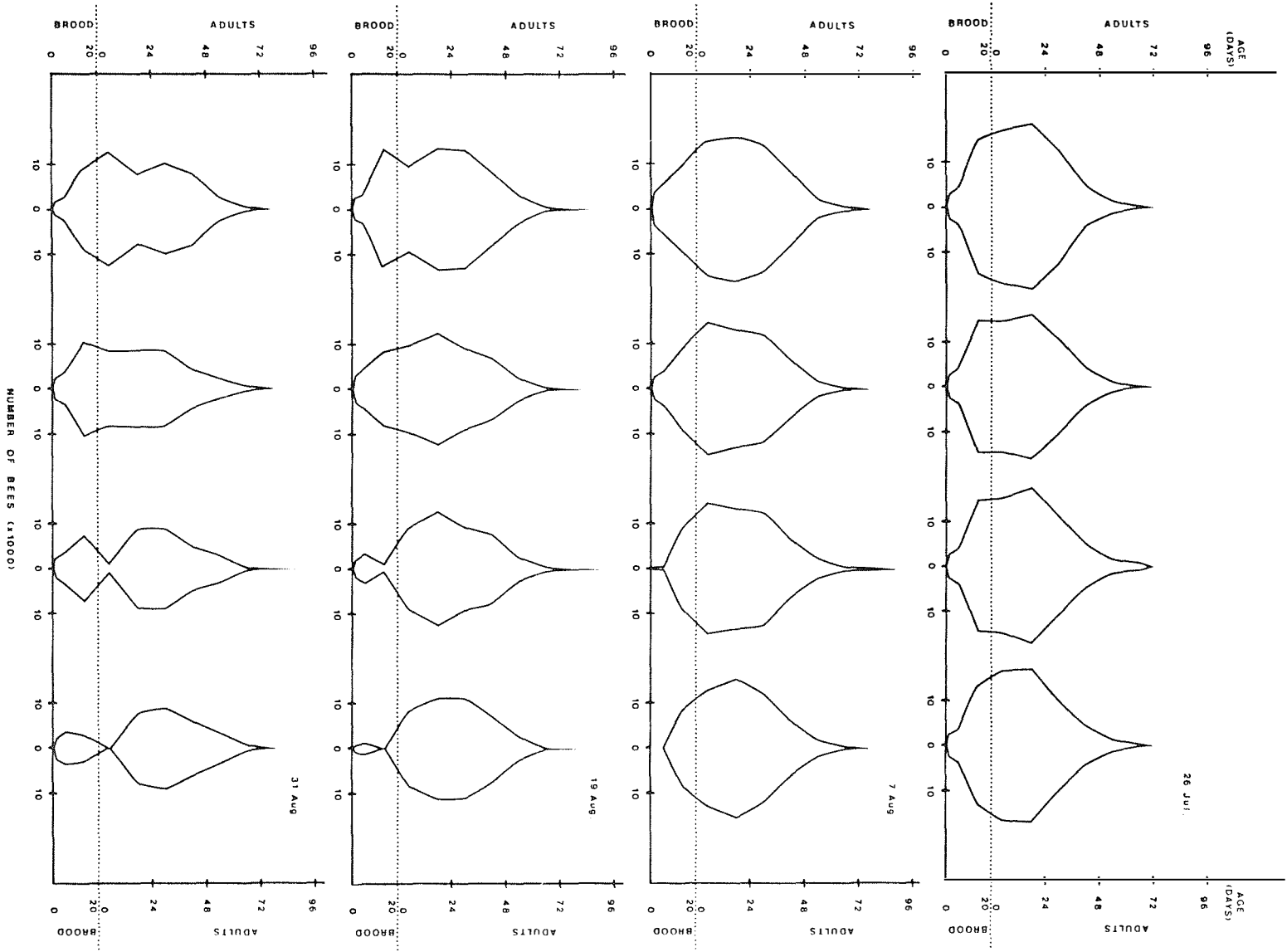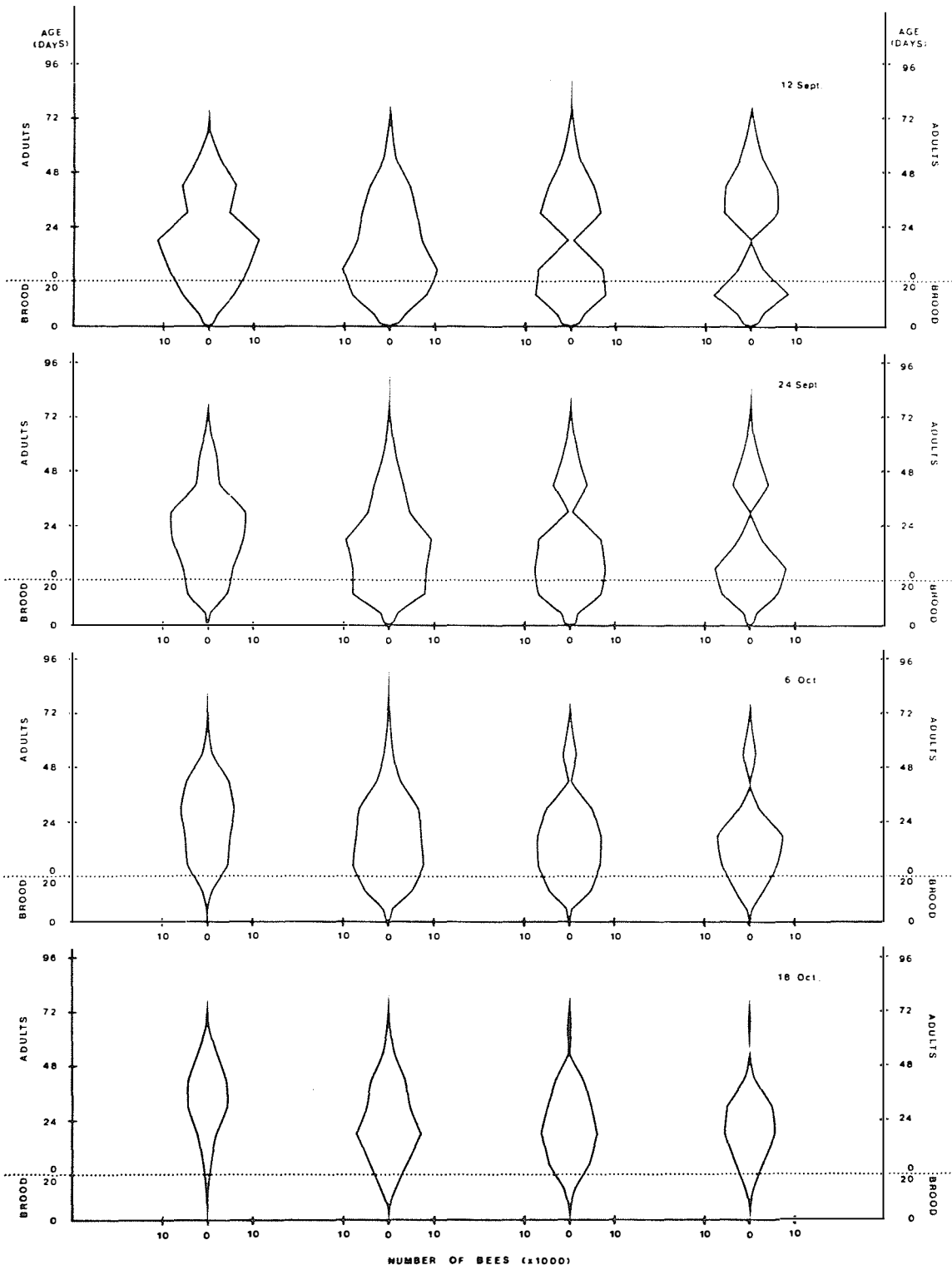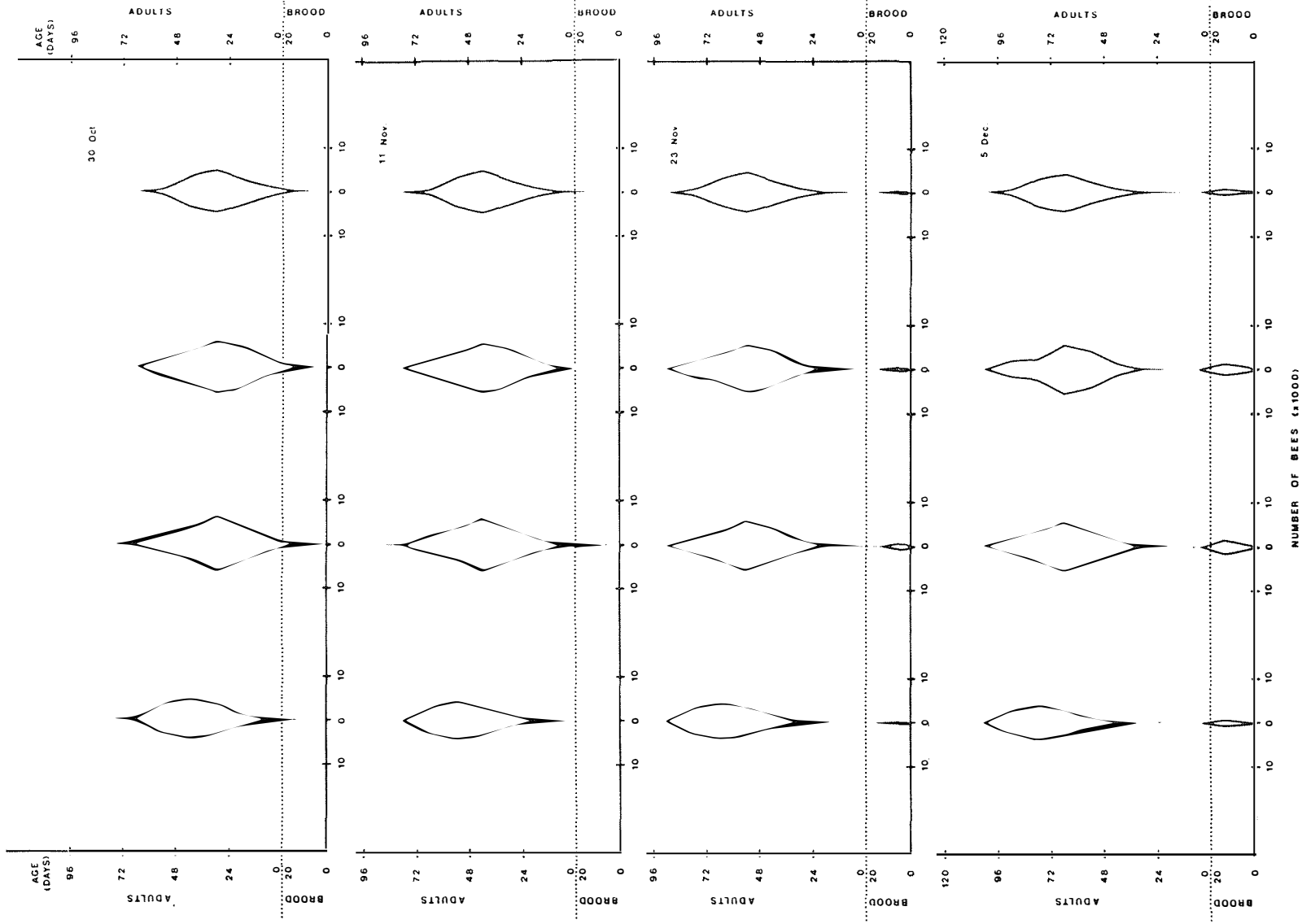
(D) upon these age distributions.

AGE (DAYS)

96
72   ADULTS
48
24
0
20   BROOD
0

24 Apr

A   B   C   D

10   0   10   10   0   10   10   0   10   10   0   10

96
72   ADULTS
48
24
0
20   BROOD
0

5 May

10   0   10   10   0   10   10   0   10   10   0   10

96
72   ADULTS
48
24
0
20   BROOD
0

17 May

10   0   10   10   0   10   10   0   10   10   0   10

96
72   ADULTS
48
24
0
20   BROOD
0

29 May

10   0   10   10   0   10   10   0   10   10   0   10

NUMBER   OF   BEES   (x1000)

NUMBER OF BEES (x1000)

AGE (DAYS)

96

72

48 — ADULTS

24

0
20 — BROOD
0

28 Jul.

96

72

48 — ADULTS

24

0
20 — BROOD
0

9 Aug

96

72

48 — ADULTS

24

0
20 — BROOD
0

21 Aug

96

72

48 — ADULTS

24

0
20 — BROOD
0

2 Sept

10 0 10   10 0 10   10 0 10   10 0 10

NUMBER OF BEES (x1000)

AGE
(DAYS)

96

72   ADULTS

48

24

0
20   BROOD

0

14 Sept

10   0   10   10   0   10   10   0   10   10   0   10

96

72   ADULTS

48

24

0
20   BROOD

0

26 Sept

10   0   10   10   0   10   10   0   10   10   0   10

96

72   ADULTS

48

24

0
20   BROOD

0

8 Oct

10   0   10   10   0   10   10   0   10   10   0   10

96

72   ADULTS

48

24

0
20   BROOD

0

22 Oct

10   0   10   10   0   10   10   0   10   10   0   10

NUMBER   OF   BEES   (x1000)

Fig. 6.2   Seasonal changes in the age distribution of

worker bees in honey bee colonies (A, control) and the

effect of fall requeening colonies on 26 July 1976

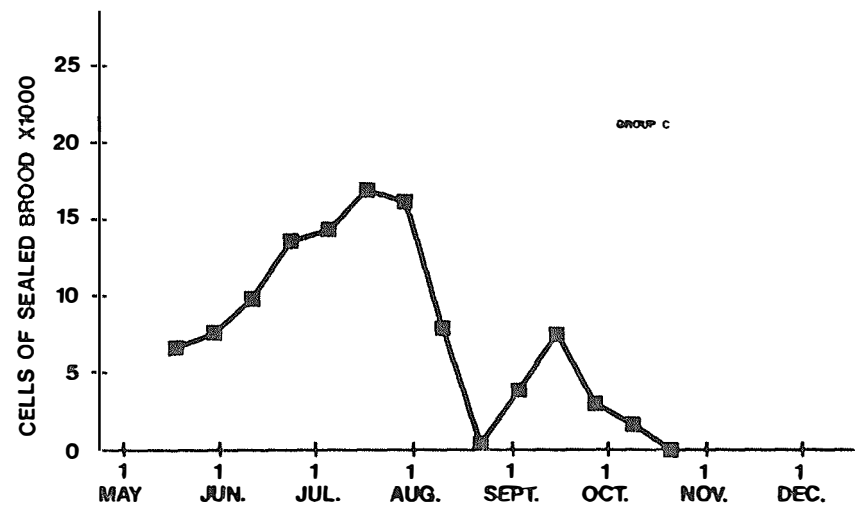with mated queens (B), queen cells (C) and supersedure

queens (D) upon these age distributions.

NUMBER OF BEES (x1000)

BROOD   ADULTS

BROOD   ADULTS

BROOD   ADULTS

BROOD   ADULTS

96

72

48

24

0 20 0

10

0

10

10

0

10

10

0

10

10

0

10

NUMBER OF BEES (x1000)

31 Aug.

19 Aug.

7 Aug.

26 Jul.

AGE
(DAYS)

0 20 0 24 48 72 96

BROOD   ADULTS

AGE
(DAYS)

96

72

48

ADULTS

24

12 Sept.

0

BROOD
20

0

10 0 10   10 0 10   10 0 10   10 0 10

AGE
(DAYS)

96

72

48

ADULTS

24

0

BROOD
20

0

96

72

48

ADULTS

24

24 Sept.

0

BROOD
20

0

10 0 10   10 0 10   10 0 10   10 0 10

96

72

48

ADULTS

24

0

BROOD
20

0

96

72

48

ADULTS

24

6 Oct.

0

BROOD
20

0

10 0 10   10 0 10   10 0 10   10 0 10

96

72

48

ADULTS

24

0

BROOD
20

0

96

72

48

ADULTS

24

18 Oct.

0

BROOD
20

0

10 0 10   10 0 10   10 0 10   10 0 10

96

72

48

ADULTS

24

0

BROOD
20

0

NUMBER OF BEES (x1000)

seasons are shown in Figures 6.1 and 6.2.

The age distribution of the various colonies, for each year, was similar between hiving and the last week of July. Colony age structures were altered when the queens were removed from the colonies and replaced using treatments B, C and D. Changes in colony age structures were more evident in colonies requeened with mated queens than when requeened with mature queen cells or with queens reared by their respective colonies from eggs or young larvae (Figure 6.1; 6.2). Although requeening provided colonies with a younger population of worker bees than was observed in treatment A, these differences were not as pronounced in December as they had been in early October. It seems that the differential age distributions were related to differences in brood rearing since the various colonies tended to approach a common age distribution once brood rearing stopped and new adults were no longer being added to the populations.

6.4.2 Sealed brood

Seasonal trends in the cells of sealed brood, as influenced by requeening are shown in Fig. 6.3 and 6.4. Requeening altered the normal brood rearing patterns. Colonies which were requeened tended to increase their brood production while colonies which were not requeened reduced their brood production. Requeened colonies also had a tendency to continue brood rearing after the older queens

Fig. 6.3   Seasonal changes in brood rearing patterns

(A, control) and the effect of requeening

colonies on 28 July, 1975 with mated queens

(B), queen cells (C) or supersedure queens
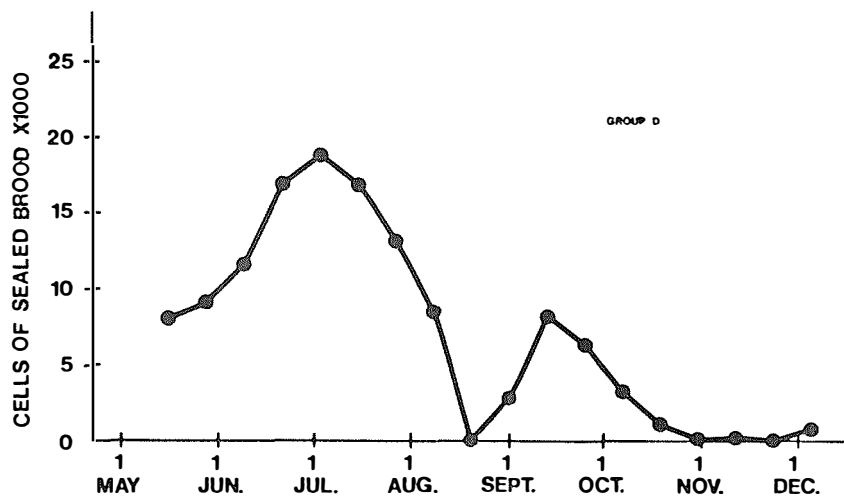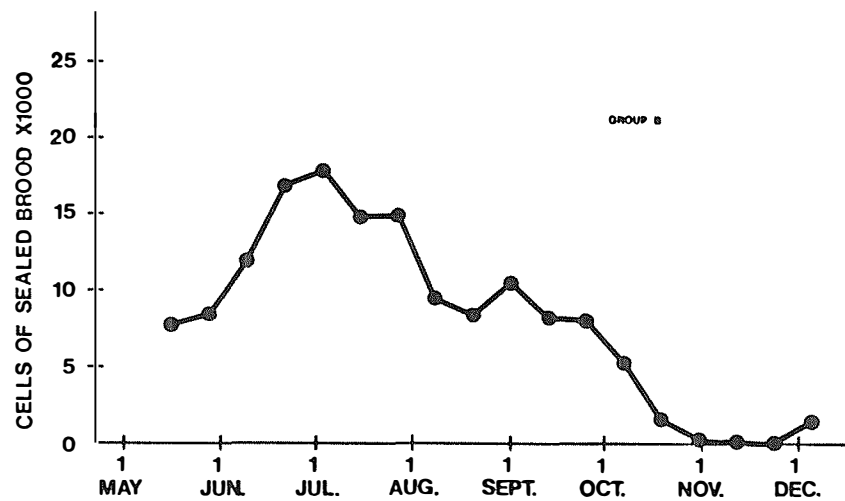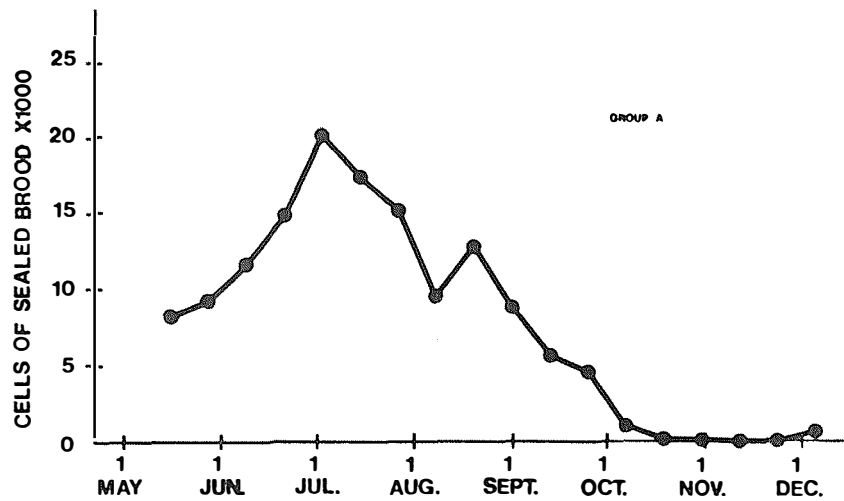
(D).
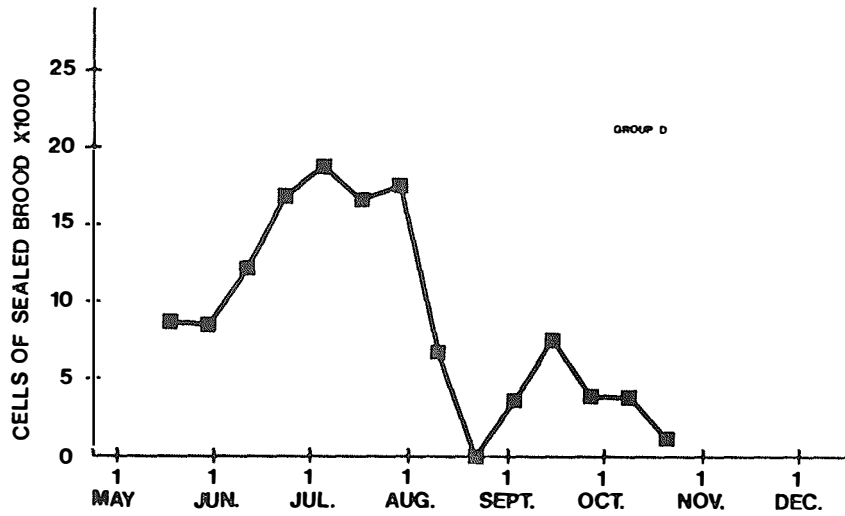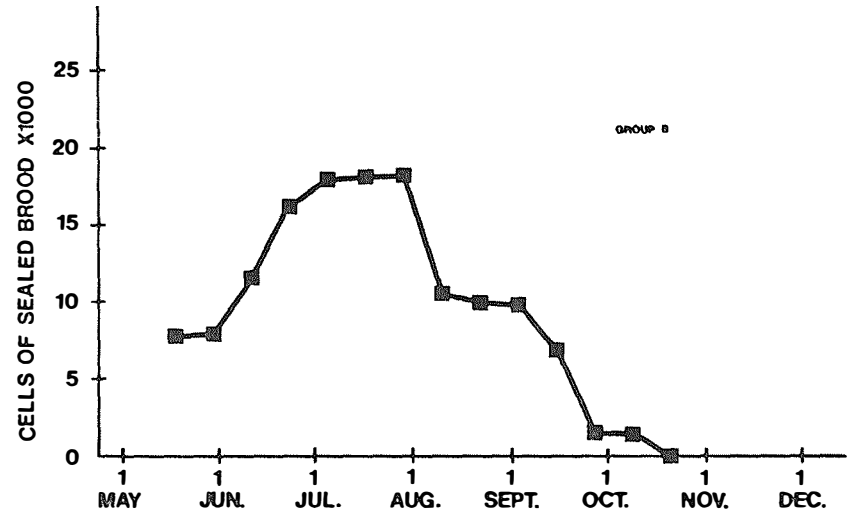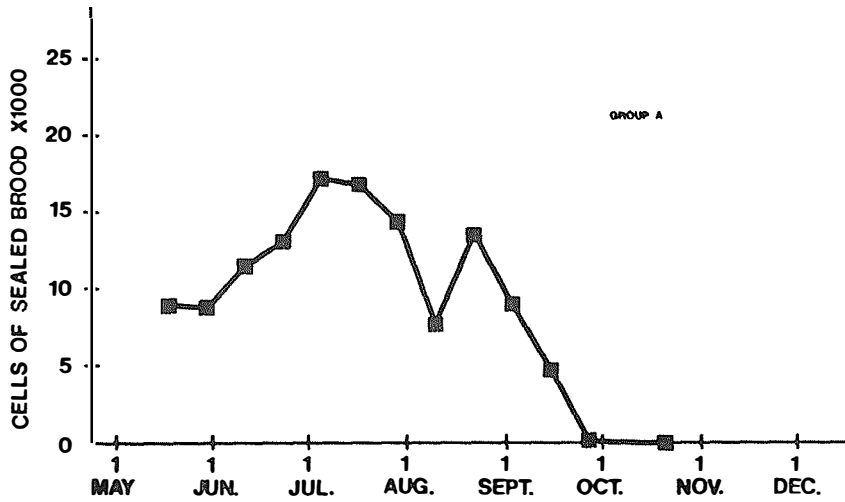
Fig. 6.4   Seasonal trends in brood rearing patterns (A,

control) and the effect of requeening

colonies on 26 July, 1976 with mated queens

(B), queen cells (C) or supersedure queens

(D).
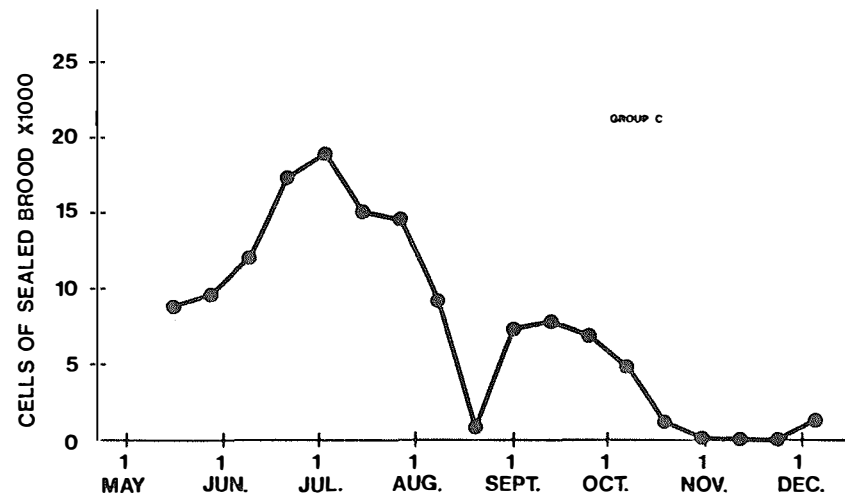
had stopped. Similar observations have been made by Free and Racey (1968) in England and by Moeller (1977) in the United States. They indicated that the queen's age is an important factor in determining the amount of brood reared by colonies in the fall.

Brood rearing did not decline as rapidly in 1976 as it had done in 1975. This problem was related to the sugar syrup fed to colonies in 1976. Brood rearing in 1976 resumed in most colonies in late November. Colonies which had been requeened appeared to be more inclined to rear brood than those which had not been requeened as requeened colonies produced significantly more brood between 24 November and 5 December, 1976.

6.4.3 Adult populations

Seasonal changes in adult populations are shown in Figures 6.5 and 6.6. Colonies tended to have larger populations in 1976 than in 1975. This may have been related to management practices as the addition of hive bodies to colonies was often delayed by one or two days in 1975 to accommodate data collection. Adult populations followed similar patterns prior to requeening, they decreased for the first twenty-four days after hiving and then increased to a maximum of approximately one hundred and eight days after hiving. Average worker bee populations continued to increase even after their queens had been removed and did not decline until after day 108. Had there not been a decrease in brood production between day 84 and day 96, adult populations may have increased until day 120. Requeening

Fig. 6.5   Seasonal changes in the adult population of honey

bee colonies initiated from 0.9 kg packages of bees

(A, control) and the influence of requeening

colonies on 28 July, 1975 with (B) mated queens,

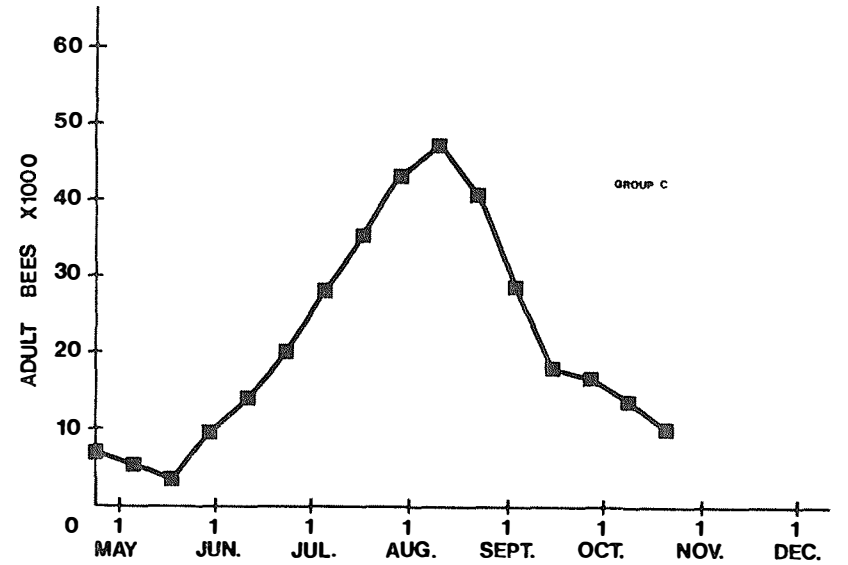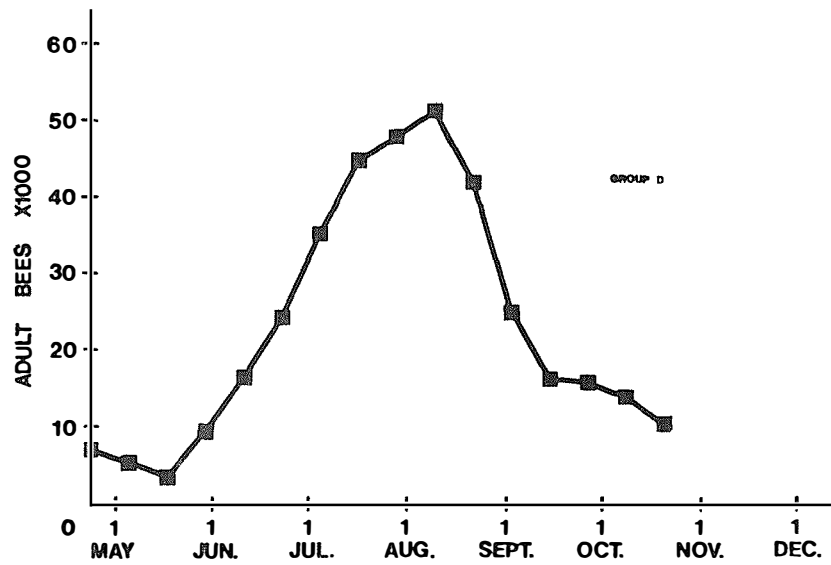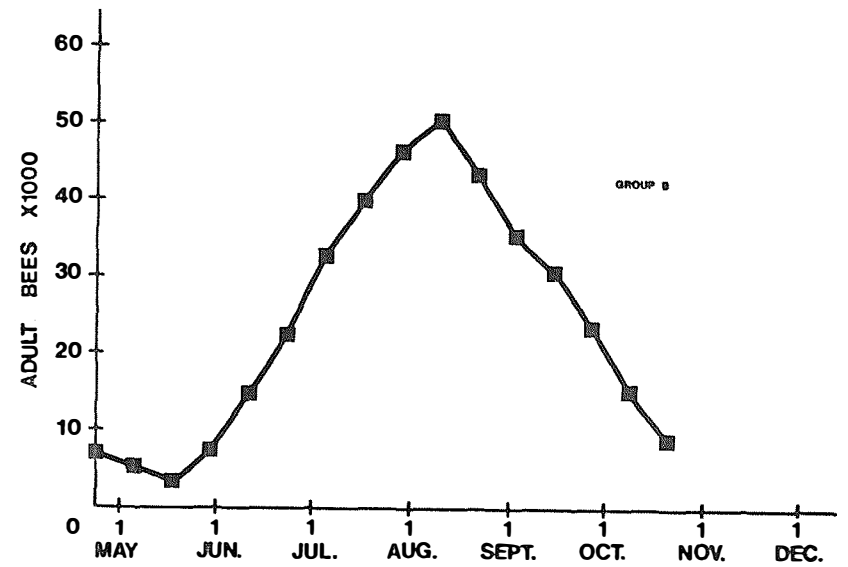(C) queen cells and (D) supersedure queens upon
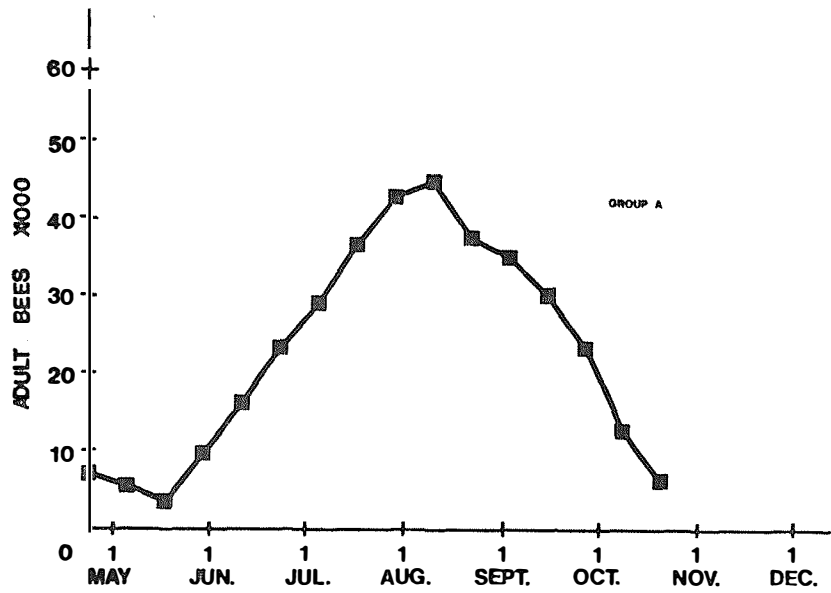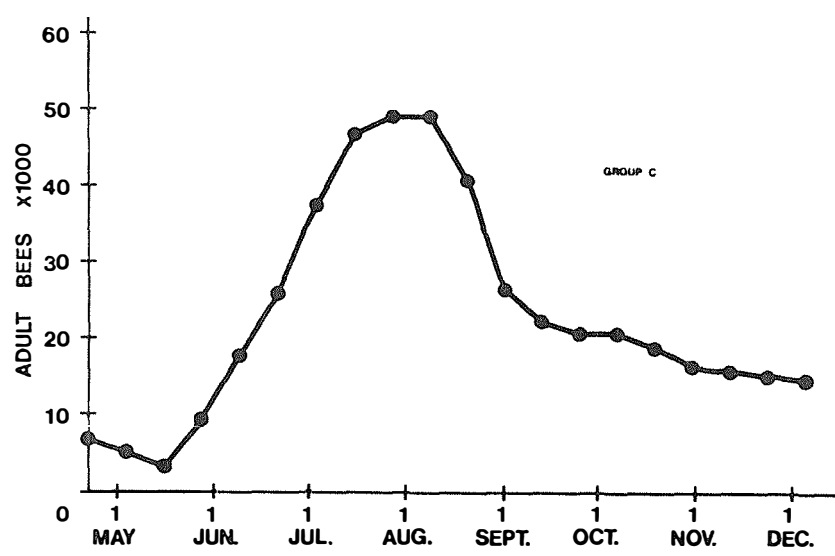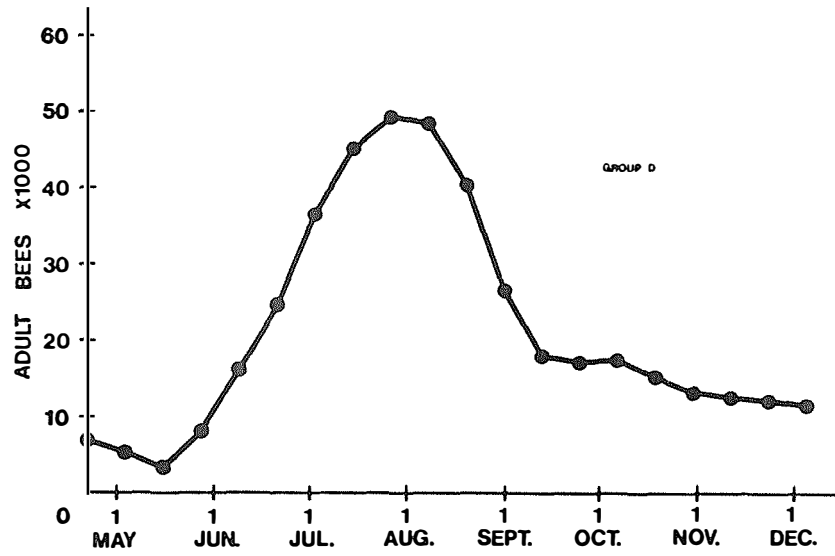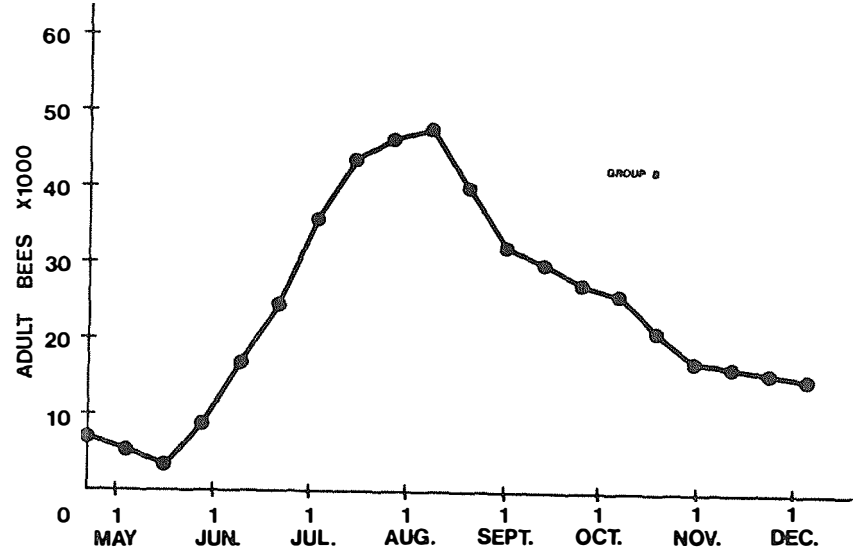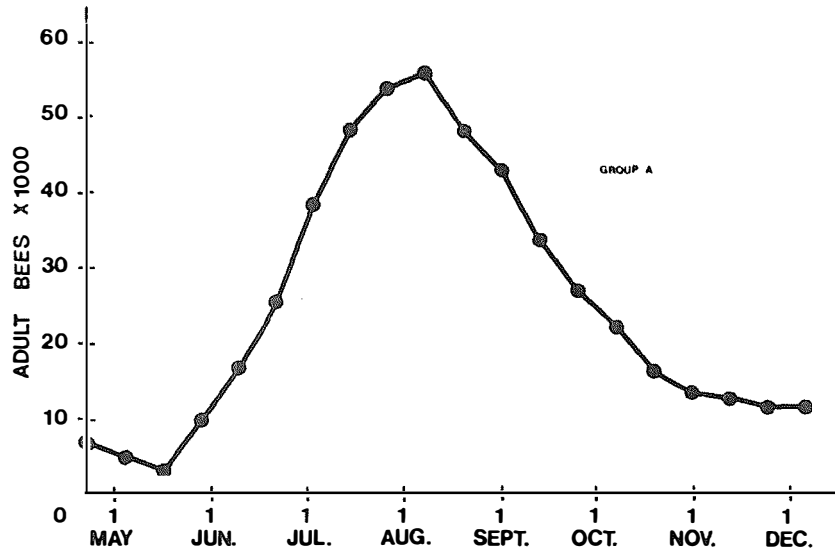
adult populations.

Fig. 6.6   Seasonal changes in the adult population of honey

bee colonies (A, control) and the influence of

requeening colonies on July 26, 1976 with mated

queens (B), queen cells (C) and supersedure queens

(D) upon adult populations.

increased the initial rate at which adult populations declined. Adult populations in treatments B, C and D declined in both years faster than did treatment A immediately after requeening. After the initial population decline, requeened colonies showed a lesser rate of decline than did treatment A. In 1976, adult populations in treatments A, B, C and D were numerically similar by early December. They contained approximately 1.2×10^4 bees. It appeared that once brood rearing had ceased within colonies there was a tendency for colony populations to converge towards a common numerical size. Adult populations declined from $5.0-6.0 \times 10^5$ bees in August to less than 1.5×10^4 bees by late November or early December, a decline of approximately seventy-five percent. If this is normal, it would seem that a method which could reduce colony populations after the nectar flow would be of significant economic value in reducing the amount of honey consumed by a colony. Although requeening reduced fall populations, a further reduction would seem possible without adversely affecting the size of the overwintering colony. Perhaps adult populations could be reduced by either killing some of the adult bees or splitting each colony in half to produce two colonies.

6.4.4 Implementation of Requeening

When colonies are to be requeened in the fall, timing is critical. If a colony is to rear its own queen or if queens emerging from queen cells are to be used in requeening colonies, requeening must be completed early enough to ensure that there will be good

mating weather and a plentiful supply of drones. However, requeening should not take place when a break in egg laying would reduce adult populations during the main honey flow. In most honey producing areas requeening should take place between the middle of July and the end of August (Richmond 1924; Gooderham 1926; Dyce and Morse 1974). Phillips and Demuth (1918a, 1918b) recommended that requeening be done at least two months before colonies are to be packed for winter or two months before the first killing frost. Under conditions found in Manitoba, fall requeening should take place between the end of July and the middle of September, depending upon whether colonies are requeened with mated queens, queen cells, or supersedure cells.

Fall requeening of colonies appears to be a reasonable approach to requeening honey bee colonies which are to be wintered. By re-queening in fall, a beekeeper can provide against old queens dying during the winter and early spring, and ensure that his colonies are headed with young queens for the next season. In addition, a beekeeper may be able to obtain a supply of queens reared under the ideal conditions found in the Canadian prairies during late June and early July. Unfortunately, fall requeening takes place at a time when many beekeepers are busy extracting honey and it is often difficult to locate queens in populous colonies. If fall requeening is to be feasible for commercial beekeepers it will be first necessary to find new and easier methods of locating the old queens.

6.4.5 Conclusions

Fall requeening of honey bee colonies (1) alters "normal" brood rearing patterns, (2) causes a shift in colony age distribution and (3) reduces fall populations without significantly altering the numerical size of the overwintering colony. It would appear that fall requeening may be a satisfactory method of providing colonies with a new queen.

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CHAPTER 7

Development of Honey Bee Colonies: III. **During Confinement to
Winter Quarters**

7.1 Summary

The development of honey bee colonies, while confined to winter
quarters,was observed from early December until mid March. Colonies
headed with fall-reared queens produced more brood during winter and
were more populous in the spring than colonies with queens which had
been present for an entire season.

7.2 Introduction

Canadian beekeepers import large numbers of package bees
annually from the United States to replace colonies killed the pre-
vious fall. However, with the replacement value of these bees
increasing significantly in recent years, many beekeepers have
altered their management practices and are now overwintering their
colonies. Colonies wintered outdoors are either arranged singly or
in groups and encased with insulation (Burke and Adie 1952; Dyce and
Morse 1974; Gooderham 1926) while those wintered outdoor are placed
inside a dark air-conditioned room for the winter (Phillips and
Demuth 1918; Gilbert 1939). When colonies are inspected in spring,
there are often large differences in colony populations; some
colonies may have 2 or 3 kg while others may have less than 0.2 kg.
As a result there is a growing interest about what factors affect

colony populations during winter.

Apart from temperature regulation in the colony during winter (Phillips 1914; Wilson and Milum 1927; Bundel 1948; Farrar 1963; Free and Simpson 1963; Owens 1971) and periodic observations on brood rearing (Jeffree 1956; Farrar 1963; Avitable 1978) and death (Schua 1955) little information is available concerning changes in honey bee population colonies during winter. The present study was undertaken to record any changes in birth and death rates within honey bee colonies during the winter and the effect such changes would have upon the age structure of an overwintering colony.

7.3 Methods and Materials

Twenty-one honey bee colonies used in previous experiments (see Chapter 6) were overwintered in single chamber Langstroth hives in a dark air-conditioned room at $6 \pm 2°C$. Seventeen colonies had previously been requeened at the end of July, using (B) mated queens, (C) mature queen cells or (D) queens reared from eggs while other colonies (A) retained their original package queens. The data from each of the four groups were therefore considered separately.

Colony populations were estimated by the procedure described in Chapter 3. Worker bee survival and brood production of individual colonies were determined from measurements taken at twenty-four day intervals. Because of problems associated with marking emerging bees during winter, worker bee survival was considered to be similar to that observed for the last group of bees marked in October.
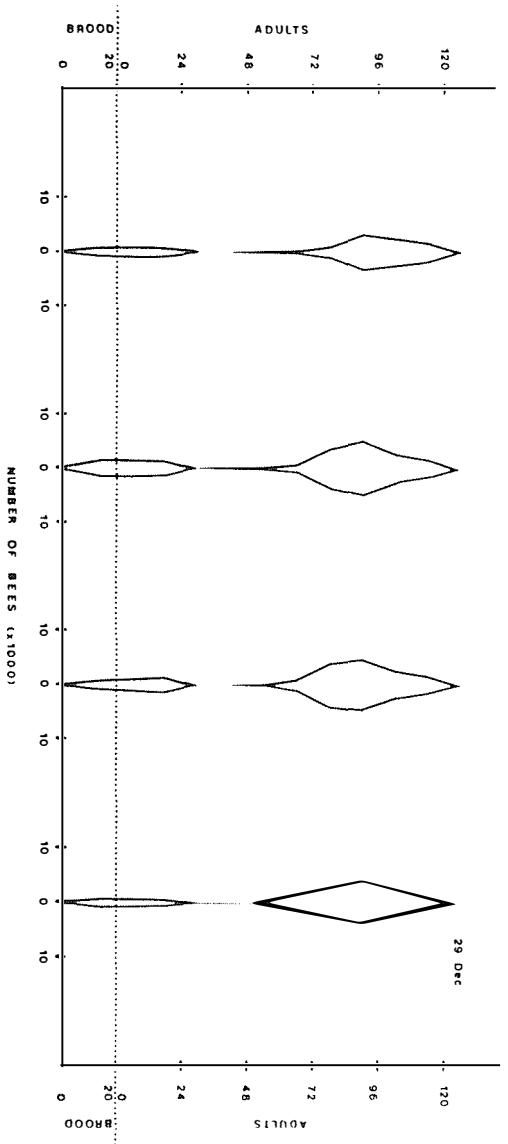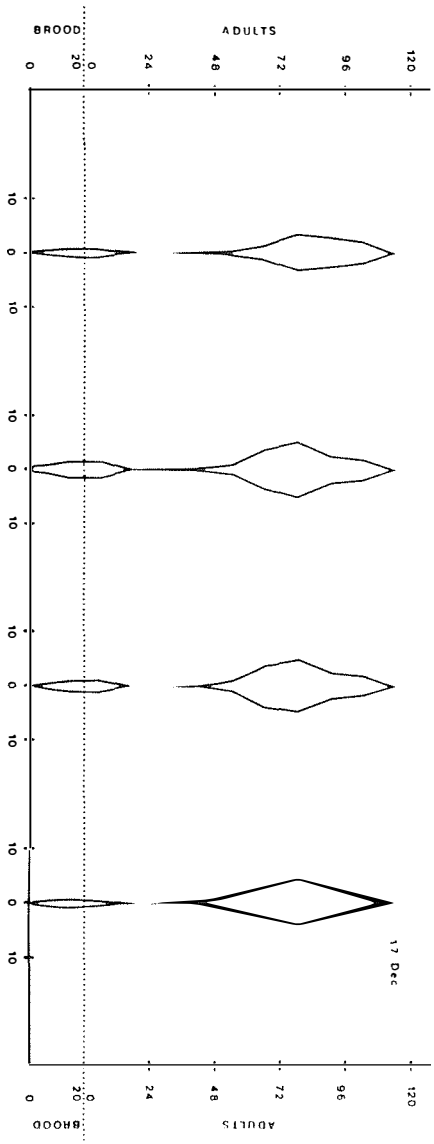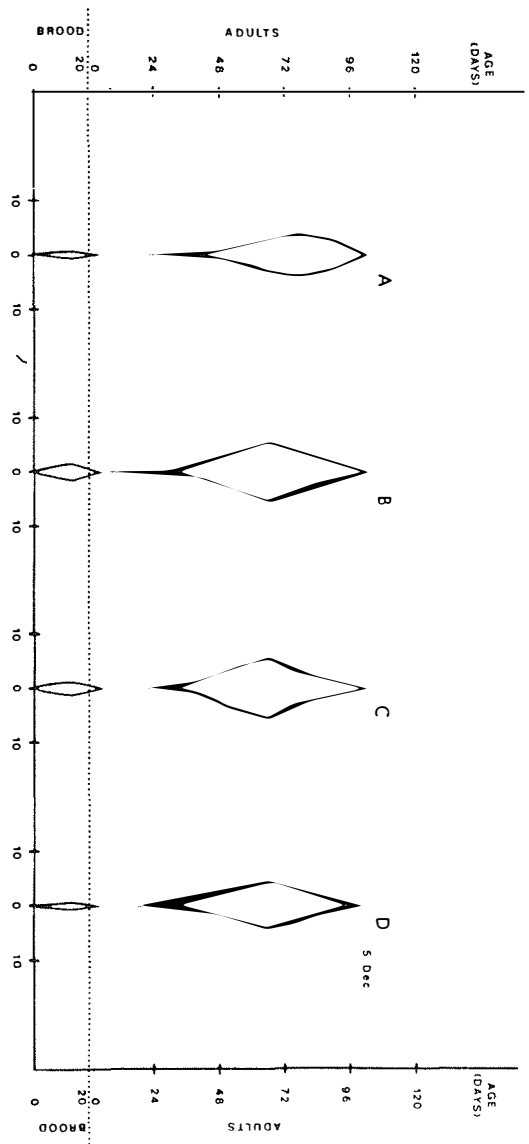
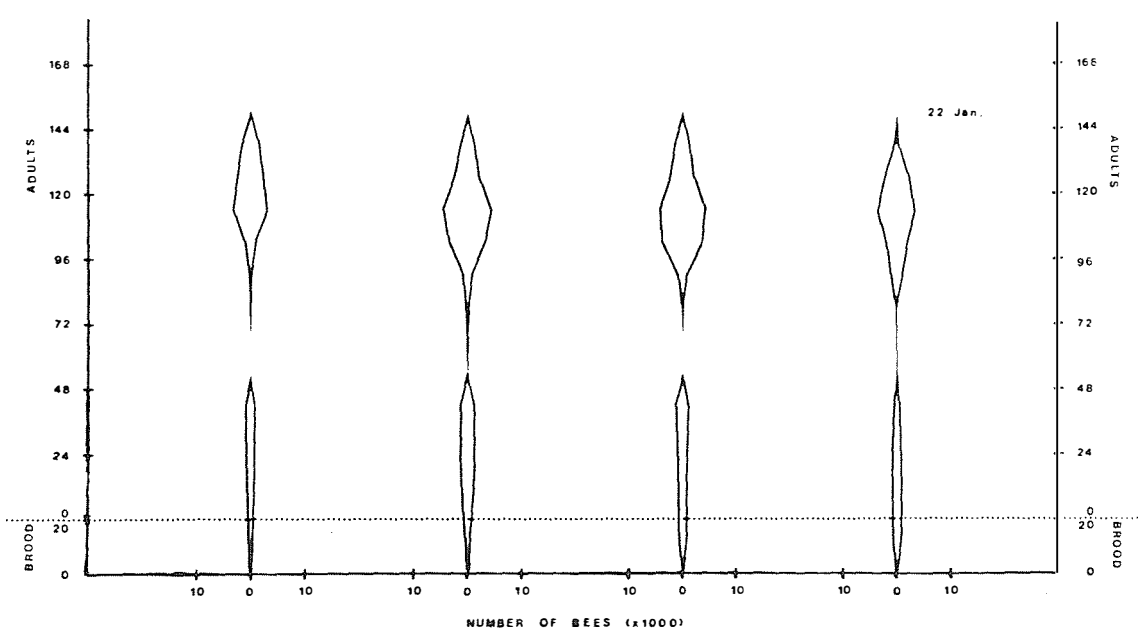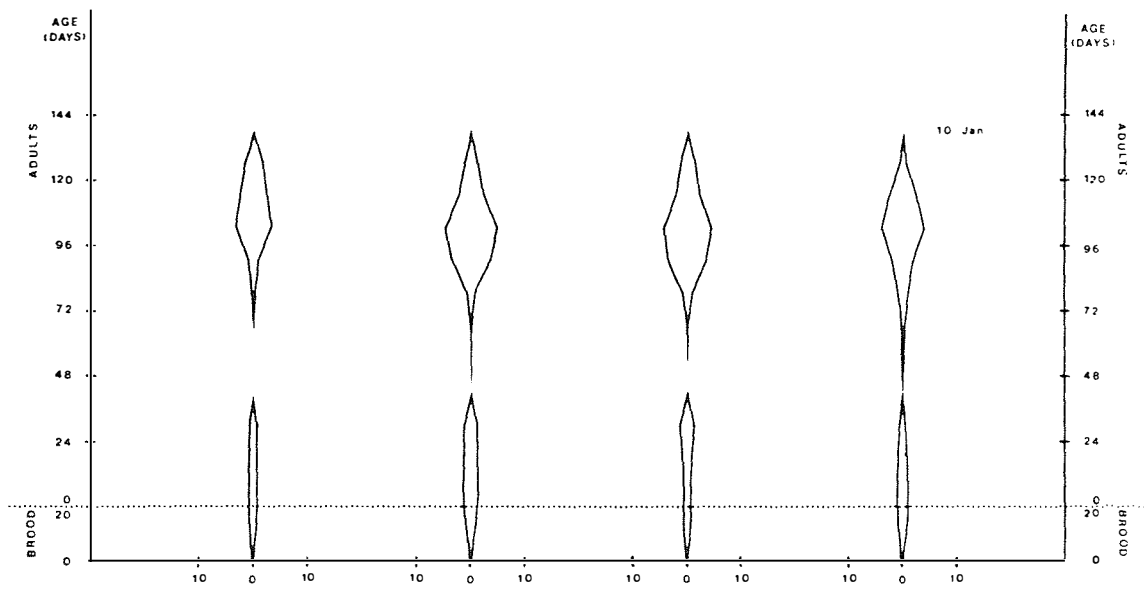## 7.4 Results and Discussion

7.4.1 Age structure

The age structure of the overwintering honey bee colony is shown in Figure 7.1. Colony age structure changed considerably from early December until mid-March. In December very few bees were more than ninety-six days of age, while in March fifty-eight percent of the worker bees were in excess of 144 days of age. Approximately one-half of the colonys' population in March were reared during the winter while the other one-half were reared in August, September or October. The "inverted pyramidal" age structure in Figure 7.1 was indicative of an aging population with few bees being reared to replace those which were dying. Consequently, the overwintered population was likely to be unstable and subject to the type of population collapse beekeepers refer to as "spring dwindling."
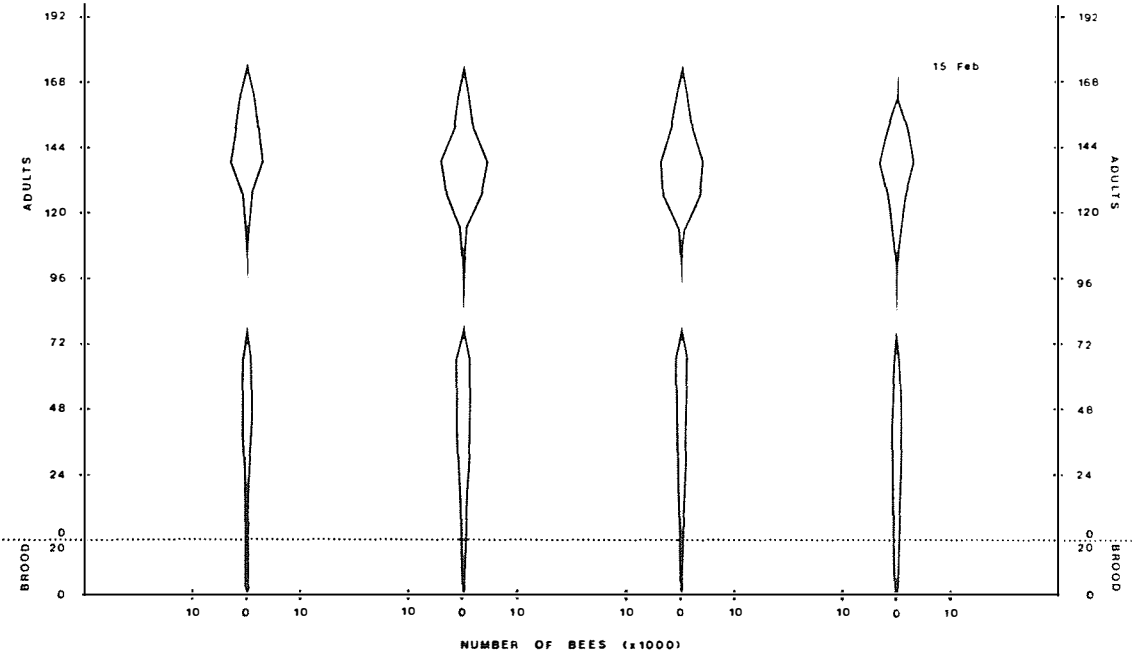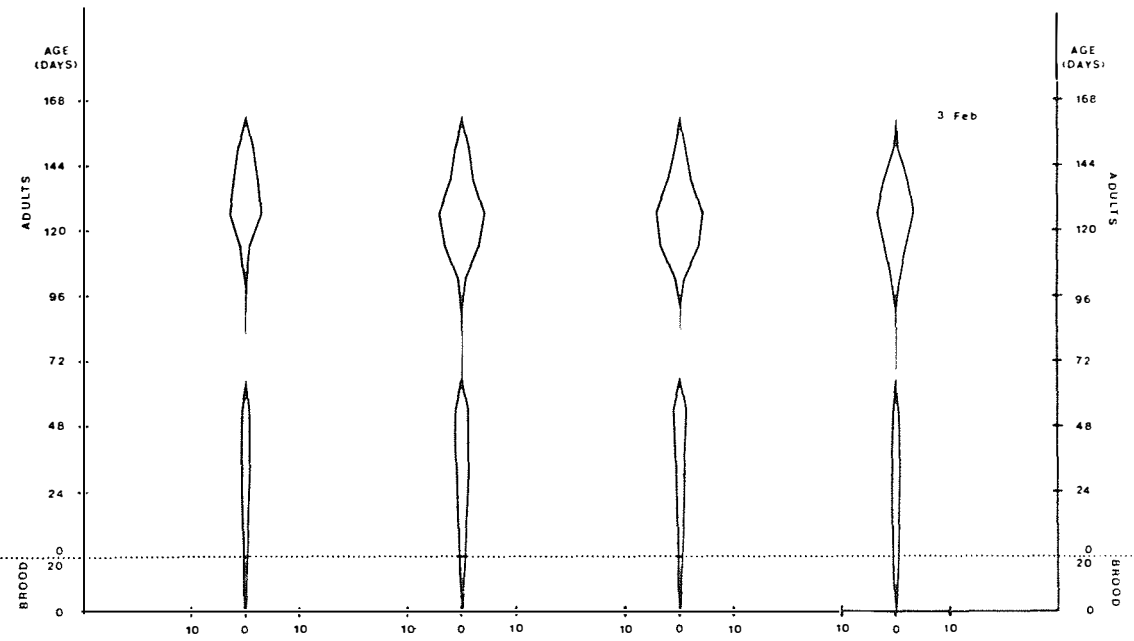
Although requeening has been shown to alter fall population age distributions (see Chapter 6) its effect during winter was less dramatic. Requeened colonies contained a larger proportion of young bees than did those which had not been requeened. The difference was largely related to small differences in brood production during the winter.
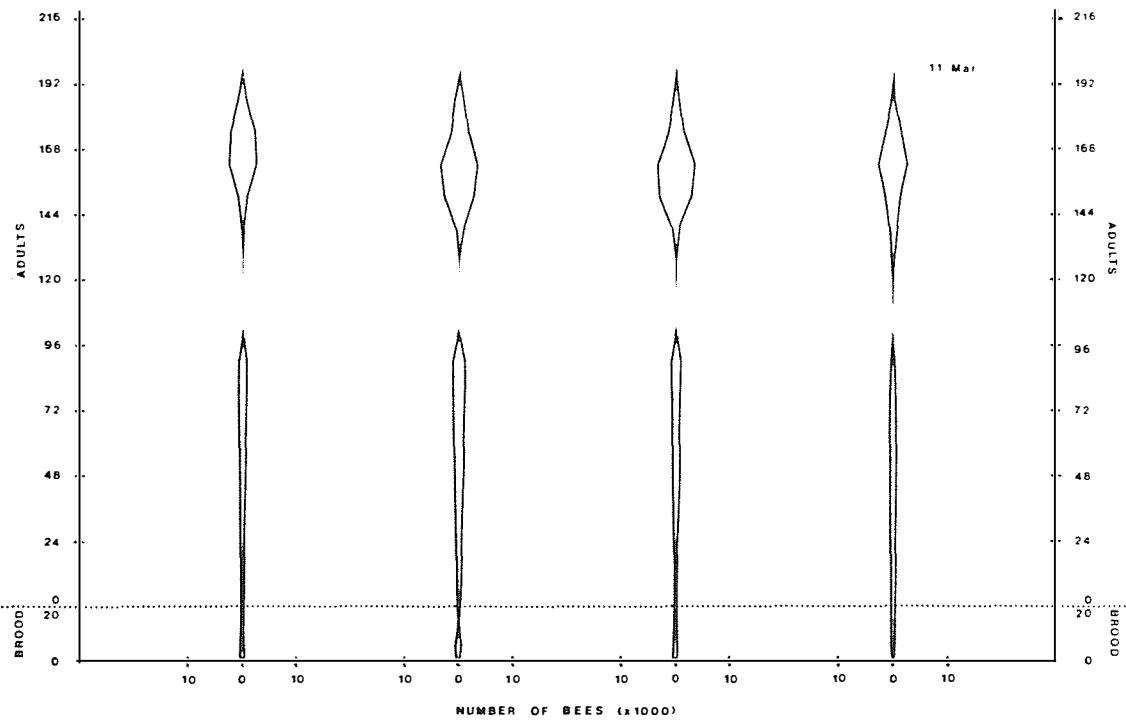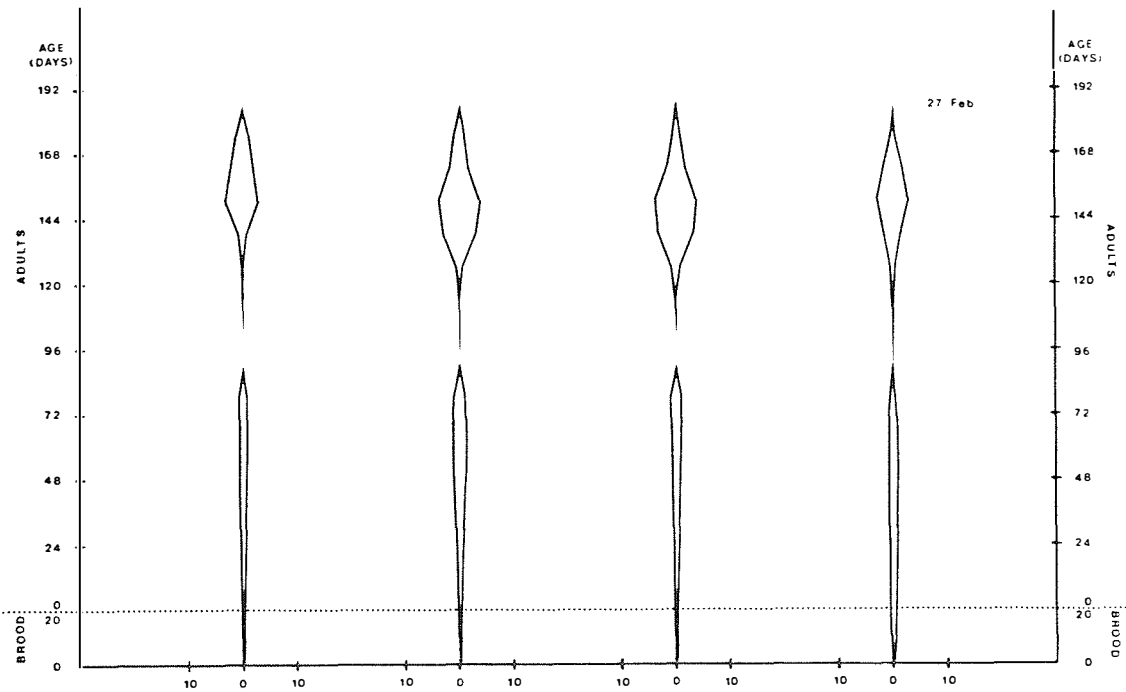
Fig. 7.1   Age structure of honey bee colonies during

confinement to winter quarters (A, control) as

influenced by requeening on 26 July, 1976 with

mated queens (B), queen cells (C) and supersedure

queens (D).

AGE (DAYS)

ADULTS

144
120
96
72
48
24
0

BROOD
20
0

10 Jan

10 0 10   10 0 10   10 0 10   10 0 10

168
144
120
96
72
48
24
0

22 Jan.

10 0 10   10 0 10   10 0 10   10 0 10

NUMBER OF BEES (x1000)

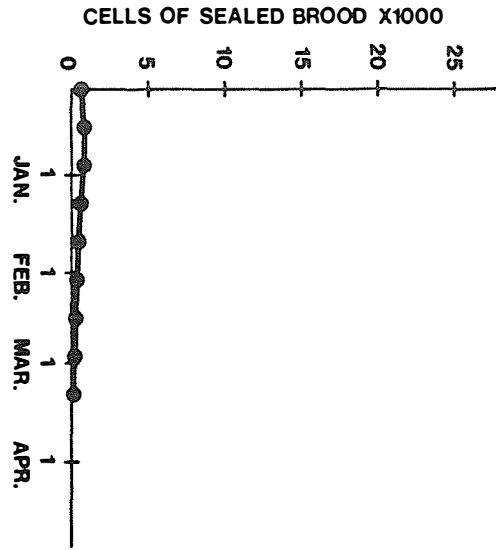NUMBER OF BEES (x1000)

NUMBER OF BEES (x1000)

7.4.2 Sealed Brood

Production of sealed brood while colonies were confined to winter quarters is illustrated in Figure 7.2. Seventeen of the twenty-one colonies observed contained pupae on 5 December when they were placed into winter quarters. The number of eggs, larvae and pupae were relatively constant from December until mid-January. It then declined. A slight increase in eggs and larvae was evident in mid-March before colonies were removed from winter quarters. The increase appears to coincide with an increase in room air temperature associated with warm external temperatures. Drone brood was occasionally observed being reared in worker cells during the winter.
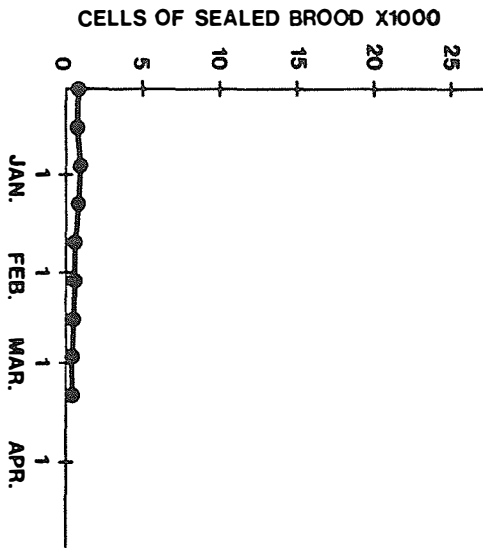
It is unclear why brood rearing should decline during the winter. If brood rearing was strongly associated with changing photoperiod as suggested by Kefuss (1978) and Avitabile (1978) one would have expected brood rearing to have decreased much sooner and to remain at a low level while the bees were confined to winter quarters. Avitabile (1978) observed brood to increase between January and March in colonies wintered outdoors. It may be that decreasing brood production observed in this study was associated more with (1) decreasing stores of honey or pollen, (2) a declining and/or aging adult population, (3) accummulation of feces in the intestinal tract of worker bees, and/or (4) adapting to a constant room temperature, than changing photoperiod.

The queen's age was observed to have an influence on winter brood production. Colonies with young queens produced more brood
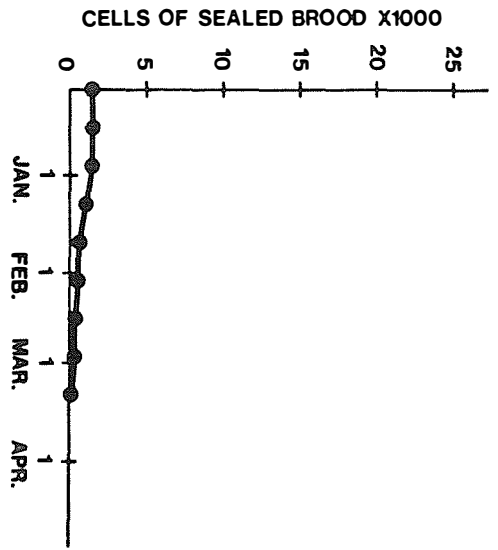
Fig. 7.2   Winter brood rearing activities of honey bee

colonies (A, control) as influenced by requeening

colonies on 26 July, 1976 with mated queens (B),

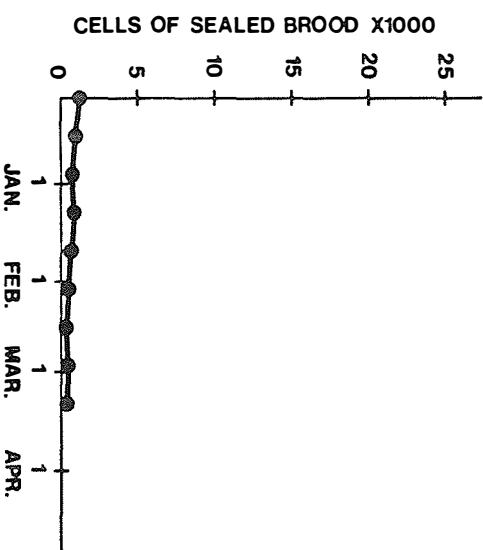queen cells (C) and supersedure queens (D).

CELLS OF SEALED BROOD X1000

CELLS OF SEALED BROOD X1000

CELLS OF SEALED BROOD X1000
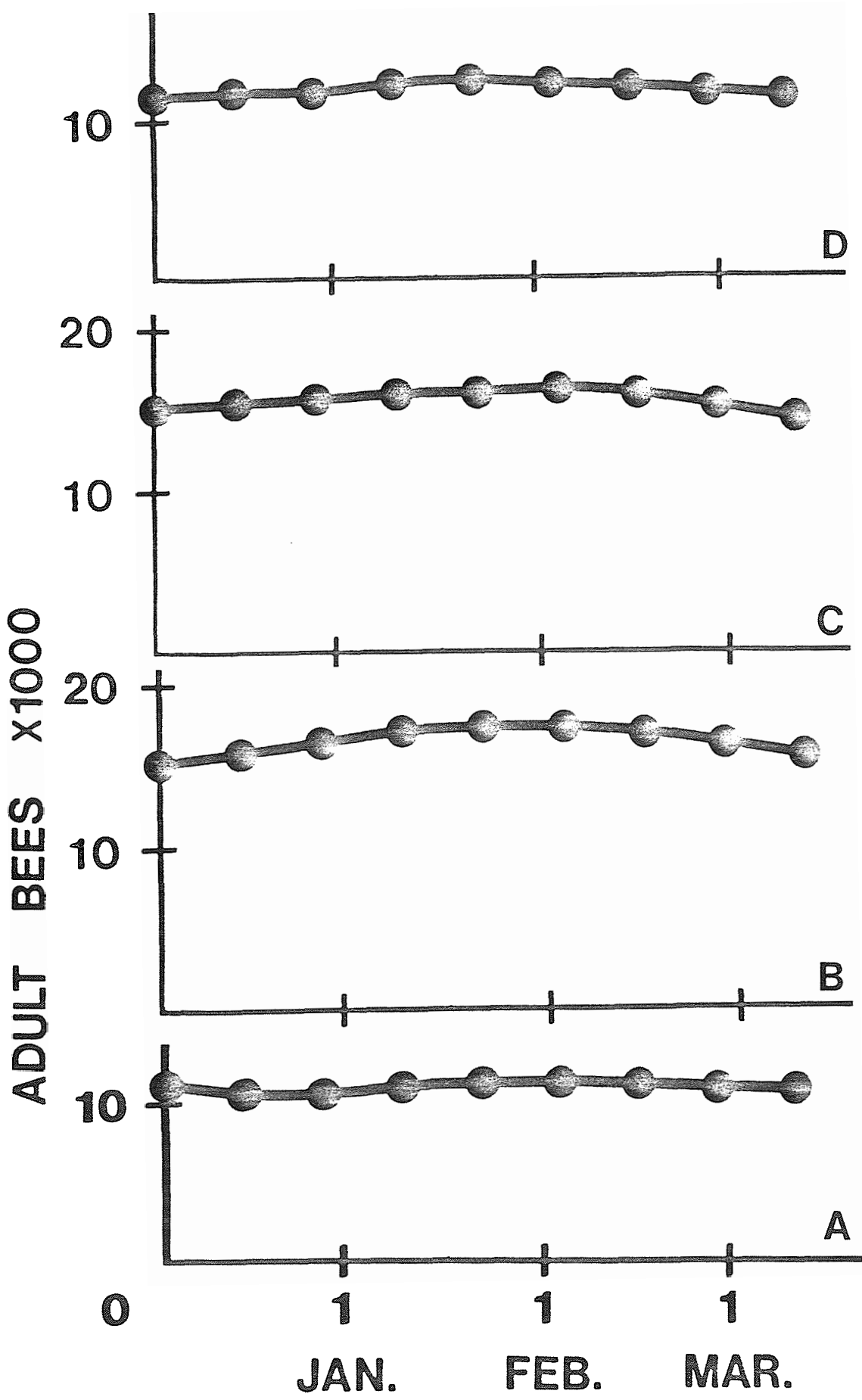
CELLS OF SEALED BROOD X1000

GROUP D

GROUP A

GROUP C

GROUP B

Fig. 7.3 Changes in adult honey bee populations during

winter (A, control) and the influence of

requeening colonies on 26 July, 1976 with mated

queens (B), (C) queen cells (C) and supersedure

queens (D).

during the winter than did those which were headed with queens which had been in the colonies for an entire season. However, these differences were not significantly different at the 5 percent level. Given the variation between colonies a much larger sample size would be required to show statistically significant differences between the various treatments.

Further study is required to determine why brood rearing declined during the winter and how it might be regulated.

7.4.3 Adult populations

Adult population trends are presented in Figure 7.3. The average adult population during the first week of December was $1.2 \times 10^3 \pm 0.1$ for requeened colonies and $1.3 \times 10^3 \pm 0.2$ for colonies which were not requeeneed; this difference was not statistically significant. During the winter adult populations increased slightly, followed by a gradual decline. The adult population was only slightly smaller in March than it had been in December. Colonies reared almost enough bees during the winter to compensate for those which had died. Adult bee mortality rates during the winter were relatively constant. The death rate increased slightly from December to March. This may indicate that a colony's ability to maintain a favourable environment within the hive is affected by long periods of confinement to winter quarters.

7.5 Conclusions

Honey bee colonies confined to winter quarters reared small

quantities of brood through the winter. The amount of brood reared decreased towards spring. Because of the brood being reared during the winter adult populations increase during the winter. However, as spring approached, a slight increase in the adult death rate coupled with decreasing brood rearing results in colony populations being slightly smaller than they were when the colonies were placed into winter quarters. Had brood rearing not occurred during the winter in the colonies their adult populations would have been significantly smaller than were observed in this study. It seems that brood rearing by colonies during the winter may be something that should be promoted if colonies are to maintain large adult populations during the winter.

7.6 References

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CHAPTER 8

Development of Honey Bee Colonies: **IV. After Confinement to Winter**

Quarters

8.1 Summary

The development of honey bee colonies following their confine-
ment to an overwintering facility for fifteen weeks was recorded.
Colonies which had been requeened the previous fall generally had
larger populations throughout the season than did colonies that
contained queens which had been active the previous summer.

8.2 Introduction

Honey bee colonies can be maintained for more than one season if
one ensures that they have adequate food, a healthy fertile queen and
protection from adverse weather conditions (Furgala 1975). In recent
years, the use of overwintered colonies has become more prevalent in
the Canadian Prairie Provinces than they once were. Since 1974, the
number of overwintered colonies in Manitoba, Saskatchewan and Alberta
has more than tripled and it is estimated that there were
approximately 100,000 honey bee colonies overwintered in 1979-1980.
Much of the increase can be attributed to the rapidity with which
these colonies are reported to develop and the large honey crops they
collect and the annual cost of replacement colonies. The present
study was undertaken to investigate the seasonal changes in colony
age structure, brood rearing and adult populations of overwintered

colonies after their removal from winter quarters and the effect fall requeening might have upon those changes.

8.3 Methods and Materials

Twenty single-chamber Langstroth hives, well supplied with pollen and honey, were overwintered for fifteen weeks in a dark air-conditioned room maintained at $6 \pm 2°C$ (Chapter 7). Seventeen of the colonies used contained young queens which had been introduced into the colonies in late July or early August of the previous year. Colonies were removed from the building during the evening and arranged in a circular pattern on bare ground. They were placed near a wind break to minimize loss and drift of bees (Jay and Harris 1979).

Colony populations were determined by the procedure outlined in Chapter 3 i.e. sealed brood was measured by placing a calibrated grid over brood combs (Nolan 1925, Moeller 1961) and adult bee survival was determined at twelve day intervals from worker bees marked at emergence with fluorescent paint (see Chapter 2). Adult bees were not marked between 11 March and 16 April, because weather conditions during this period did not allow bees to be marked. Hence, adult worker bee survival between 11 March and 16 April was considered to be similar to that observed for worker bees marked 28 April.

Additional hive bodies were supplied as required. Empty combs were placed in the brood area, between May 22 and August 2 to provide adequate space for brood rearing.
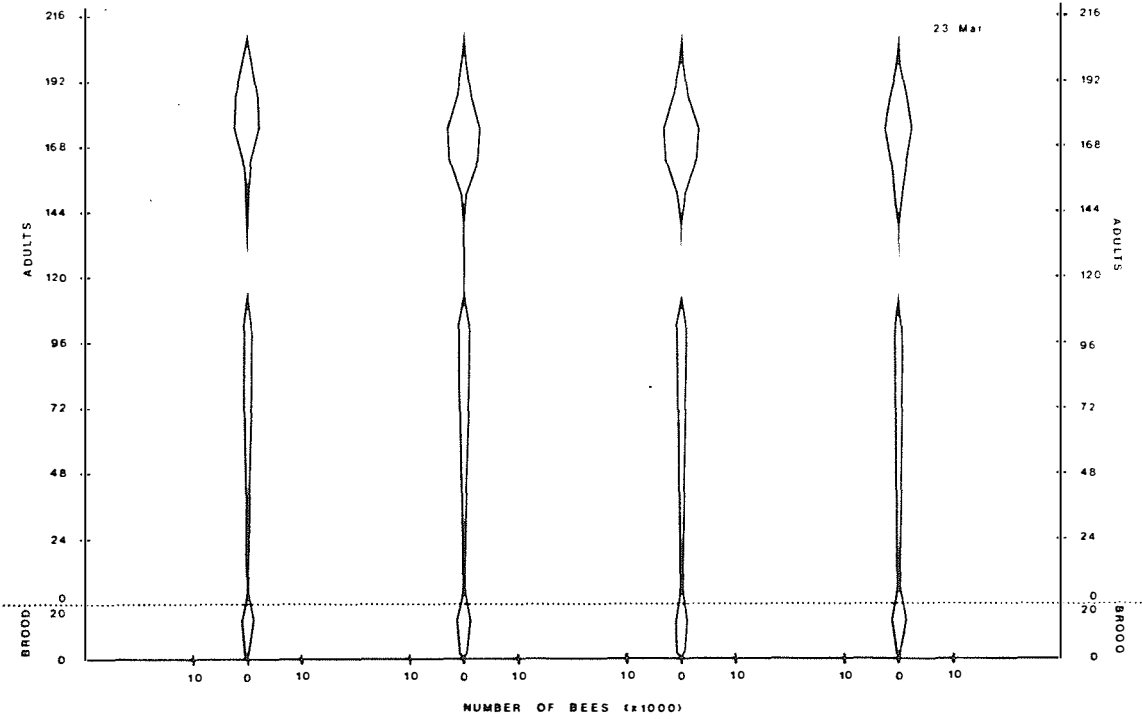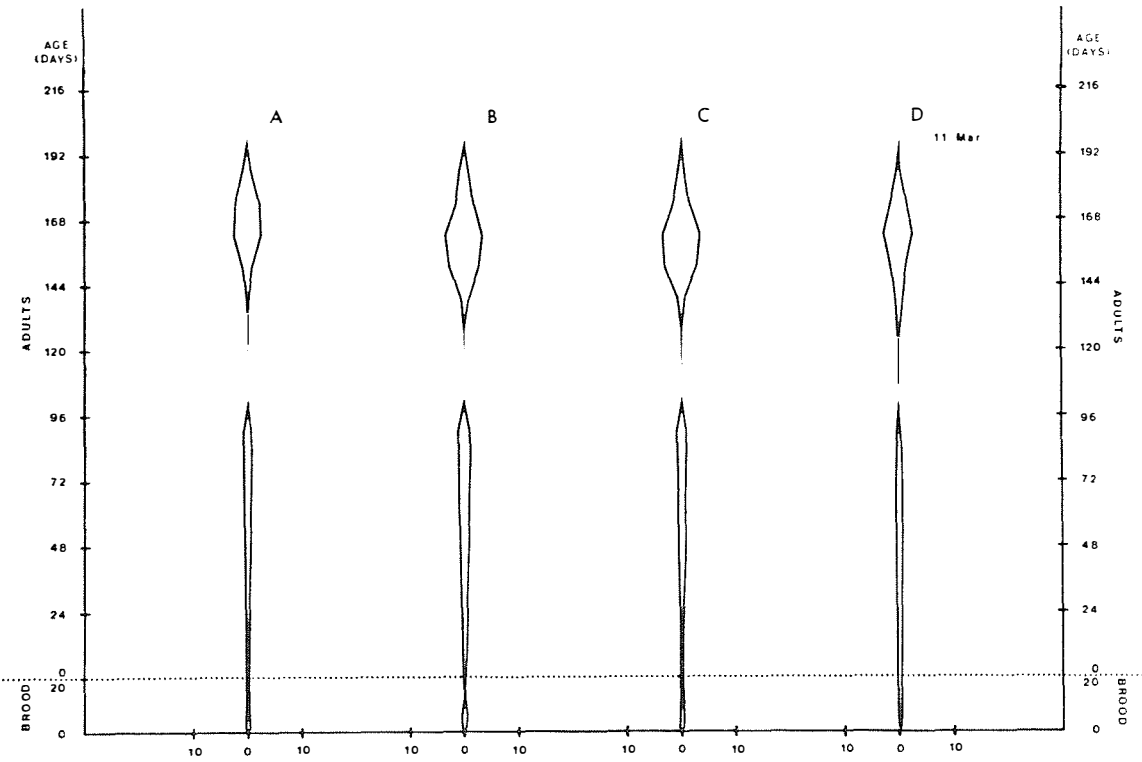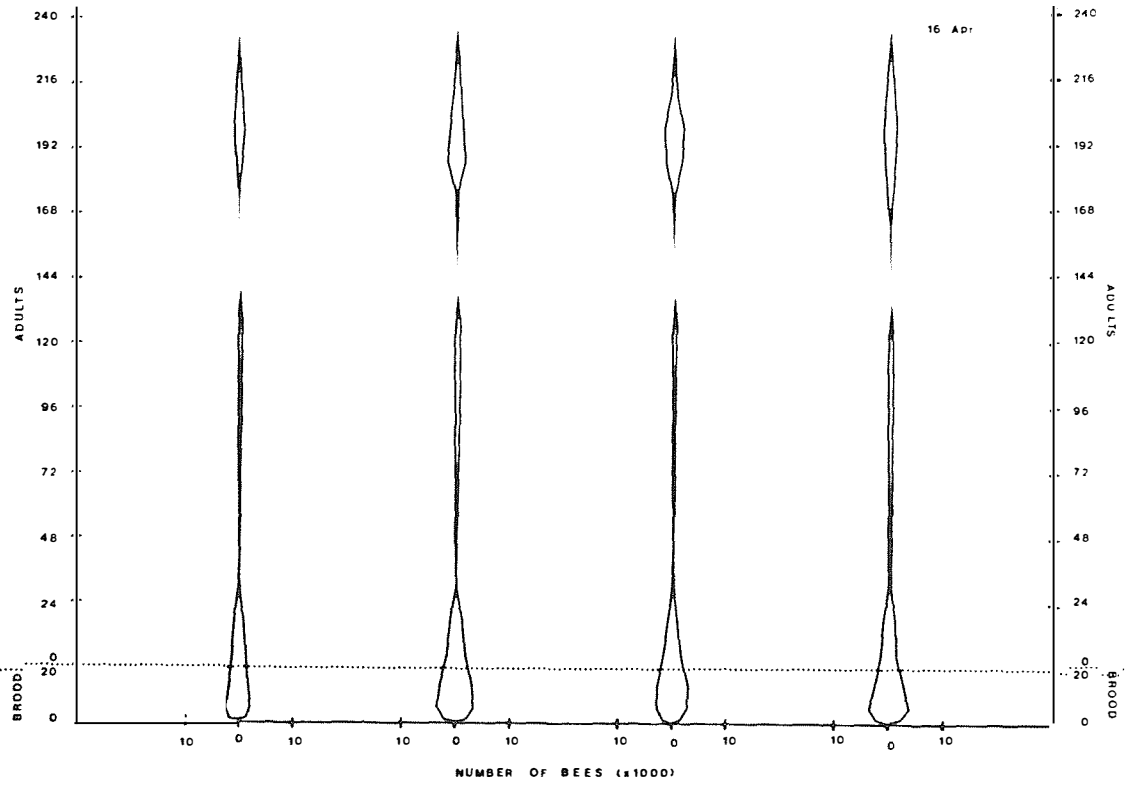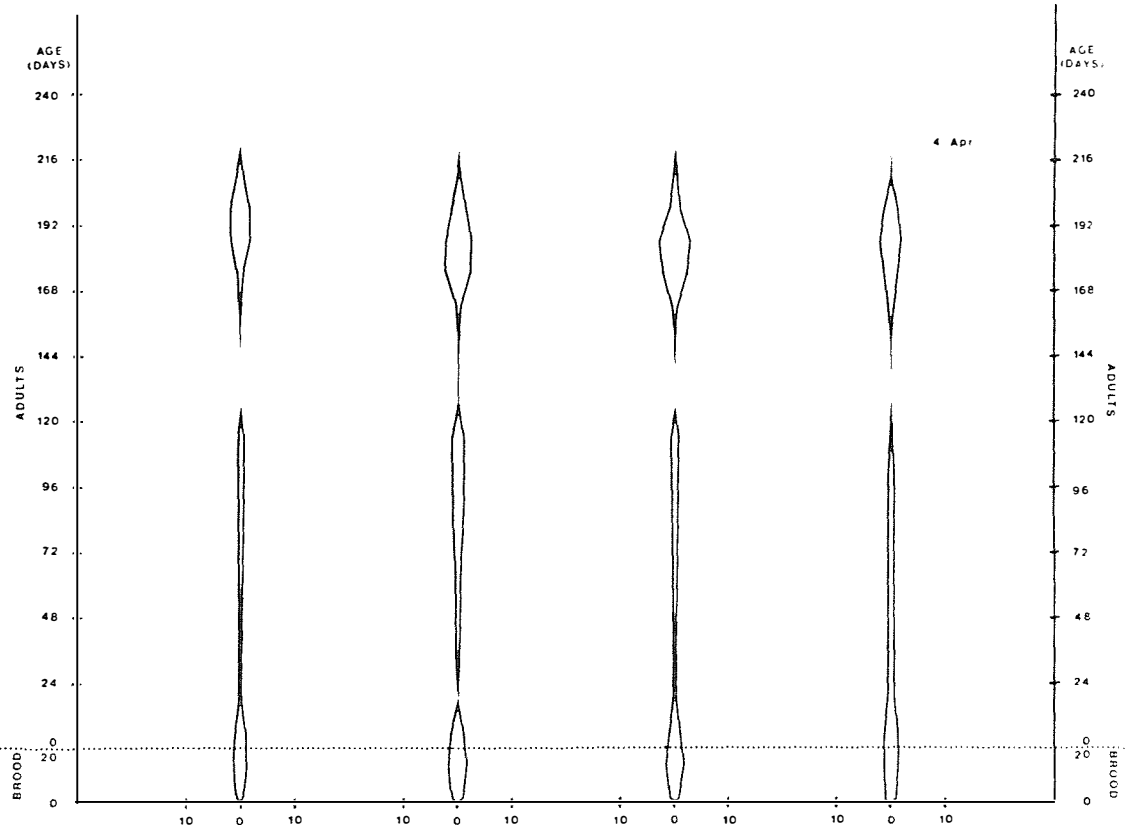
8.4 Results and Discussion
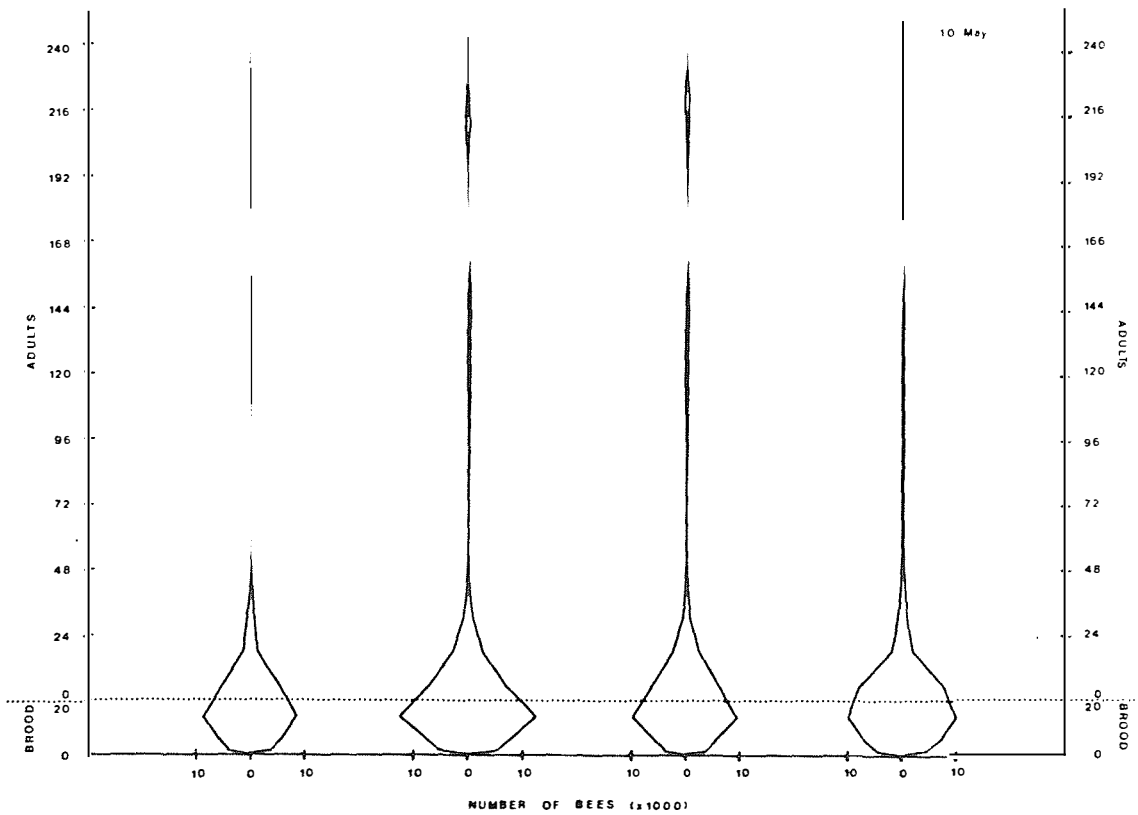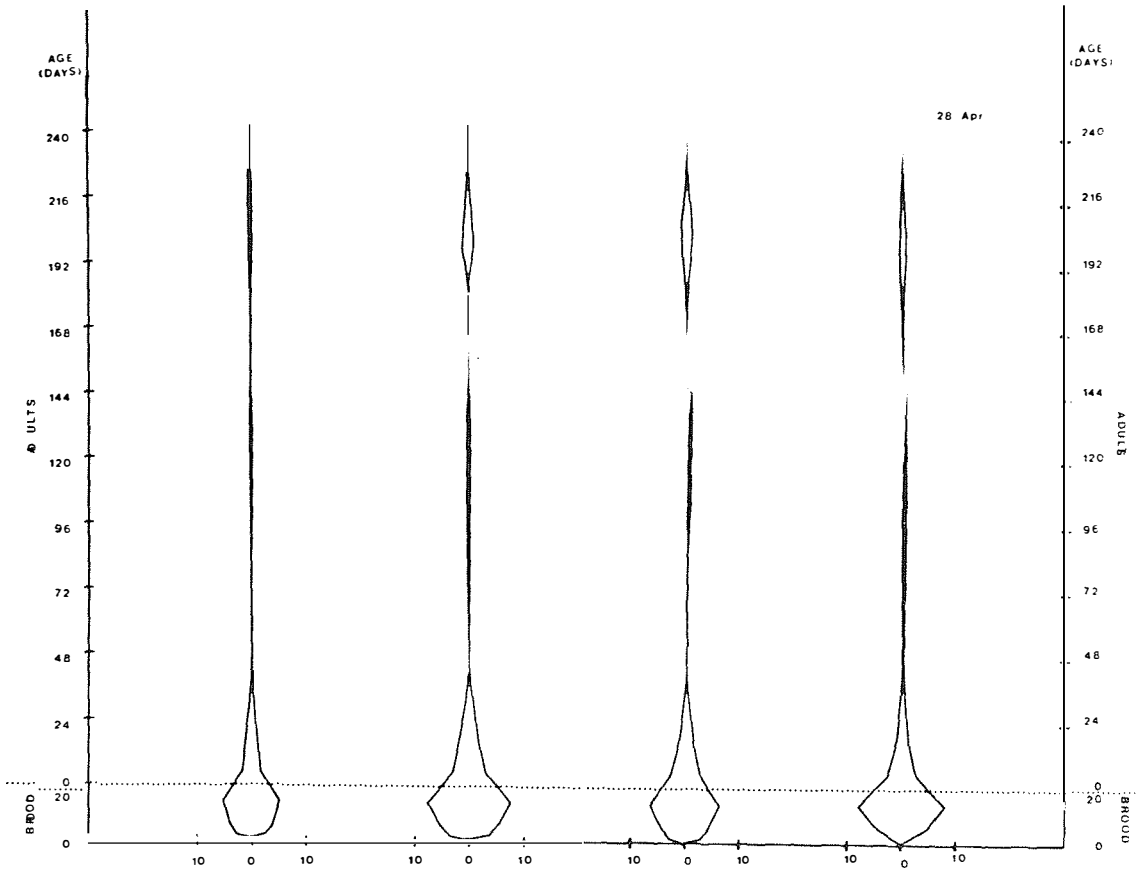
8.4.1 Colony Age Structure

Colony age structure from 11 March to 2 August is presented in Figure 8.1. Since colonies contained queens which differed with respect to their age and method of introduction (see Chapter 6) each group was considered separately. Overwintered colonies were composed predominantly of bees over seventy-two days of age when they were removed from winter quarters. A large population of old bees and a small population of young bees was indicative of an aging population with few bees being reared to replace those dying. Because there were few replacement bees being reared in April and March, a rapid decline in the adult population would appear to have been predictable colonies with free flight. Because there were few replacement bees being reared in March and April and because bees from colonies with free flight have higher mortality rates than those confined to hives (Fukuda and Seckiguchi 1966), a rapid decline in the adult population would appear to have been predictable.
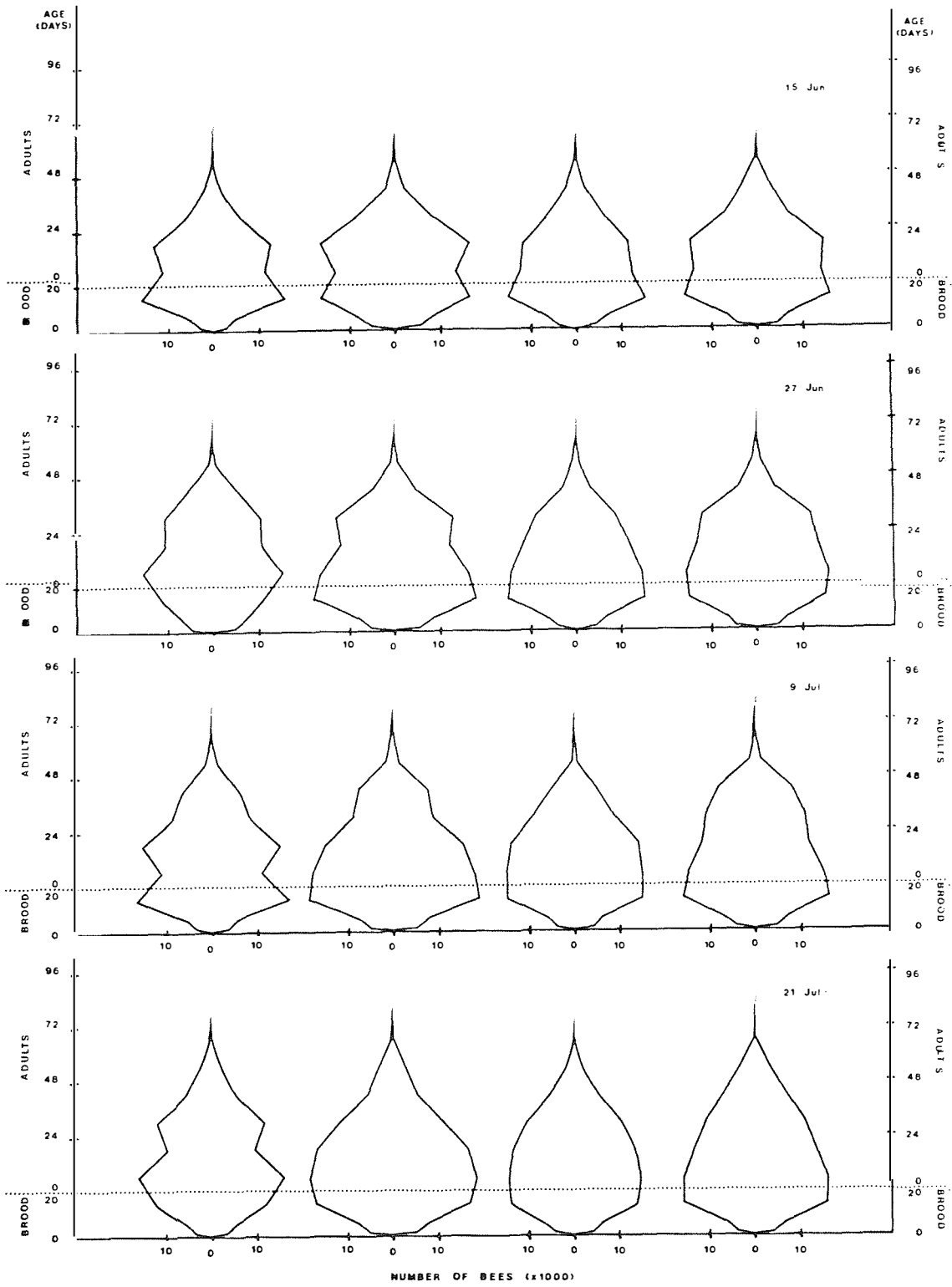
Between March and early July colony age distribution changed considerably. In July, there were few bees older than seventy-two days. The majority of the adult bees were less than thirty-six days old. The importance of encouraging colonies to rear large amounts of brood can be deduced from the summer age distribution, for if brood production is reduced at some period colony adult population increase may be postponed. For example, the well defined indentation in colony age structure observed on 15 June which was related to a reduction in the number of adult bees entering a particular age
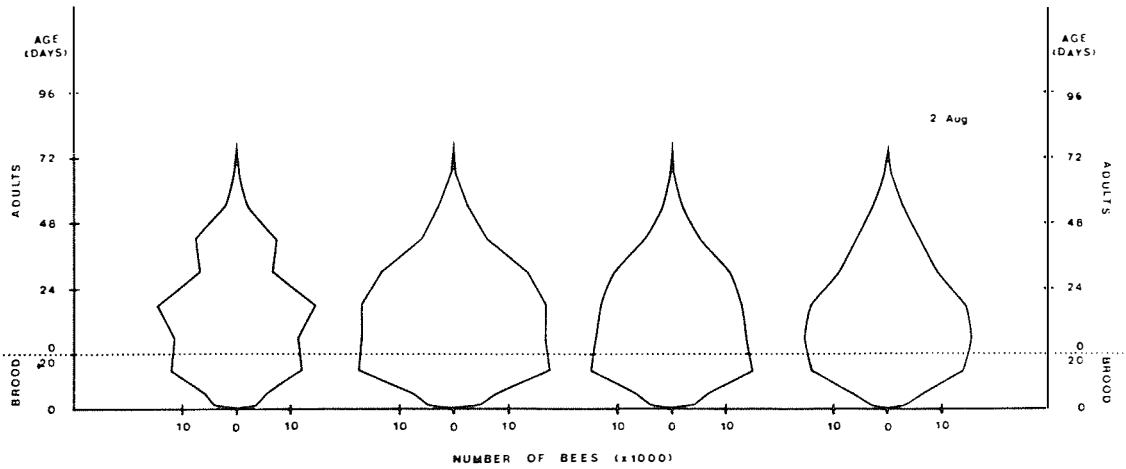
Fig. 8.1 Seasonal changes in the age distribution of worker

honey bee populations in overwintered honey bee

colonies (A-D) and the effect of requeening

colonies on 26 July, 1976 with mated queens (B),

queen cells (C) and supersedure queens (D).

NUMBER OF BEES (x1000)

NUMBER OF BEES (x1000)

AGE
(DAYS)

AGE
(DAYS)

28 Apr

240

240

216

216

192

192

168

168

144

144

ADULTS

ADULTS

120

120

96

96

72

72

48

48

24

24

0
20

0
20

BROOD

BROOD

0

0

10   0   10   10   0   10   10   0   10   10   0   10

10 May

240

240

216

216

192

192

168

166

144

144

ADULTS

ADULTS

120

120

96

96

72

72

48

48

24

24

0
20

0
20

BROOD

BROOD

0

0

10   0   10   10   0   10   10   0   10   10   0   10

NUMBER OF BEES (x1000)

NUMBER OF BEES (x1000)

class, could be traced to the reduced brood rearing in early May (Fig. 8.2).

Seasonal trends in the ratio of brood to hive bees were different to that previously observed (see Chapter 5). In overwintered colonies the optimum ratio was maintained for a longer period of time than observed in package colonies (Jay 1974; Chapter 5). Brood did not decrease as the forager population increased as previously observed (see Chapter 5) since adequate brood space was provided. This may be directly attributed to the author placing of empty combs in the brood area and thus providing space for the queen to deposit eggs.
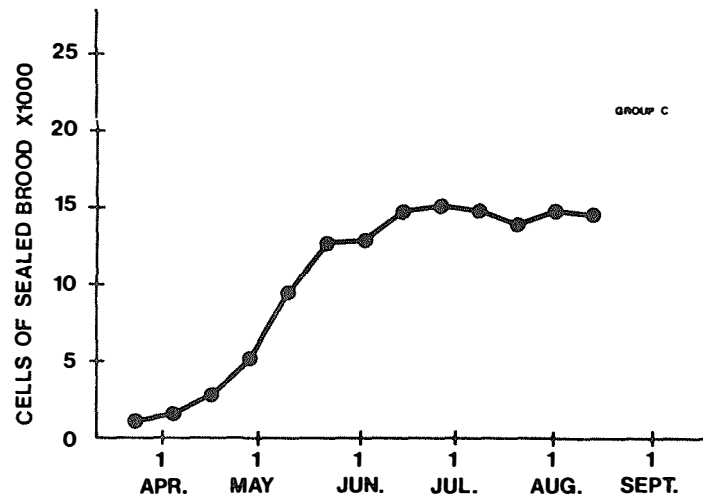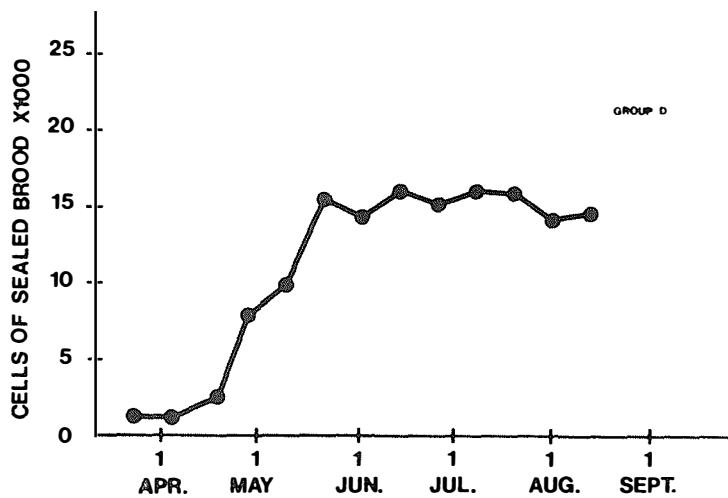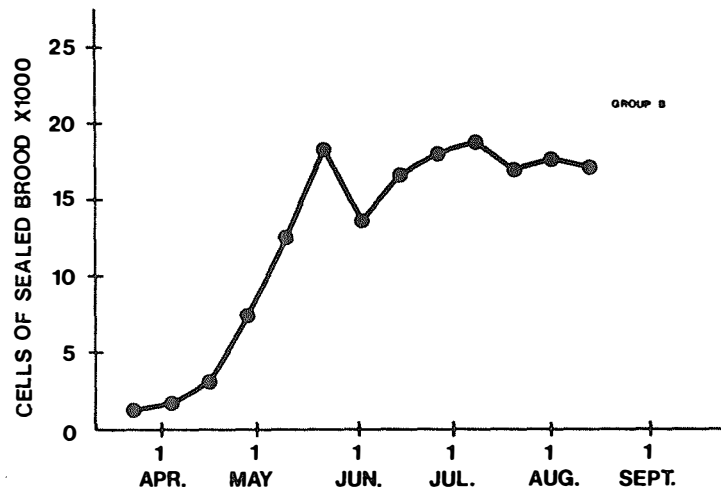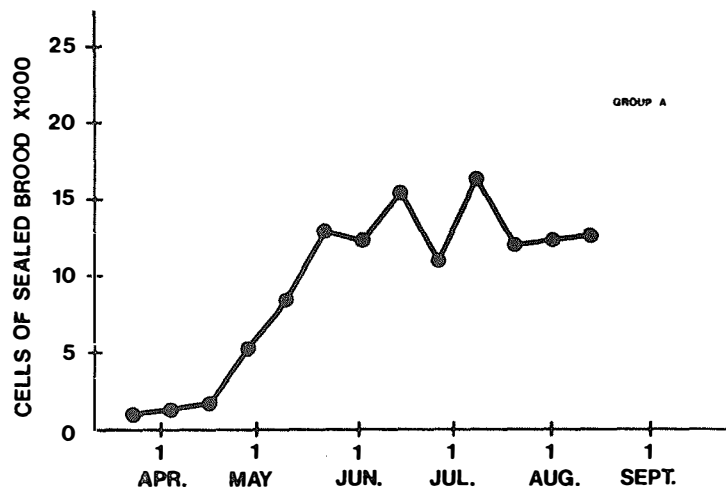
Overwintered colonies had more bees of foraging age during the honeyflow than did colonies developing from 0.9 kg packages of bees (see Chapter 5). This seems to be related to the high brood rearing found in overwintered colonies.

A comparison of colonies in treatment A, B, C and D indicates that the requeened colonies tended to develop faster and to attain larger populations than those which were not requeened, although there was considerable variation within each group.

8.4.2 Brood

The seasonal brood rearing curves of the overwintered colonies are presented in Figure 8.2. Brood rearing trends were similar in various treatments in the initial phases of colony growth. Brood rearing increased rather slowly in March and early April followed by

Fig. 8.2   Seasonal changes of brood rearing in 1977 in

overwintered honey bee colonies (A, control) as

affected by requeening colonies on 26 July, 1976

with mated queens (B), queen cells (C) and

supersedure queens (D).

a dramatic increase after mid April when pollen and nectar was available. A slight decline in brood rearing was evident in early June. This decline seems to have been associated with the collection of large quantities of dandelion honey which may have restricted the space available for the queen to deposit eggs. Following the addition of empty combs, brood rearing increased and appeared to reach a plateau after mid June. Fluctuations in brood rearing were more obvious in colonies containing the original package queens than those which had been requeened the previous fall. Requeened colonies, produced more brood than did those colonies containing the original package queens. Differences in amounts of brood of various treatment were especially evident in the initial phases of brood expansion. The differences in brood production by individual colonies were probably related to initial adult populations of the overwintered colony and the queen's age and genetic constitution.

There was a relatively large standard error associated with brood production in overwintered colonies as compared to those pre- viously observed (Chapter 5) which had been started from 0.9 kg of worker bees. Had colonies been equalized at some point in April or May the quantity of brood produced by the various colonies may have been less variable and differences between colones may have reflected genetic differences of their queens.

The brood curves for overwintered colonies were different from those observed for package colonies in Manitoba (Smirl and Jay 1972, Nelson and Jay, see also Chapter 5) and those observed for other overwintered colonies in different geographical areas (Nolan 1932,

Bodenheimer and Nerya 1938) were probably related to the climate, initial colony size, prevalence of flowering plants and the type of colony management employed.

8.4.3 Adult Populations

Seasonal changes in adult populations are presented in Figure 8.3. Adult populations decreased for the first forty-eight days after their removal from winter quarters. They then increased until a maximum adult population was attained. The timing of this maximum population differed between colonies.

Requeened colonies tended to produce more bees than those which contained the original package queens after they were removed from winter quarters. Population differences in colony size were also apparent for colonies of each group. Minor differences in initial adult populations were accentuated during the summer as a consequence of differential reproductive rates of the respective queens and their colonies. Colonies in groups A, C and D attained maximum populations in July and then leveled off, while colonies in group B tended to increase until the experiment was terminated in mid-August. Maximum adult populations tended to be larger in requeened colonies than in those which had not been requeened. Some of the requeened colonies were almost twice as large as those which had not been requeened. It is not known how much of this difference can be attributed to the queen's age or her genetic constitution. Colonies headed with queens, mated in July, tended to have larger populations than those headed with queens mated in August. Perhaps differences in adult

a dramatic increase after mid April when pollen and nectar was available. A slight decline in brood rearing was evident in early June. This decline seems to have been associated with the collection of large quantities of dandelion honey which may have restricted the space available for the queen to deposit eggs. Following the addition of empty combs, brood rearing increased and appeared to reach a plateau after mid June. Fluctuations in brood rearing were more obvious in colonies containing the original package queens than those which had been requeened the previous fall. Requeened colonies, produced more brood than did those colonies containing the original package queens. Differences in amounts of brood of various treatment were especially evident in the initial phases of brood expansion. The differences in brood production by individual colonies were probably related to initial adult populations of the overwintered colony and the queen's age and genetic constitution.

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The brood curves for overwintered colonies were different from those observed for package colonies in Manitoba (Smirl and Jay 1972, Nelson and Jay 1972, see also Chapter 5) and those observed for other overwintered colonies in different geographical areas (Nolan 1932,

Fig. 8.3 Seasonal changes in adult honey bee populations

in 1977 (A, control) and the effect of

requeening colonies on 26 July, 1976 with mated

queens (B), queen cells (C) and supersedure

queens (D) upon honey bee populations.
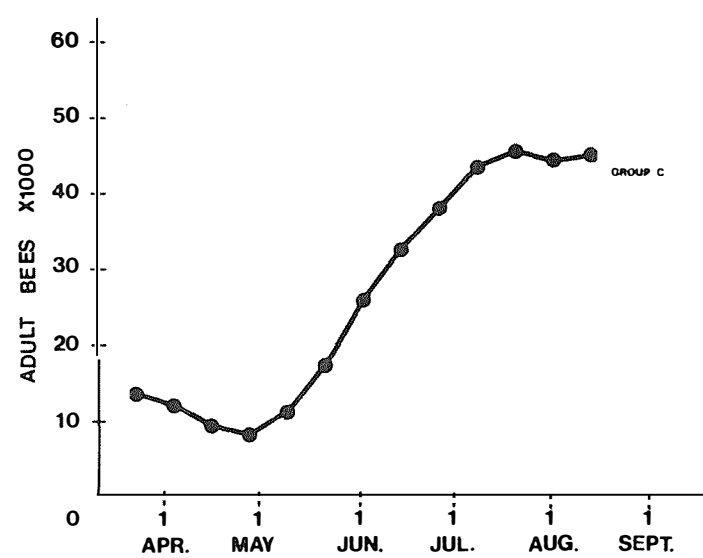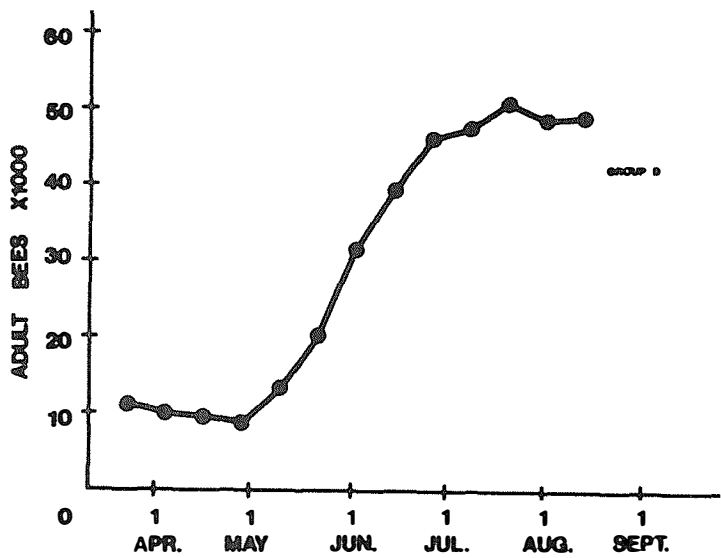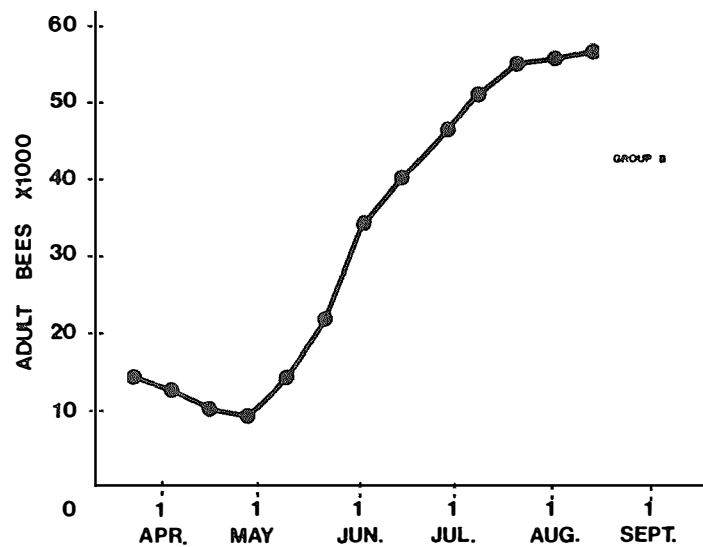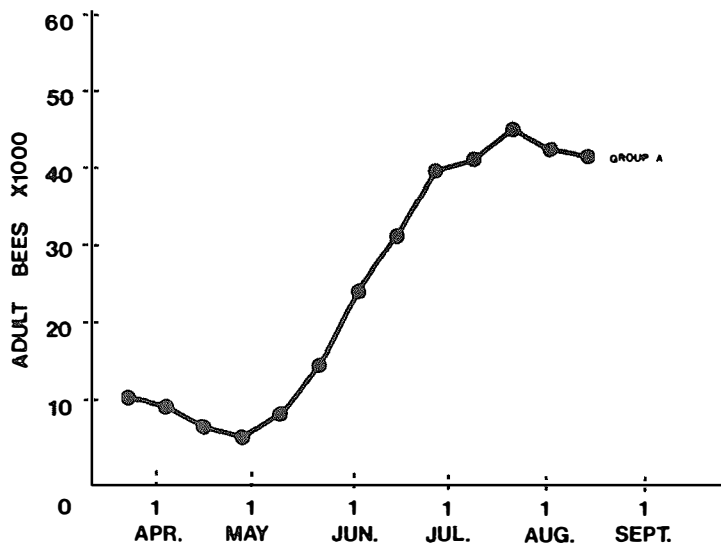
populations may be related to (1) favorable mating conditions in July (i.e. warm sunny weather) and (2) an abundance of drones.

Adult populations were much larger in the colonies used in this study than those reported by Jeffree (1955) and Farrar (1937). Several colonies, (25%) were estimated to have contained between 60-80,000 adult bees. The larger populations may be attributed to the overwintering of an adequate population of worker bees, a favorable climate, good management practices and local cropping practices.

8.5 Conclusions

Overwintered honey bee colonies are extremely variable with respect to adult populations and the amount of brood reared throughout the season. In general, those colonies which started the season with small worker bee populations were unable to produce the large populations found in colonies which overwintered with medium or large populations. Growth rates of overwintered colonies can decrease if space is not provided for honey collected during the early honeyflows. Colonies with the largest adult populations were affected more than were colonies with smaller populations.

Colonies which were requeened the previous fall tended to have larger adult populations and lower queen losses than did colonies which retained the original package queens. Overwintered colonies also had larger populations earlier than did colonies started from 0.9 kg of worker bees. This may account for the larger crops of honey beekeepers have obtained from over-wintered colonies.

8.6 References

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