SOME FACTORS AFFECTING THE ORIENTATION OF
DRONE HONEY BEES (*Apis mellifera* L.)

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by

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A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

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ABSTRACT

Currie, Robert William. M. Sc. The University of Manitoba, October 1982. Some factors affecting the orientation of drone honey bees (*Apis mellifera* L.).

The acceptance, longevity and survival of drones introduced into honey bee colonies, along with the effects of age, apiary layout and coloured hives on the number, direction, and distance that drones "drift" were examined in this study.

Drones of known ages were marked and introduced into colonies of honey bees. These colonies were examined on a regular basis before the time of drone flight and the numbers and locations of marked drones were recorded.

The acceptance of introduced drones appeared to be related to climatic conditions. Days with cool temperatures, rain and few hours of "bright" sunshine were correlated with low drone acceptance. More drones were accepted by queenless colonies than queenright ones.

The mean longevity of adult drones was 13 $\pm$ 3.3 days. The longevity of drones in queenless colonies was similar to that found in queenright colonies.

Drones first drifted at 5 days of age but generally began drifting at 7 days of age. Large proportions of drones drifted from their parent colonies by 13 to 15 days of age. Many drones drifted more than once; some drifted to as many as three hives. Drones continued to drift until at least 24 days of age.

Drones drifted between hives that were spaced up to 150 m. apart and some drifted to other apiary layouts up to 450 m. away.

Drones appeared to show directional tendencies when drifting. In rows that faced north or south drones tended to drift more to the west, and in rows facing east or west drift was greater towards the south.

The proportion of 13-15 day old drones that drifted from the parent colony was 48%. None of the apiary layouts tested controlled drift completely. However, when coloured boards, horseshoe layouts, or paired colony layouts were used, numbers of drones drifting appeared to be reduced.

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Introduction

Workers often make orientation errors and enter other colonies. The drifting of worker honey bees can result in unbalanced colony populations, and in the transmission of bee diseases causing management problems in commercial apiaries. The orientation of workers in Manitoba has been extensively researched by Jay (1965, 1966a,b, 1968, 1971). Queens also make orientation errors. Orientation errors made by queens can reduce the success of mating. The orientation of queens was studied by Dixon (1979). Orientation errors made by drones can result in the transmission of bee diseases and may result in reduced success of matings. Although drones are thought to drift two to three times more than workers (Free 1958), little research has been done on the orientation of drones. This study was conducted to determine what factors influence the orientation of drones, how much they drift, how far they drift, and if apiary layouts that reduce the drifting of workers (Jay 1966a,b, 1968) can reduce the drifting of drones.

CHAPTER I

LITERATURE REVIEW

Introduction

Drones are male honey bees and are not involved in the collection of either pollen or nectar. They spend a great deal of time inside the hive yet do not contribute to the maintenance or defense of it. Their only known function is mating with virgin queens. Because drones do not contribute to brood production, pollination or honey production, they have been researched far less than workers and queens. Research on drones could aid breeding programs, help in controlling the spread of bee diseases and improve the efficiency and quality of mating.

In this study it was necessary to obtain large numbers of drones of the same age for use in experiments. Therefore information relevant to the rearing methods used, is included in this review.

Aspects of drone biology including the survival of adults, the acceptance of drones by colonies, the purpose of drone flight, the areas to which drones fly, and the time of day at which drones fly are important to an understanding of drone orientation and therefore are also reviewed here.

Growth and Development of Brood

The queen lays male eggs in the larger (drone) cells (Woyke 1963a, Koeniger 1969). Drone eggs hatch within 48-144 hours (Phillips 1928, Wedmore 1932, Allen 1959).

The larvae are fed by worker bees until the drone cells are capped. Colonies rearing drones require much pollen (Bichtler 1952). Cell capping usually occurs 6 days after the eggs hatch (Allen 1959, Matsuka *et al*. 1973). After the cells are capped the larvae spin a cocoon; this takes about 54 hours (Jay 1964). The prepupal stage lasts about 80.2 hours and pupal development takes about 8-17 days (mean 10 days, Jay 1963). The imago remains in the cell for about 20 hours before emergence.

Most studies report the total duration of the immature stages to be 24 days (Jay 1963). However, Fukuda and Ohtani (1977) found that in the peripheral areas of the hive, where colonies usually rear drones, the length of development was 25 days. Total developmental time can range from 20-28 days (Jay 1963). Fluctuations in developmental time are likely caused by variations from the normal brood nest temperature of 34-35° C.

Regulation of Drone Brood by the Colony

Lack of food and adverse environmental conditions can decrease drone production by colonies (Hofmaster 1927, Allen 1963, Taber 1964, Fukuda and Ohtani 1977). Workers regulate the amount of drone brood by eating it (Woyke 1977). Eggs and unsealed larvae are eaten more often than is sealed brood (Fukuda and Ohtani 1977).

Only 55.8% of the eggs survive to the adult stage (Fukuda and Ohtani 1977). Survival is lowest in the egg and unsealed brood stage. Survival in the capped brood stage is stable regardless of the month or time of year. However, drone prepupae (in the capped stage) are sensitive to vibration and temperature changes (Gontarski 1957). Survival of drone brood in autumn is greater in queenless than in queenright colonies (Woyke 1977).

Life Expectancy and Survival of Adults

Reports on the length of life of adult drone honey bees have been highly variable. Averages of 54 days (Howell and Usinger 1933, Lavrekhin 1947) 21.2, 22.8, and 23.5 days (Witherell 1972, Jaycox 1961, Drescher 1969) have been found. Kepena (1963) found that 50% of the drones died before 21 days of age. Drones can live up to a maximum of 66 days (Witherell 1965a).

Some authors believe that drone life spans vary seasonally. Garofalo (1972) found average life spans to be 37 days in spring and 40 days in summer, and Fukuda and Ohtani (1977) found the mean length of life of drones to be 13.89 days in summer and 32-42 (mean 38.09) days in autumn.

The mortality rate of drones is higher than that of workers, especially during the first five days after emergence (Fukuda and Ohtani 1977). However, mortality is relatively low until the first 5-10 days after emergence, after which the death rates increase sharply. This period corresponds to the beginning of flight activity (Witherell 1972, Ohtani and Fukuda 1977). The percentage of drones surviving decreases with increased number of flights and increased age (Witherell 1972). Flight activity appears to greatly increase the mortality of drones. Oertel (1956) suggested that the amount of food carried, the age of the drone, its natural enemies and death through mating, influence the survival of drones during flight. Witherell (1972) suggests that natural enemies are the most important factor influencing mortality of drones in flight. Birds and possibly dragonflies may be major predators of drones.

Worker bees take their first flights at a later age than do drones and as a result their period of high mortality comes at a later age than does that of drones (Fukuda and Ohtani 1977). Drones have higher survival rates later in the season which probably result from decreased flight activity in autumn (Fukuda and Ohtani 1977).

Fukuda and Ohtani (1977) found that the shape of the survival curves did not change and life expectancy of drones was not lowered by the process of drone eviction by workers in the fall. However, it was suggested that few drones may have been evicted from these colonies because the colonies had many young drones and abundant honey stores.

Adult Behaviour

Drones have never been observed feeding while outside the colony. Mindt (1962) found that drones, returning to colonies, have empty honey stomachs, indicating that no food is ingested on flights. Drones can receive food from worker bees (Oertel *et al*. 1953, Free 1957, Orosi-Pal 1959, Bobrezecki 1968) and consume honey from cells (Phillips 1922, Free 1957). Drones are fed almost exclusively by workers for the first three days of their adult life (Free 1957). Drones continue to receive occasional meals from workers until they are 17 days old. Drones occasionally beg food from other drones but no food transfer occurs between them (Ohtani 1974). Drones do not regurgitate food for workers (under natural conditions) (Hoffman 1966). Drones have a diurnal feeding rhythm with maximum food consumption occurring at 12:30-13:30 hours (Burget 1973). This corresponds to the period before flight activity.

Drones have a preferred temperature of 35° C. in the hive (Cahill and Lustick 1976). However, thermal preferences may vary with age (Ohtani and Fukuda 1977). Younger drones tend to prefer the warmer parts of the hive (sealed brood area) and older drones stay in the cooler areas (empty comb area).

Drones also show phototropism and are strongly photopositive at all stages of their adult life after one day of age (Berthold and Benton 1970).

Expulsion of Drones

In the fall or under periods of nectar dearth, drones are forced to the outside combs of the colony by the workers, then to the walls, and finally to the bottom boards before being expelled from the colony (Levenets 1956). The expulsion of drones is a very gradual process taking several weeks in the fall (Morse *et al*, 1967). No more than 10-15 drones are evicted per day. Drones are not evicted from queenless colonies even if little forage is available (Free 1957, Woyke 1977).

Certain workers specialize in aggressive acts (Dathe 1975). Free (1957) has shown that young drones (6.9 days old) receive food from young workers (9.8 days old) at the same time as older drones (23.0 days old) are being attacked by older workers(21.2 days old). Workers bite drones and pull them from the hive, but do not sting them (Mindt 1962, Ohtani 1974, Free 1957).

Factors that may influence the rejection of drones by a colony include: environmental temperature, the presence of workers with developed ovaries, the presence of a queen, the amount of sealed and unsealed brood, the activity of the colony, the amount of forage collected, the amount and condition of honey stores, the strain of bees and their odour (Alber 1955, Levenets 1956 , Orosi-Pal 1959, Taber 1964, Morse et al. 1967, Holmes and Henniker 1972, Free and Williams 1975, Free 1977).

Sexual Maturity

Drones must be sexually mature so that the queen can be successfully fertilized. Sexual maturity has been assessed on the basis of a number of different criteria. Drones 9-23 days old will pursue virgin queens (Zmarliki and Morse 1963b). They will evert genitalia when 10 days old or older but most evert between the ages of 13-23 days (Kurennoi 1953b, Ruttner 1966). Englert (1967) found that matings involving drones under 14 days of age are unsuccessful. The concentration of sperm in the vas deferentia and seminal vesicles of drones is greatest at 8-9 days of age (Jaycox 1961) but an optimal number of sperm enter the queen's spermatheca when drones are 14 days of age (Woyke and Jasinski 1978).

Present data indicate that drones must be at least 9 days old to allow successful mating with the queen, the optimal age being about 14 days.

Sex Pheromones

Drones are attracted to queens by pheromones released from the queen's mandibular glands (Gary 1962). The most attractive fraction of the mandibular gland secretions is 9-oxodec-2-enoic acid (Gary 1962, Butler and Fairey 1964). Two isomers of 9-oxodec-2-enoic acid exist, a cis and a trans isomer (Doolittle et al. 1970). Drones are 200-400 times more sensitive to the trans acid than the cis acid.

The sex pheromone appears to be attractive only above heights of 5-10 m. (Gary 1962, Ruttner and Ruttner 1971). The height at which attractance occurs varies with wind speed (Butler and Fairey 1964). Drones can be attracted from a maximum distance of 60 m. away (Butler and

Fairey 1964).

Mating

Several drones mate with a single queen (Triasko 1957, Roberts 1944, Woyke 1956). Taber (1954) predicted up to 20 drones could mate with a queen. In temperate climates an average of 7 drones mate with a single queen (Peer 1956, Taber and Wendel 1958). The number of drones mating with a queen may be higher in subtropical climates (Adams et al. 1977). Thus large numbers of drones must be reared to obtain successful matings with queens (Konopacka 1968). Sladen (1920) found 59 drones per queen were required in an isolated mating station on an island.

Drones mate with queens outside the colony (Rothschild 1955) completing the mating process while in flight (Gary 1963, Woyke and Ruttner 1958). However, drones do occasionally pursue queens that are walking on the ground (Dixon 1979) and pairs can drift to the ground while mating (Wieghtman 1951).

Drones are initially attracted from the windward side by the queen's pheromone (Gary 1963). Attractance of drones is greatest at wind speeds of 5-7 m./sec. but mating is hindered at wind speeds of greater than 5 m./sec. (Bol'Shakova 1978). Drones cannot detect concentration gradients of the sex pheromones and probably use anemotaxis in locating the queen (Butler and Fairey 1964). When the queen's scent is detected drones fly directly upwind for about 9 m. or until the queen is sighted. This cycle is repeated until the queen is found, the drone becomes too fatigued or it loses the scent entirely. Drones may not be able to respond to the queen's odour in still air.

Visual stimuli are as important as olfactory stimuli in assisting drones in locating queens (Strang 1970). While on mating flights drones must pass within 1 m. of a queen to see her (Butler and Fairey 1964). Drones are more attracted to darker colours and more compact shapes (Strang 1970, Gerig 1971). Moving objects appear to be more attractive than stationary objects (Gary 1963).

Drones are also attracted to drone swarms which form quickly once the first few drones have found the queen (Gary 1963). Elusive movements of the queen provide a distraction within the swarm that results in drones collectively darting in one direction to form what is termed a "drone comet". Comets disintegrate quickly if there is no object to follow.

Drones approach queens from the posterior ventral side and orient to the lowest end of the queen (Gary 1963). In normal flight the queen's abdomen is held lower than its head. The position of the drone and queen while mating is drone superior (Gary 1963).

Drones mate and separate from the queens within 1-6 sec. of mounting (Gary and Martson 1971). Drones die within 0-198 mins. (mean 92.4 mins.) after their genitalia are everted (Witherell 1965a).

Location of Mating

Whether drones locate queens on mating flights or whether queens locate drones is still not clear. Many authors believe that drones gather regularly to mate with queens in areas termed "drone assemblies" (Ruh 1960, Jordan 1967, Kobel 1967, Cooper 1969) or "drone congregation areas" (Muller 1950, Zmarlicki and Morse 1963a, Ruttner and Ruttner 1963, Gerig 1969, Strang 1969). Congregation areas are defined as areas where drones gather regularly, in a location that remains constant over time, irrespective of the presence of a queen (Ruttner and Ruttner 1971).

Drones follow virgin queens (or sex attractant lures) vigorously within congregation areas but only short distances beyond them (Zmarliki and Morse 1963a, Ruttner and Ruttner 1963, 1965a, Gerig 1972). Drones fly over congregation areas for 10-15 minutes before returning to their hive (Ruttner and Ruttner 1971).

Some evidence has been found to support the theory that congregation areas exist. Drones are attracted in greater numbers to sites farther from an apiary than to sites closer to it (Zmarliki and Morse 1963b, Ruttner and Ruttner 1966, 1971). Drones fly to congregation areas regularly and revisit the same congregation areas (Ruttner and Ruttner 1963, 1966, 1968). The geographical location of congregation areas remains constant over time (Ruttner and Ruttner 1965b, 1968, 1972, Strang 1970). Drones of different races and different species of honey bees use the same congregation areas (Ruttner and Ruttner 1972, Ruttner 1973). Queens returning from mating flights have usually mated with several drones or not at all (Ruttner 1966). This may indicate that only queens that find congregation areas, successfully mate with several drones.

Drones are thought to locate congregation areas primarily on the basis of visual cues (Ruttner and Ruttner 1972). Drones may fly towards near and distant physical features of the landscape (Ruttner and Ruttner 1966). Boundaries of congregation areas appear to be marked by some form of vertical relief in the landscape (Strang 1970, Ruttner and Ruttner 1971). Light intensity may also be used as a cue to mark boundaries in congregation areas (Praagh and Ruttner 1975). Congregation areas are usually found in hilly or mountainous regions (Doolittle 1892, Ruttner and Ruttner 1965c, Strang 1970). In flat country, congregation areas are not well defined (Ruttner and Ruttner 1965c).

The alternate theory to the use of congregation areas for mating is that drones fly at random and are attracted to the queen during her mating flight by her sex pheromones. Butler and Fairey (1964) suggest that the rapidity with which drones find queens may indicate that drones are abundant and widely dispersed and that queens have an efficient system of attraction. Butler and Fairey (1964) found no areas in which drones congregated. They pointed out that there is no evidence that queen honey bees are attracted by drones. This seemed especially unlikely as drones were so highly adapted to locating queens. Occasions in which drones have been heard or seen in certain places may be the result of the presence of queens in those places. Butler and Fairey suggested that the presence of a crippled queen in an area may result in the queen's scent persisting for several days and result in drones congregating at places where they had previously smelled a queen.

Flight Activity

The earliest that drones begin to fly is four days after emergence from the cell (Howell and Usinger 1933, Kurennoi 1953a, Kepena 1963). All drones have usually taken their first flight by 15-18 days of age (Howell and Usinger 1933, Kurennoi 1953c, Drescher 1969). Reports on the average age at which drones make first flights vary; 5-7 days of age (Howell and Usinger 1933), 6-10 days (by 82-90% of drones) (Kurennoi 1953c), 9-12 days (by 78.6% of drones) (Kepena 1963) or 9-18 days (Drescher 1969). Witherell (1970) found that the average age of first flights was 7.96 days.

Drones usually fly only later in the day. Most authors believe drone flight begins between 11:00-14:00 hours (mean 12:28 h.) and ends between 16:00-18:00 h. (mean 17:22 h.) (Howell and Usinger 1933, Kurennoi 1953c, Oertel 1956, Lavrekhin 1960, Ruttner 1966, Taber 1963, Drescher 1969, Tuchashvili 1969, Garofalo 1972, Strang 1971, Bol'Shakova 1978). Maximum flight activity occurs between 14:00-16:00 h. (mean 15:07 h.). Drone flight activity can begin as early as 09:00 h. (Tuchashvili 1969).

Time of flight for _Apis mellifera_ drones is temporally separated from _Apis cerana_, _Apis florea_, _Apis dorsata_ and _Apis indica_, (Lavrekhin 1960, Ruttner _et al_. 1972, Koeniger and Wijayagunasekera 1976). Peak periods of flight activity for _A. florea_, _A. cerana_, _A. indica_ and _A. dorsata_ are 13:30 h., 16:30 h., 17:00 h. and 18:20 h. respectively (Koeniger and Wijayagunasekera 1976, Lavrekhin 1960). The peak period of flight activity of _A. mellifera_ was around 15:00 h. Temporal separation of flight is necessary because virgin queens of _A. florea_, _A. dorsata_, _A. cerana_, and _A. mellifera_ all use 9-oxodec-trans-2-enoic acid as a sex attractant for drones (Shearer _et al_., 1976). Tuchashvili (1969) has shown that slight variations in drone flight time can occur between strains of _A. mellifera_. A Mid-Russian strain flew between 10:00-17:00 h. with peak activity occurring between 14:00-16:00 h., while a Kuban strain flew between 9:00-18:00 h. with peak activity between 15:00-16:00 h. However, considerable variation in flight times can occur between colonies, the flight times of drones being dependent on many environmental factors (Taber 1964). Therefore, it is difficult to judge if variations in flight time reported between strains of drones are significant.

The flight rhythm of drones can also vary seasonally. Taber (1964) found that average drone flight time was 14:00-16:00 h. in June, but was 2 hours earlier in April. Taber hypothesized that drones fly at a later time and flight becomes more concentrated when temperatures become warmer and days become longer as the season progresses. This hypothesis is partially supported by Bol'Shakova's (1978) findings that towards the end of the flight season the length of the flight day was reduced from 4 to 2.5 h. Drones were also found to accumulate around tethered queens between 15:00-16:00 h. in June but from 14:00-15:00 h. later in the season. It appears that the average time of day for drone flight may reach a peak in mid-summer and decline again towards fall.

Drone flight occurs at the same time of day in different geographic locations and different time zones (Lavrekhin 1960, Taber 1964). Taber proposed that a circadian rhythm exists to control drone flight time. He suggested that drones may set their internal clocks in the morning using light as a cue.

A number of other environmental factors influence flight activity and one, or a combination of these, may control time of drone flight. These factors include temperature, wind speed, humidity, and light (Bol'Shakova 1978, Howell and Usinger 1933, Witherell 1970). Drones usually fly at temperatures above 18-20° C. (Ruttner 1976, Bol'Shakova 1978). Drone flight can occur at between 15-18° C. (Drescher 1969, Bol'Shakova 1978). However, flights at these temperatures were only 1-2 minutes long (Drescher 1969). Howell and Usinger (1933) found that drone flight activity was not correlated with ambient temperature. Flight activity peaked about 2 hours after the daily temperature was at a maximum (at 13:00 h.) and drones did not fly at 10:30 h. when temperatures were equivalent to temperatures at the time of peak flight activity (at 15:00 h.).

Wind speed also influences flight activity. Bol'Shakova (1978) found that drone flight was not affected by winds of up to 7m./sec. (25.2 km./h.). Oertel (1956) found that released drones could not return to colonies if temperatures were low and wind speed was 8-16 km./hr.. Howell and Usinger (1933) found a slight increase in wind velocity each day at the time of drone flight but they believed that wind did not initiate flight behaviour.

Drone flight time may be regulated by relative humidity, or the evaporation rate of the environment (Howell and Usinger 1933, Witherell 1970). Howell and Usinger (1933) found that the saturating power of the environment had a curve similar to that of the temperature, except that the peak was at 14:00 h.. Relative humidity was more closely related to peak flight activity (Howell and Usinger 1933, Witherell 1971). Drones flew at times of the day (14:00-16:00 h.) when relative humidity was lowest (30%). However, if drone flight time is regulated by relative humidity, it is difficult to explain why drones are attracted by queen pheromone lures in higher numbers and at faster rates as the humidity increases (Bol'Shakova 1978). Queens attracted the greatest number of drones at 70-80% relative humidity.

Howell and Usinger (1933) believed that light intensity was only important in regulating drone flight time late in the day (at around 17:00 h.) when intensity was low enough to prevent flight. Ultraviolet light intensity is known to increase from 295.5 uu. at 10:30 h. to 307 uu. at 16:38 h. and corresponds very well with Howell and Usinger's flight time curve (Luckiesh in Howell and Usinger 1933). It is thought that variations in ultraviolet light may be a more important factor in regulating drone flight times than actual light intensity (Howell and Usinger 1933).

Tuchashvili (1969) found that flight activity decreased with decreased light intensity. Drones in shaded colonies stop flying if light intensity is reduced by cloud even though drones from unshaded colonies keep flying (Taber 1964). Bol'Shakova (1978) measured cloudiness on a scale of one to ten and found that cloudiness up to a scale of 8 did not affect flight activity but few drones flew when the sky was completely overcast. Drones in hives facing south-east flew earlier than did drones in hives facing south-west (Taber 1964). This may result from drones perceiving light from the sun's rays at the hive entrance in the south-east facing hives at an earlier time than by those in the south-west facing hives.

If environmental conditions (light, temperature, wind clouds) were unfavourable for flight on preceding days, drones flew earlier on the next day (Oertel 1956, Taber 1964). Several factors have been correlated with the flight time of drones but it is not known which, if any, of these factors provide cues stimulating drone flight activity, or if an internal rhythm is involved. Factors which may provide a time cue are: perception of light in the morning, relative humidity, evaporation rates, temperature, light intensity, fluctuations in the ultraviolet spectrum (Howell and Usinger 1933, Witherell 1970, Taber 1964).

Duration of Flight and Interflight Time

Drones fly chiefly for the purpose of mating but also make flights for orientation and defecation (Witherell 1971). Howell and Usinger

(1933) found drones make shorter flights (1-6 mins.) for orientation and longer flights (25-30) for mating. However, Witherell (1971) found some 7 day old drones made flights of 40-68 mins. in duration. As these drones were not yet sexually mature and, therefore, must have been on orientation flights, Witherell suggested the definition of "orientation flights" should be based on age criteria and not on flight durations. The first to fifth flights for orientation usually last from 1-6 mins. (Howell and Usinger 1933, Drescher 1969).

Flight duration varies with weather, age, flight experience, time of day, time of year, and quantity of food carried (Garofalo 1972, Howell and Usinger 1933, Witherell 1971). Drones take shorter flights, 4.6-10 minutes long on cloudy or windy days (Witherell 1971). Duration of flights tends to increase with increase in age (Witherell 1971). The longest flights were taken by drones 31-40 days of age. Older drones, with the most flight experience made the longest flights. Flights in all age classes of drones tended to be longest during the period of peak flight activity (14:00-16:00 h.). The first flight of the day tended to be the longest (32.60 ± 21.82 minutes) while the second and third flights averaged 15.84 (± 20.56) minutes and 29.84 (± 15.45) minutes respectively. Subsequent flights varied between 1-49 minutes. Garofalo (1972) found flight duration varied with time of year. Average flight duration was 26 mins. in spring and 36 mins. in summer. Witherell (1971) suggested that flight duration of drones was also regulated by the amount of food carried in the crop. This theory is supported by Orosi-Pal (1959) who found that drones seldom feed before taking orientation flights.

The duration of flights is highly variable and can range up to 3 hours and 27 minutes long. Witherell (1971) found that without considering age and other factors, mean flight duration was 32.56 ($\pm$22.49) minutes. This figure is close to the flight durations reported by other authors for mating flights; 20 mins. (Butler 1939), 10-60 mins. (mean 30 mins.) (Drescher 1969), 25-30 mins. (Howell and Usinger 1933).

Drones return to the colony from flights presumably because their food reserves are depleted (Free 1957). Time spent in the colony between flights tends to decrease as flight frequency increases (Witherell 1971). Interflight time between the first and second flights was significantly longer than in the succeeding hive stays. Duration of hive stays between flights was longer after flights of greater than 60 minutes than for flights of 30 minutes. However, the difference in hive stay times were not statistically different. The mean length of time spent in the colony between flights reported are 17.14$\pm$24.42 mins. (Witherell 1971), 21.56$\pm$ 22.79 mins. (Mikhailov 1928), and 3-4 mins. (Minderhoud 1932).

Number of Flights

Drones can make up to 94 (mean 25) flights over their life span (Witherell 1971). Half of the drones fly 30 or more times and 13.5% fly 60 or more times. Drones are reported to make between 2-8 flights and average between 2-4 flights per day (Kurennoi 1954, Drescher 1969). Howell and Usinger (1933) reported an average of 3.1 flights per day and Witherell (1971) found drones seldom made over 3 flights per day. The number of flights per day can be as high as 17 (Howell and Usinger 1933).

Area of Flight

Drones are thought to occupy the flight region between 10-40 m. above ground level while workers range 1 to 8 m. above ground (Ruttner and Ruttner 1963). Drones fly between 10 to 30 m. above tree top height.

Speed of flight is estimated at around 6-10 mph. (12-10 km./h.) (Oertel 1956). Drones are thought to consume more honey during flights than do workers and can carry enough honey reserves to fly several kilometers.

Drones returned to colonies from up to 5 km. away in capture/release tests (Levenets 1954, Konopacka 1968). However, only a few drones (2%) returned from that distance. Fifty percent returned from 1 km. and 80% returned from 200 m. away from their original colony. Ruttner and Ruttner (1966) found that drones flew to areas up to distances of 5 km. on a regular basis and could fly to areas up to distances of 7 km. Peer and Farrar (1956) and Peer (1957) studied the mating of the honey bee and found that matings between queens and drones occurred across distances of up to 10.1 miles (16 km.). If queens fly a maximum of 5 km. (Ruttner and Ruttner 1971) this would indicate that drones could fly distances of up to 11 km. on mating flights. However, drones flying that far do not necessarily have enough food reserves to return to the hive.

Peer (1957) found that the success of mating between queens and drones from different colonies was lower as the distance between colonies increased. Queens that mated successfully with drones from colonies that were 16.2 km. apart began laying eggs at later dates than did queens mating with drones from colonies 6.1 to 9.8 km. apart.

Orientation to the Colony

Drones that are unsuccessful on mating flights, or which are on orientation flights, must return to their colony for food and shelter. The process of how drones orient to their home colonies is poorly understood. Capture and release tests have shown that drones can return to their colonies within 46.5 minutes from 5 km. away (Levenets 1954).

The direction from colonies, where drones were released, has no effect on the rate or success of returns (Oertel 1956).

Oertel (1956) found that drones could successfully return to colonies even if both antennae were removed; thus they apparently do not use antennae in orienting. It is probable that they use only visual cues. Oertel attempted to determine if drones used the sun to help them locate their hive. Drones were confined in a tent and prevented from seeing the sun or the sky. Drones found their way back to the colony in the forenoon and afternoon whether the sky was cloudy or not. This led Oertel to conclude that drones do not use the position of the sun as an aid in orienting to their colony. However, if drones have a biological clock they may be able to keep track of sun position internally and compensate for the differences in it.

Oertel (1956) felt drones used landmarks to find their way back to the hive. No tests have been done as yet to verify this hypothesis. However, Ruttner and Ruttner (1966) and Strang (1970) have shown that drones may use optical cues in the form of near and distant physical features of the landscape in the location of "congregation areas".

Bees have been shown to have magnetic remanence (Gould et al. 1978). If placed in total darkness on a horizontal plane, workers eventually orient their dances towards the cardinal points of the compass (Gould 1980). A honey bee possesses a substance called magnetite which may be used in the detection of magnetic fields. Honey bees have a higher sensitivity to fluctuations in the earth's magnetic field than do homing pigeons. It is possible that fluctuations in the earth's magnetic field may aid drones in orienting to their home colonies using a method similar to that used by pigeons.

Khalifman (1951) concluded that drones placed in different colonies tended to remain in the colonies to which they were more closely related. Differences in brood food were thought to cause this "change in homing instinct". It was proposed that if brood combs are placed in strange colonies this may contribute to subsequent "drifting". Drifting is the movement of drones to colonies other than their original colony. Adult drones were marked and then placed in different colonies and the percentage of drones drifting back to the colonies in which they were reared, was measured. As these drones must have been at least of flight age (6-7 days old) to be able to drift from these colonies, it seems more likely that these drones picked up the colony odours as adults. When placed in colonies with similar odours, drones may remain more closely allied to these colonies than to colonies that were not related.

Drones appear to retain a memory of the cues they use in orienting to their home colony. Foged (1953) found that colonies, moved more than 1 km. away from their original sites, had worker and drone bees returning to the old site. Two days later 2/3 of the bees returning were drones. Bees continued to return for up to 4 days and were mostly drones. This indicates that the drones must have retained some form of memory of the location of the old site for a period of at least 4 days.

Butler (1939) suggested that drifting of drones may be influenced by weather, time of year, and the presence or absence of virgin queens. Butler (1939) marked drones in four colonies and noted their presence in colonies throughout the season. Only 6 drones drifted throughout the season and only one was found in a mating nucleus. Butler concluded that virtually no drift of drones occurred between hives in his apiary, despite the fact that there were droneless nuclei with virgin queens present. Levenets (1951) found rates of drift of 1.75%, 1.47%, and .85% repectively for Italian, Bashkir and Caucasian stocks of bees. It was concluded that drift does not vary significantly between different races of drones. Drift generally occurs on the first orientation flight and then chiefly to the strongest hives in the rows. Drones generally remain in colonies to which they first drift. Levenets found queenless colonies and colonies with virgin queens, did not attract or retain drones. However Free and Spencer-Booth (1961) found that more drones from queenright colonies drifted to queenless, than to queenright colonies. Drones expelled from queenright colonies did not drift to queenless ones.

Drones were reported to drift 2 to 3 times as much as do workers (Free 1958, 1961). The percentage of drones drifting ranged between 8.6-80% between trials. Goetze (1954) placed colonies of *A. mellifera mellifera* bees in an apiary containing *A. mellifera carnica* and *ligustica* colonies. When colonies of *A. mellifera* were subsequently examined, just over half the drones present had originated from *carnica* or *ligustica* colonies. Witherell (1965b) had levels of drift of 11.43% and 12.25%. He also concluded that drones drift more readily to a nearby hive than one that is farther away. Twelve percent of marked drones drifted to a colony 30.5 cm. west, while .25% drifted to a colony 3.8 m. east. Drones also fly to hives that face different directions than their own hive.

Drones as Vectors of Disease

Drones are potential vectors of honey bee diseases because: 1. they are susceptible to the same microbic and parasitic infections as are workers, 2. They retain the powers of flight when diseased, 3. they drift between colonies (Moreaux 1953).

Drones are susceptible to acarine mites, Forrest disease (virus), sacbrood (virus) and an infective dysentery (Moreaux 1953, 1959). Drones of all age groups can become infected with Nosema apis (Bailey 1972). However, fewer drones than workers became infected with Nosema in enzootically infected, undisturbed honey bee colonies. Drones are as susceptible as workers to the sacbrood virus (Bailey and Fernando 1972). The sacbrood virus does not affect the longevity of drones but infected drones fly at an earlier age than do non-infected drones.

Drones transmit these diseases when drifting between colonies. Drones from colonies severely infected with acarine disease are still able to fly, while this is not so with infected workers (Moreaux 1953). Drones have been implicated in transferring acarine disease to a colony 30 m. away. Hanko and Lemakova (1971) found that high frequencies of all age groups of drones infected with Nosema apis flew to neighbouring and distant colonies. The ability of drones to maintain and propagate pathogens of honey bees, along with their tendencies to drift between colonies and ability to continue flying when diseased, make them serious, potential vectors of bee diseases. Further studies on the transmission and spread of bee diseases between colonies and apiaries should take into consideration the role of drones as potential vectors of bee diseases.

CHAPTER II

MATERIALS AND METHODS

General Methods

Rearing of Drones for Experiments

Drones were reared from a yellow strain of bees in single storey Langstroth hives containing 7 to 8 frames of worker bees. Drone comb was placed between brood combs of colonies for one day to allow the comb to be cleaned by the worker bees. The queen was placed on the drone comb and enclosed within a single frame queen excluder; thus the queens were "forced" to lay eggs in the drone comb. These colonies will be referred to as "starter colonies". Frames with eggs were removed from the queen excluder after two days and placed between frames of worker brood within the starter colonies.

Worker brood and young worker bees were added continually to the starter colonies to maintain the worker population and to help prevent the destruction of drone brood. During periods of honey flow "starter colonies" were supplied with boxes containing empty comb to prevent the drone comb from being filled with honey by the worker bees.

When the drone brood was in the capped stage, it was transferred from the "starter colonies" to "rearing colonies". The "rearing colonies" consisted of double storey hives containing 16 to 18 frames of worker bees. Drone brood was transferred from the "starter colonies" because the proportion of drone brood in a colony must not be too high or the workers will eat the brood (Allen 1958). Drone brood was transferred to rearing colonies when it was capped because at this stage of development it can be handled with the least damage (Fukuda and Ohtani 1977). Drone brood was incubated in the rearing colonies until the 23rd to 24th day of its development.

At 23 days from the time the eggs were laid all adult drones were brushed off the frames of drone brood which were then transferred from the rearing colonies to an incubator set at 30^{o} C. Drones were allowed to emerge in the incubator overnight and were then marked the next morning.

Marking Technique

Drones were marked using a modified version of the Harris technique (1979). A 3cc. disposable plastic syringe with a curved plastic tip (Bertholet , unpublished) was used to mark the drones. Syringes were filled with " Pactra Aero Gloss" dope. One to three dots of different colours were applied to the thorax of each drone.

Drones, reared from different colonies, were allowed to thoroughly mix in the incubator prior to being marked. All drones were marked within 15-20 hours after emergence so that their ages could be determined over time. They were all marked at the University of Manitoba apiary after which they were transported to the test sites.

Handling and Transportation of Marked Drones

Marked drones were picked up by the hind leg using forceps. They were then stored, and transported in plastic cylinders, 125 mm. long by 44 mm. in diameter. The cylinders were enclosed at one end with a 16 mesh plastic screen and had plastic lids on the other end (W.H.O. 1963). The tubes were lined with 16 mesh plastic screen to provide a surface that the drones could grip. No more than 50 drones were placed in each container. Water and honey were provided for the drones through the screened end of the tube. Drones were transported in these containers until they were introduced to colonies; they were stored no longer than 6 hours.

Description of Colonies

All experimental colonies consisted of single storey Langstroth hives except for the large square experiment in which 5 frame nuclei were used. All hives were painted white, had similar lids and bottom boards and were placed on hive stands 9 cm. high. At the beginning of each experiment, colony populations were equalized (i.e. colonies consisted of the equivalent of 3 frames of worker bees, 3 frames of brood, and one queen). Additional boxes had to be added to the hives of the isolated colony experiments (in 1981) to prevent swarming.

Introduction of Marked Drones to Colonies

Hardware cloth with 8 mm. squares (i.e. three squares to the inch) was placed between the brood chamber and a hive box. The hives were then left for 10 minutes to allow the bees time to "settle down" and then 100 drones (per hive) were released onto the hardware cloth. The bees were then gently smoked after which hive lids were placed on top of the empty boxes.

All drones were introduced in the evening just prior to sunset. The hive boxes and hardware cloth were removed the following day after the drones had joined the colonies by passing through the screen.

Data Collection for Experiments

Colonies were examined to determine the number of marked drones that had survived and to what hives they had drifted. Colonies were examined early in the morning before drone flight began (i.e. before 9:00 a.m.) and the number of marked drones found in each hive was recorded. All frames, lids, walls and bottom boards of the hives were examined. In addition each hive used in an experiment and each hive within 800 m. was searched for marked drones.

Most experiments consisted of hives placed in rows which were numbered one through five from left to right as the observer faced the entrances.

Hives were examined one day after the marked drones were introduced and when drones were 7, 13, 15 and 21 days old. If weather conditions prevented drone flight, examinations were delayed one day. In some experiments however, extra examinations were done between the 7, 13, 15, and 21 day periods.

Experimental Sites

In 1980 three experiments were conducted at the University of Manitoba campus.

All other experiments in 1980 and 1981 were conducted at the University of Manitoba Glenlea Research Station.

Scale Colony and Weather Records

A "scale colony" was placed on a platform scale at the University site in 1980 and 1981. Weight gains and losses were recorded to determine when the nectar flow took place.

Weather data were obtained from Environment Canada for the two sites (i.e. Winnipeg International Airport and Glenlea Research Station).

Rain, wind, hours of bright sunshine, and mean daily temperature records were recorded.

Experiments

Data obtained using the general methods described above were used in, the determination of acceptance of drones by colonies, the longevity and survival of adult drones, and their drifting behaviour. Unless stated otherwise the methods follow those outlined in the general methods.

Acceptance of Drones by Colonies

Colonies were examined to determine the percentage of drones accepted by colonies on each date when drones were introduced during 1980 and 1981. Examinations of colonies were done on the day after introduction and when drones were six days old. The percentage of drones accepted by different colonies on a particular date was averaged.

In 1980 drones were introduced to colonies located at the University site on three occasions (i.e. 3 July, 7 July, and 10 July). All other introductions in 1980 and 1981 took place at the Glenlea site.

In 1980, drones were introduced into 3 colonies each on 3 July, 7 July, 10 July, 20 July, and on 25 July; into 4 colonies on 14 August, and into 6 colonies on each of 15 July and 10 August. In 1981, drones were introduced into 1 colony on 13 August; 2 colonies on each of 26 June and 12 August, 3 colonies on each of 9 July and 31 July; 4 colonies on each of 20 July and 28 July; 8 colonies on 3 August and into 13 colonies on 10 August.

Introductions were also made into queenless colonies in 1981, into 2 colonies on 20 July and into 1 colony on 31 July and 3 August.

The Longevity and Survival of Drones

Drones that were introduced to colonies were also used to determine drone survival and longevity by continuing colony examinations until marked drones were no longer found. The number of marked drones found in all of the colonies examined (i.e. including drifting drones) were recorded.

The mean longevity of adult drones was calculated (using a frequency distribution) from the number of drones that were accepted by a colony one day after introduction. The class mark of the last age class of drones dying was the midpoint between the age of the drones on the last examination when they were found in colonies and their age on the next day.

The survival of drones was determined in 3 different colonies at the University site on 3 July 1980. All other drone survival trials were conducted on 26 July (2 colonies), 9 July (3 colonies), 20 July (4 colonies), 31 July (2 colonies), 3 August (6 colonies), and 12 August (1 colony). The longevity and survival of drones in queenless colonies was recorded on 20 July, 31 July, and 3 August.

Drone Loss from an Isolated Colony vs. Loss and Drift from Groups of Colonies

Drones were introduced into colonies located at least 2 km. from any other colonies. Thus no drifting of drones to other colonies was probable. The percentage of drones surviving in these colonies was compared simultaneously to that of drones in groups of hives where drones drifted. The survival of drones in the groups of colonies was determined, by two methods, one including the drifting drones and one excluding the drifting drones.

The survival of drones in isolated colonies was compared to the survival of drones from groups in four trials during 1981. Two trials were conducted beginning 29 June, one beginning 9 July, and one beginning 12 August. The arrangement of the groups (see page 34) of colonies was not the same in all four trials. The trial shown in figure 30, includes data from the arrangement of hives in the 1 m. experiment (figure 1). The trials shown in figures 31 and 32 include data from the arrangement of hives in the 5 m. experiment (figure 2). The trial shown in figure 33 includes data from the arrangement of hives in the 50 m. experiment.

To compensate for variation in the acceptance of marked drones introduced to different colonies in the "loss" trials (figures 30-33) a "base line count" was done before drone flight began (i.e. before drones were 7 days old). Subsequent survival of drones was calculated as a percentage of the base line count.

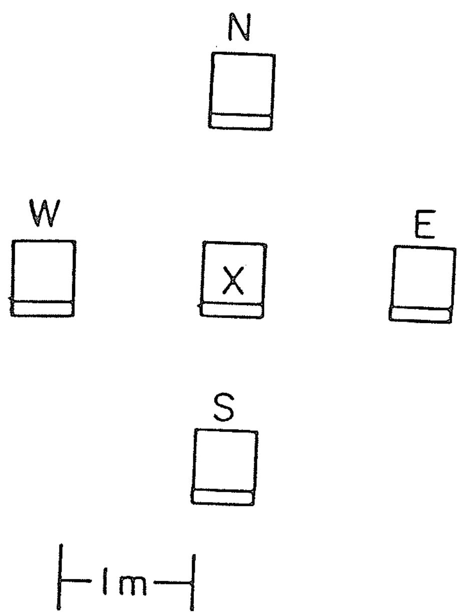
Effect of Age of Drones on Drifting

The effect of the age of drones on their drifting behaviour was tested in a row of 5 colonies (see straight row experiment page 9). Marked drones less than 12 hours old, were introduced into three hives in the row. The colonies were examined every one to three days (see table 2) to determine the number of drones that drifted.

The drifting of individually marked drones was also examined. This experiment was repeated in two different groups of hives. In one trial the marked drones were introduced into the large square layout shown in figure 6. Ten drones were placed in the centre colony of each row. In the second trial, 20 individually marked drones were placed in the centre hive of the arrangement of hives shown in figure 2. Colonies were examined 5 times (see tables 3 and 4) and drifting of marked drones

Figure 1 . Arrangement of hives in the 1 m. experiment. (The "x" indicates the colony into which drones were introduced).

Figure 2 . Arrangement of hives in the 5 m. experiment. The "x" indicates the colony into which drones were introduced).


N
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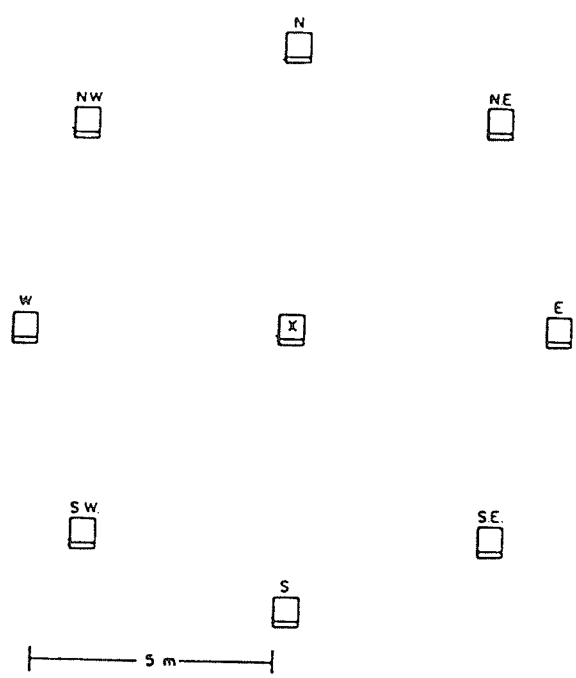
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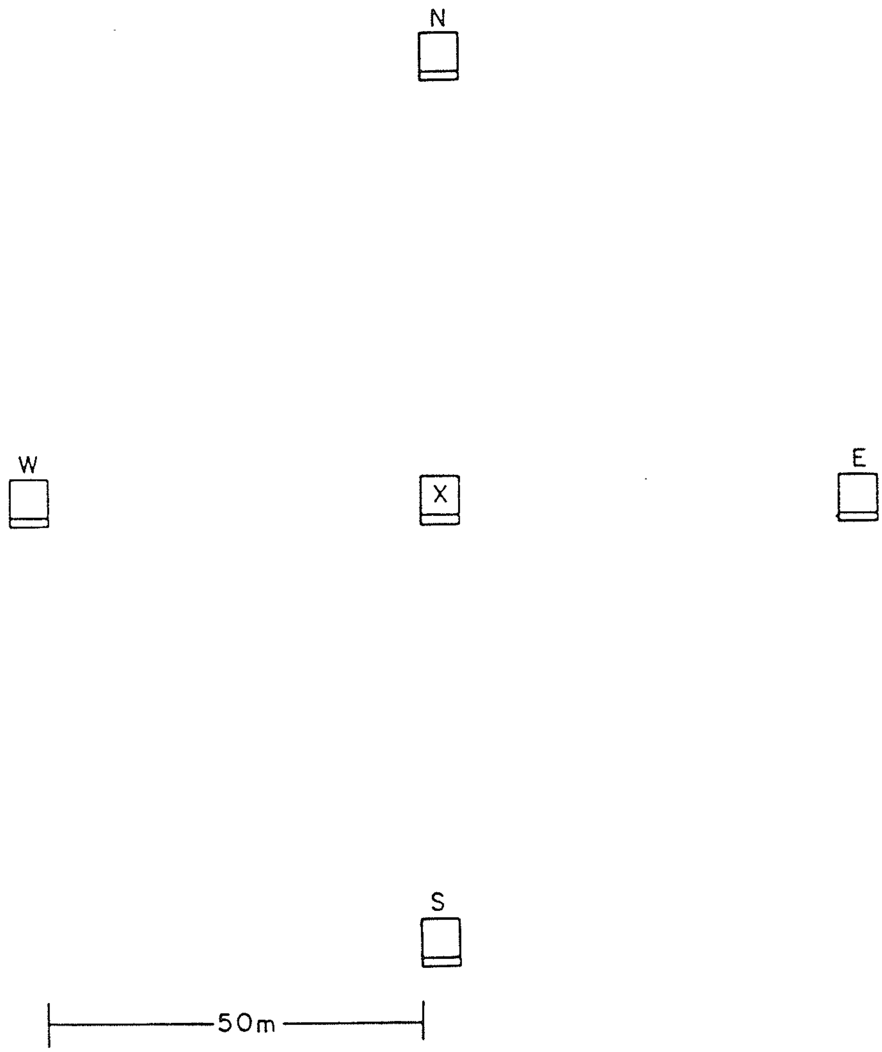
5 m

Figure 3 . Arrangement of hives in the 50 m. experiment. (The "x" indicates the colony into which drones were introduced).


N
W
X
E
S
50m

was recorded.

Distance and Direction of Drone Drift

Distance. In the one metre experiment hives were arranged as shown in figure 1 . Four hives were placed at the cardinal points of the compass 1 m. from the central hive. All hive entrances faced south. The marked drones were introduced into the central colony. Colonies were examined and the total number of drones that drifted to the four surrounding colonies was recorded. The direction of the hives to which drones drifted was also noted.

In the 5 m. experiment hives were arranged as shown in figure 2 . Eight hives were placed at distances of 5 m. around the central hive. Drones were introduced into the central colony. In the 5 m. trial (a) all hive entrances faced south, but in the 5 m. trials (b and c) all hive entrances faced north (see table 6).

The arrangement of hives in the 50 m., 100 m. and 200 m. experiments are shown in figure 3 ; hives were placed at 50 m., 100 m. and 200 m. respectively. Four hives were placed around the central colony at the cardinal points of the compass. The marked drones were introduced into the central colony of each group.

Drift between Apiary Layouts. The distance and direction that drones drifted between apiary layouts (i.e. groups of hives) were recorded twice during 1980. In the first trial, three separate apiary layout experiments were placed in a north-south line as shown in figure 4 . In a second trial five apiary layouts were arranged in an east-west line as shown in figure 5 . The numbers of drones drifting between the apiary layouts were recorded.

Large Square. The "large square" consisted of four rows of five hives spaced 1 m. apart to form a square (see figure 6). The four rows faced the cardinal points of the compass with their hive entrances facing the outside of the square (see figure 6). Marked drones were placed in the centre colony of each row. The direction of drift within rows and between rows of the square was recorded. The proportion of drones drifting from each row was also noted. This experiment was replicated twice (on 15 July 1980 and 10 July 1981).

Straight row. The direction of drift was also measured in rows facing west. The rows consisted of 5 hives spaced 1 m. apart with all entrances facing west. Marked drones were introduced into colonies in positions 1,3,and 5 (see figure 7) except for the trial conducted on 15 July, 1980 where drones were introduced only to the centre colony. Five replicates of this test were conducted (3 July and 15 July 1980; 20 July, 3 August and 10 August 1981).

Paired colonies. The direction of drone drifting was also recorded in paired colonies that were placed 1 m. apart with hive entrances facing south (see figure 8). Marked drones were placed in both colonies. Three replicates of this trial were conducted (15 August 1980, 20 July, and 28 July 1981).

Drifting of Drones Within Different Apiary Layouts

Straight rows

To determine the amount of drone drift, data were obtained from straight row experiments and large square experiments. The colonies were examined when the drones were between 13-15 days old. The proportion of

Figure 4 . Arrangement of three apiary layouts. (Each apiary layout is represented by ⬡).

Figure 5 . Arrangement of five apiary layouts. (Each apiary layout is represented by ⬡).

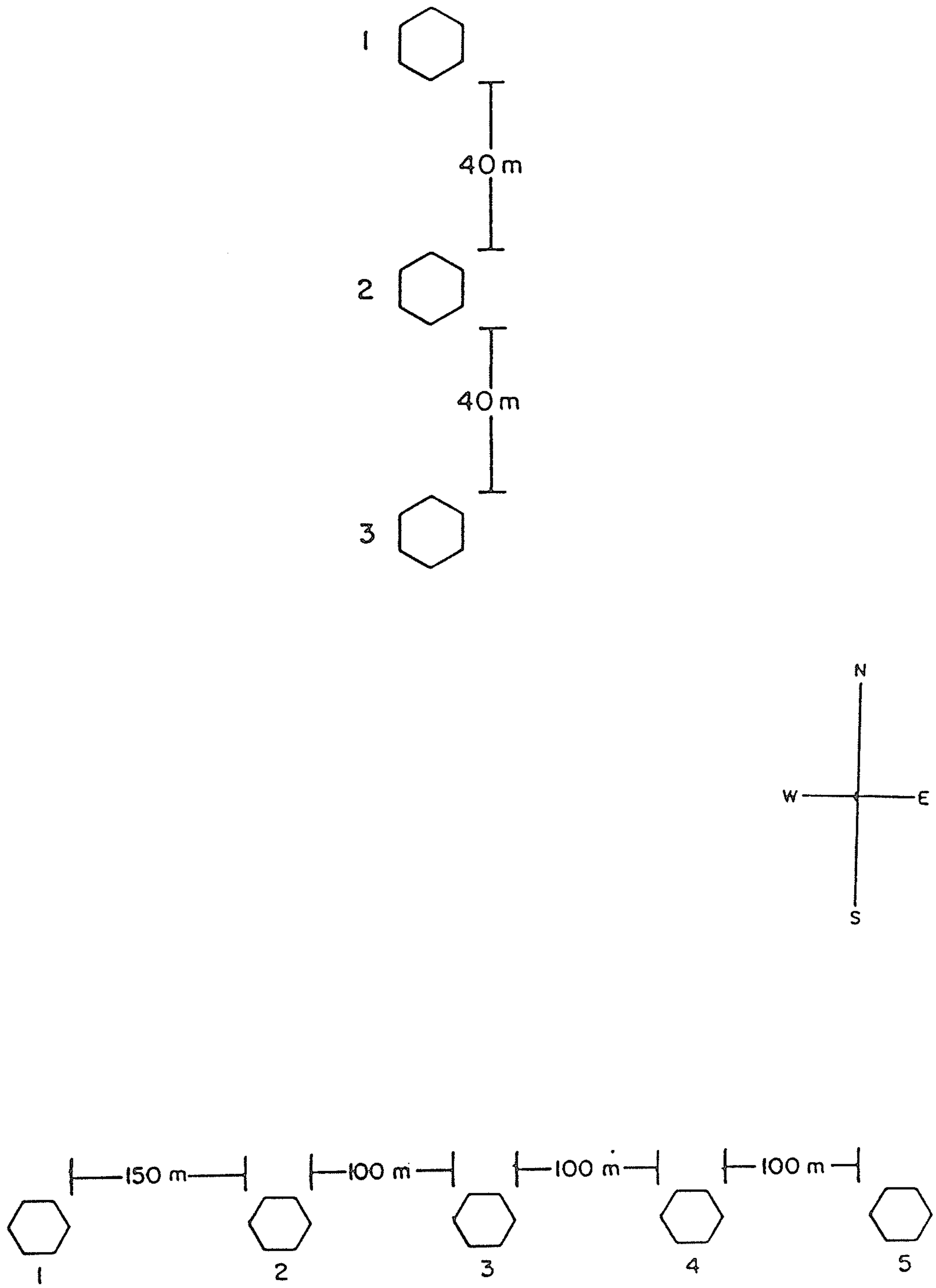
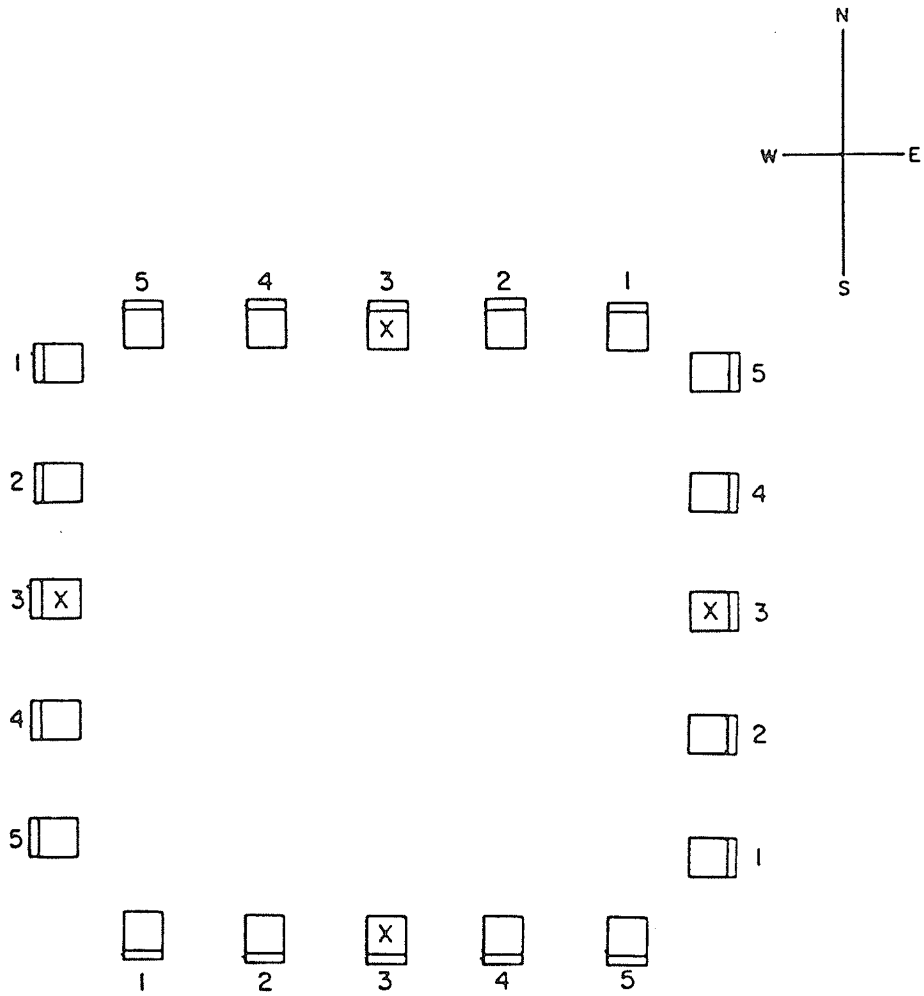

1
40 m
2
40 m
3
N
W
E
S
150 m
100 m
100 m
100 m
1
2
3
4
5

Figure 6 . Arrangement of hives in the large square apiary layout.


N
W
E
S
5
4
3
2
1
X
1
2
3
4
5
X
5
4
3
2
1
X
1
2
3
4
5
X

drones drifting from the parent colonies was recorded.

Drift. The percentage of drift from the parent colony was calculated for each specific age group. The number of drones found in colonies outside the parent colony was divided by the total number of drones found in all colonies of the same age. This yields the proportion of drones that drifted from the parent colony.

The straight row apiary layout was also used as a "control" in experiments to compare the amount of drift that occurred in different apiary layouts. Controls were done concurrently with the apiary layout experiments. The pattern of drone drifting within the straight row layout was also examined.

Offset entrances

Drift was examined in a straight row of hives with offset entrances arranged as shown in figure 9. Five hives were spaced one metre apart. Hives 1 and 4 had entrances angled N.W., hives 2 and 5 had hive entrances S.W., and hive 3 faced west. Marked drones were introduced into hives 1,3, and 5 in the row. Three replications were done (on 15 July 1980, 3 August 1981 and 10 August 1981).

Coloured boards

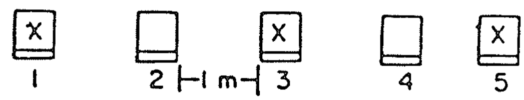
Drift was examined in a straight row of five hives spaced lm. apart that had coloured boards placed over their hive entrances. The arrangement of the coloured boards, and the colonies which received drones are shown in figure 11. Four trials were done in 1980 and 1981. Two of the trials had coloured boards over the entrances of hives 1,3, and 5 (10 July 1980, 15 July 1980) while the other two trials had coloured boards over

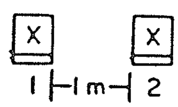
Figure 7 . Arrangement of hives in the straight row apiary layout.

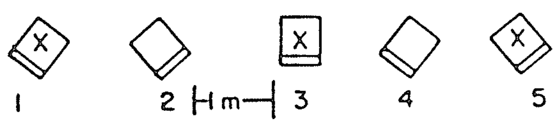
Figure 8 . Arrangement of hives in the paired colony apiary layout

Figure 9 . Arrangement of hives in the offset entrance apiary layout.

Figure 10. Arrangement of hives in the horseshoe apiary layout.


X
X
X
1
2
1 m
3
4
5


X
X
1
1 m
2


X
X
X
1
2
1m
3
4
5

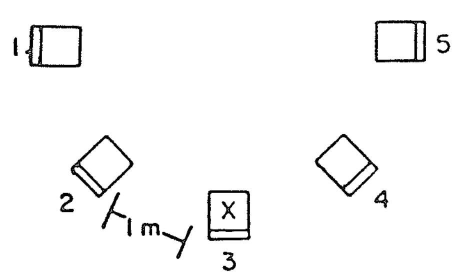
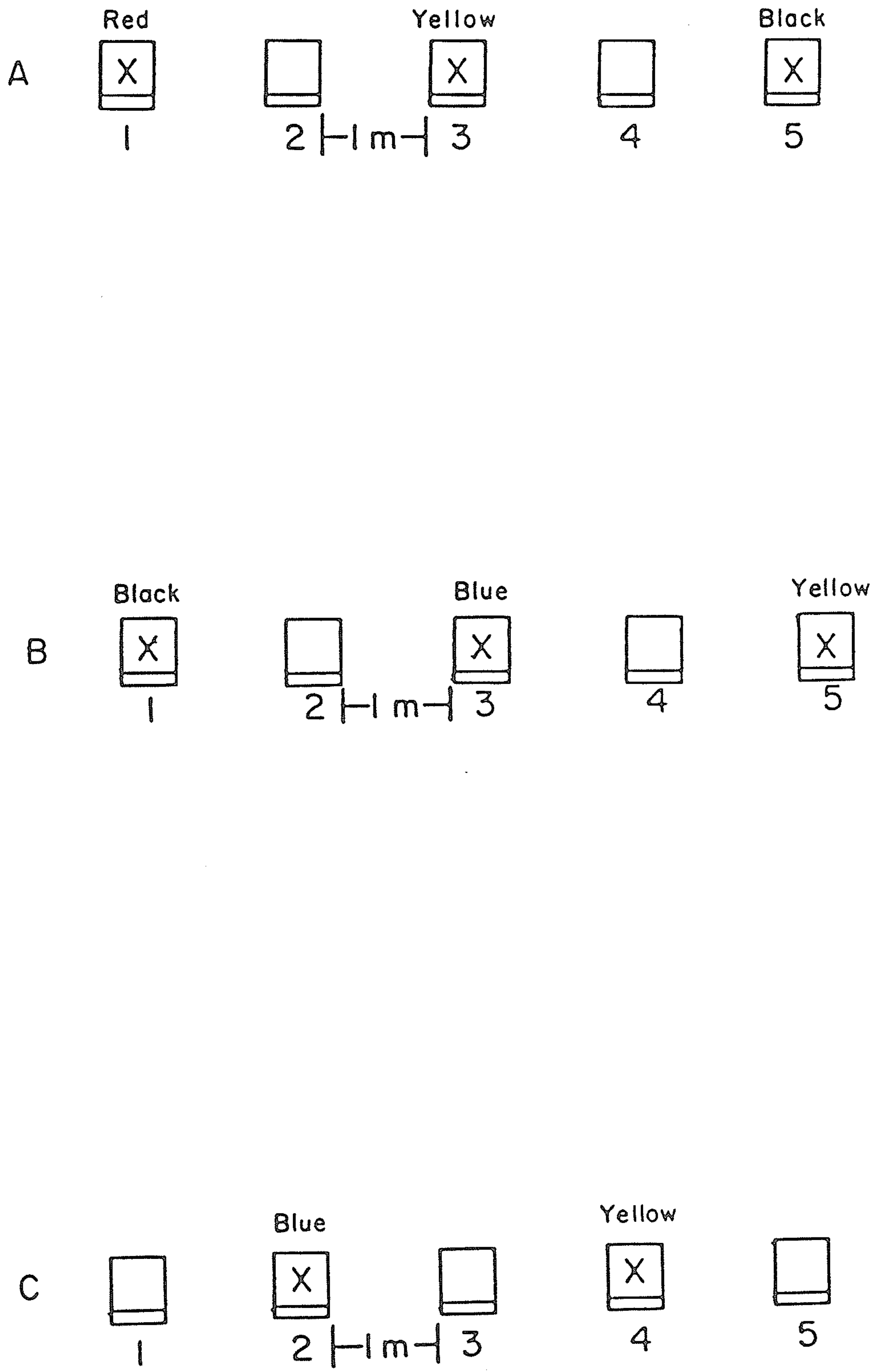

1
5
2
1m
X
3
4

Figure 11. Arrangement of hives in the coloured board apiary layouts. (The colours of the boards placed over the hive entrances are indicated).


A
Red
Yellow
Black
1
2
1 m
3
4
5
B
Black
Blue
Yellow
1
2
1 m
3
4
5
C
Blue
Yellow
1
2
1 m
3
4
5

the entrances of hives 2 and 4 (3 August, 1981, 10 August, 1981). The trial on 10 July was performed at the University site. The other trials were conducted at the Glenlea site.

Horseshoe

Hives in the horseshoe layout were spaced one metre apart as shown in figure 10. Drones were introduced into hive 3. The hive entrances faced towards the outside of the horseshoe. Three trials of the horseshoe design were done. On 15 July, 1980, the horseshoe faced south and in 1981 the horseshoe faced west in trials on 3 August and 10 August.

Paired Colonies

(see paired colonies p.35). To determine the amount of drift occurring between paired colonies, the drift occurring from both colonies was pooled.

Statistical Analysis

Comparisons of drone acceptance by colonies and of the mean longevities of drones were analyzed using t-tests.

Drone drift in the 1 m., 5 m., 50 m., and 100 m., experiments was tested to see if it conformed to a random (or poisson) distribution by using a Chi-square. The direction of drift in the 50 m. experiment was analyzed using a binomial distribution.

The analysis of the direction of drone drift and the comparisons between the amount of drift in different apiary layouts were based on Chi-square criteria.

CHAPTER III

RESULTS

Acceptance of Drones Introduced into Colonies

The initial acceptance of drones by colonies ranged from 39 to 96% in 1980 (mean 70±7.9) and 33 to 84% (mean 58±5.6) in 1981 (figures 12 and 14). Significantly more drones were accepted by the time they were 6 days old in 1980 (mean 58±7.4) than in 1981 (mean 38±6.2) ($P<0.05$) (figures 13 and 15). Twelve percent and 20% of the drones died between the first and second examination in 1980 and 1981 respectively.

The initial acceptance of drones was significantly greater in queenless colonies ($P<0.05$) than in queenright colonies (figure 14). However, the number of drones accepted by queenless colonies by the time drones were 6 days old was not significantly greater than in queenright colonies ($P>0.05$). The number of drones accepted into a queenless colony on 20 July, 1981, was lower than the number accepted into queenright colonies.

Temperature, precipitation, hours of bright sunshine and scale colony data for the periods during which drones were introduced in 1980 and 1981 are shown in figures 16 to 23.

Drone Longevity

The mean longevity of adult drones ranged from nineteen days to seven days (table 1). The mean longevity of drones from all dates sampled throughout 1981 was 13 ± 3.3 days (table 1). No drones lived longer than 51 days in this study (figure 25).

The mean longevity of drones in queenless colonies was not significantly higher than in queenright colonies ($P > 0.05$).

Survival Curves

The number of drones, accepted by a colony, was often less than 50% (figures 26 to 29). Survival rates of drones were fairly constant from the time of the first examination (second point on graph) until the end of the preflight period (i.e. before 6 days of age) on 3 July, 1980 and 12 August, 1981 (figures 24 and 26). However in the other trials some drone mortality did occur in the preflight period (figures 25 and 27 to 29).

The number of drones accepted by queenless colonies was higher (12 to 50%) but survival rates were similar after introduction (figures 27 to 29).

Drone Survival in Isolated Colonies vs. Survival in Groups of Colonies

The number of drones surviving in isolated colonies was similar to the number surviving in groups of colonies when drifting drones were included (figures 30 to 33). However the number of drones surviving in groups of colonies was up to 50% lower (see figures 30 to 33) than in isolated colonies if drifting drones were not included.

Effect of Age of Drones on Drifting

Generally, drones did not drift until they were seven days old (table 2). Observations from later experiments indicated that drones could drift as early as 5 days of age (e.g. table 16, 3 August, 1981). However, drifting by 5 and 6 day old drones was rare. The proportion of drones drifting from the parent colony indicated that large numbers of drones (66%) drift by the time they are 15 days old (table 2). The proportion of drones drifting from the parent colony tends to increase with age.

Drones can make more than one error in orientation (table 3). Drones made as many as 3 changes in position between hives within three examination periods (table 3, trial A). Although low numbers of drones were used in tests (because of the difficulty in marking large numbers of drones with individual markings), the results indicate that drones often drifted more than once. Some that drifted more than once, actually drifted back to the parent colony.

The number of drones that changed hives between examinations remained fairly constant (table 4). However, there appears to be a slightly greater number of bees (not significant) changing hives in the 13 day examination (trial A, table 4) which coincides with the large numbers of 9 to 13 day old drones that drifted (shown in table 2). Fifty-two to 54% of drones did not drift from their parent colonies (table 3).

The Distance and Direction that Drones Drift

The distance of drift. Drones drifted to colonies 1 m., 5 m., 50 m., and 100 m. from the central colony (table 5). Drones did not drift to the colonies that were 200 m. away. Between 29-63% of 13-21 day old drones drifted to colonies at distances up to 50 m. (table 5). The percentage of drones drifting from their parent colonies, to colonies at distances of 100 m., was 15 to 17% (table 5). Drones 8 days old did not drift farther than 5 m. (table 5).

Direction and distance. In the 50 m. and 100 m. experiments (figures 35 and 36) drift was not random ($P < 0.01$); drones drifted only to the colonies north and south of their parent colony (table 6). In the 50 m. experiment (trial A) drones drifted to the colony in the north. The 50 m. experiment (trial B) and the 100 m. experiment were done concurrently starting on 12 August, 1981. In the 50 m. experiment (trial B) drift was greater to the colony in the south than in the north ($P < 0.05$) (table 8). In the 100 m. trial drones drifted only to the south (table 8). Wind data for the dates on which the 50 and 100 m. trials were conducted are presented in table 7.

In the 1 m. experiment drifting of drones was not random ($P < 0.05$); i.e. significantly more drones drifted to the east and west than to the north and the south ($P < 0.05$) (table 6). In the 5 m. experiments (trials A and B) the drifting of drones was not significantly greater to any single hive ($P > 0.05$)

The drifting of drones in the 5 m. experiment, trial C, was not random ($P < 0.001$); 16 drones drifted to the colony in the north-west position.

Direction and Distance of Drift Between Apiary Layouts

Up to 60% of the drones drifted between different apiary layouts (i.e. groups of hives) (tables 8 and 9). When groups of hives were arranged in a north-south line (table 8); significantly more drones drifted from the centre groups (2) to the groups 40 m. south than to the group 40 m. north in (3 of 5 readings $P < 0.05$). When five groups of hives were arranged in an east-west line (table 9), the drifting of drones from group 3 was greater to apiary layouts in the west than to those in the east; however, this trend was significant in only one of 3 examinations ($P < 0.01$).

More drones from group 3 (table 8) drifted to groups 40 m. north than to colonies 80 m. north ($P < 0.05$ in 4 of 5 examinations). However the drifting of drones from group 1 was greater to the group 80 m. south than to the group 40 m. south (table 8) $P < 0.05$ in 3 of 5 examinations).

Drones drifted between groups (1 and 5) that were 450 m. apart, table 9. Drones also drifted between groups (1 and 2) that were separated by 150 m. (table 9).

Direction of drift in rows. In rows facing north, significantly more drones drifted to the colonies west of the centre colony in replicate 1 ($P < 0.05$ in 2 of 4 trials), but in replicate 2, significantly more drones drifted to the colonies to the east of the centre colony ($P < 0.05$ in 3 of 4 trials) (table 10). In rows facing south, drone drifting was greater to the west of the centre colony (in 2 of 4 examinations, $P < 0.05$ in replicate 1 and in 1 of 4 examinations in replicate 2 , ($P < 0.01$). In rows facing east more drones drifted to the colonies to the south in both replicates 1 and 2 ($P < 0.05$) in 1 of 4 readings in both trials 1 and 2. Drones from the row facing west showed no significant tendency for drift to either the north or south of the centre colony in either replicate.

Drones also drifted between the rows of the large square (table 11). Drift from a side (row of hives) of the square tended to be higher to sides of the square that were adjacent to it, than to the side that faced directly opposite (tables 13 and 14). The two exceptions to this general tendency of drone drift were (1) the drones drifting from the east row in replicate 1, in which large numbers of drones (6-10) drifted to the west row and (2) the drones from the south row in replicate 2 where a single drone was found in the north row. In replicate 1 the west row received significantly more drones from the north and south row than did the other rows (in 5 of 6 trials $P < 0.05$ or greater).

The proportion of drones drifting from their parent colony was not significantly different in rows facing different directions (figures 34 and 35).

Although no directional tendency of drift was observed in the rows facing west in the large square experiments (table 10), other experiments that were conducted using rows of hives facing west did show a directional tendency for drone drift. Drift from the centre colony (in a row of 5 hives) was examined in five trials with a total of 24 examinations.

Drift was significantly higher towards the south on 11 examinations ($P < 0.01$ or greater) and significantly higher towards the north once ($P < 0.025$). In the 12 examinations where there was no significant drift to either direction, drift was higher towards the south 9 times (table 12). Other data and analyses are shown in table 12.

Drift from hives (1 and 5) at the ends of the rows also indicated a weak tendency for higher numbers of drones to drift towards the south (from hive 1) than towards the north (from hive 5) (see table 13). Drift was significantly greater towards the south in 3 examinations ($P < 0.05$ or greater) and was not significantly greater towards the north. In examinations where there was no significant difference in drift to either direction, drift was greater towards the south 9 times, greater towards the north 7 times and equal in both directions twice.

<u>Direction of drift in paired colonies</u>. The directional tendency of drift from paired colonies facing south is shown in tables 20-22. Drift was

measured in three trials with 14 hive examinations (table 14). The amount of drift was significantly greater towards the west (from hive 2) on 8 examinations, ($P < 0.05$ or greater). In examinations where there was no significant difference in drift to hives in either direction, drift was higher towards the west 5 times and higher towards the east once (table 14).

Effect of Apiary Layout on the Number of Drones that Drifted

Amount of drift occurring in straight rows. The proportion of 13-15 day old drones drifting in straight rows is shown in table 36. The percentage of drones drifting from the parent colony ranged from 10-80% and the total drift during 1980 and 1981 was 49% (table 15).

Offset entrance layout. The use of apiary layouts with offset entrances did not significantly reduce drifting of drones below the levels found in controls (see table 16). The drifting of drones in this pattern was often higher than the control layout but was significantly higher ($P < 0.005$) only during one examination.

Coloured board layout. The proportions of drones drifting in apiary layouts with coloured boards above the hive entrances, are shown in tables 17 and 18. In the trial conducted on 10 July 1980, the results of examinations done when drones were 7 to 13 days old were not considered because a virgin queen was present in hive three.

Drifting in the coloured board layout was significantly lower than in controls on only 2 of 14 examinations in the four trials ($P < 0.05$). In the 12 examination in which drift was not significantly different from the controls, drift was lower on 8 examinations (table 19).

Horseshoe layout. Drift from colonies in a horseshoe formation was significantly lower than in controls on 2 of 10 examinations in 3 trials ($P<0.005$ or greater). In the 8 examinations in which drift in the horseshoe layout was not significantly different from the controls, drift was lower on 8 examinations (table 19).

Paired colony layout. Drift from colonies in the paired colony layout was significantly lower than in controls during 4 of 12 examinations in 3 trials (table 20). In the 8 examinations in which drift in the paired colony layout was not significantly different from the controls, drift was lower on 6 examinations (table 20).

The Pattern of Drift Within Apiary Layouts

Straight rows. In straight rows of 5 colonies placed 1 m. apart, the drifting of drones was not consistently higher from the centre colony of the row than from the end colonies of rows (see figures 36 to 38).

Aside from the direction effect mentioned earlier, drift was not consistently higher to any hives in the row (table 21).

Offset entrances. Drift in the offset entrance layout is shown in table 22. Drift was not consistently higher to any colonies in the row.

Coloured board layout. In the trial conducted on 10 July, 1980, many drones drifted to the centre colony of the row during examinations done when drones were between 8-12 days old (table 23). During this period a virgin queen emerged in the centre colony of the row. The centre colony of the row had a yellow board over the hive entrance (figure 11). In other trials, colonies with yellow boards over the hive entrances (hive

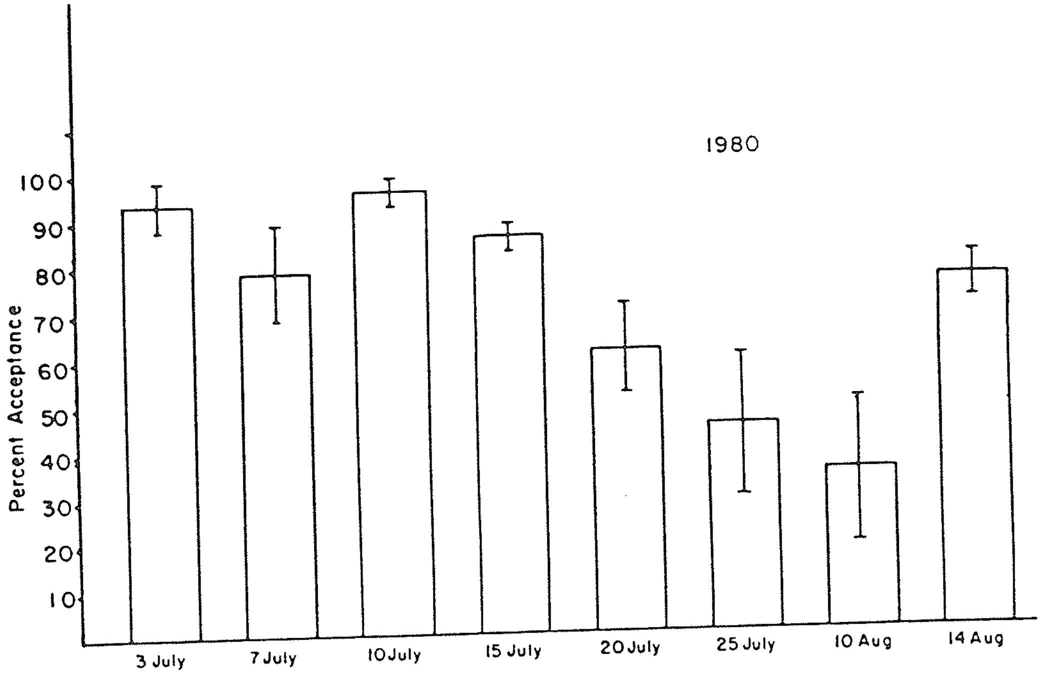
5 on 15 July, 1980 and hive 4 on 3 August and 10 August, 1981) did not attract drones (see table 22).

Horseshoe. In the horseshoe layout (figure 10) most drones drifted from the centre colony to the colonies on either side of it (table 24).

Paired colonies. The pattern of drift in paired colonies is described in the section on direction of drone drifting (see page 51).

Figure 12. The mean acceptance of drones introduced into colonies on the day following introduction for specified dates during 1980. The vertical bars indicate standard errors.

Figure 13. The mean acceptance of drones introduced into colonies (when drones were 6 days old) for specified dates during 1980. The vertical bars indicate standard errors.


1980
Percent Acceptance
100
90
80
70
60
50
40
30
20
10
3 July
7 July
10 July
15 July
20 July
25 July
10 Aug
14 Aug

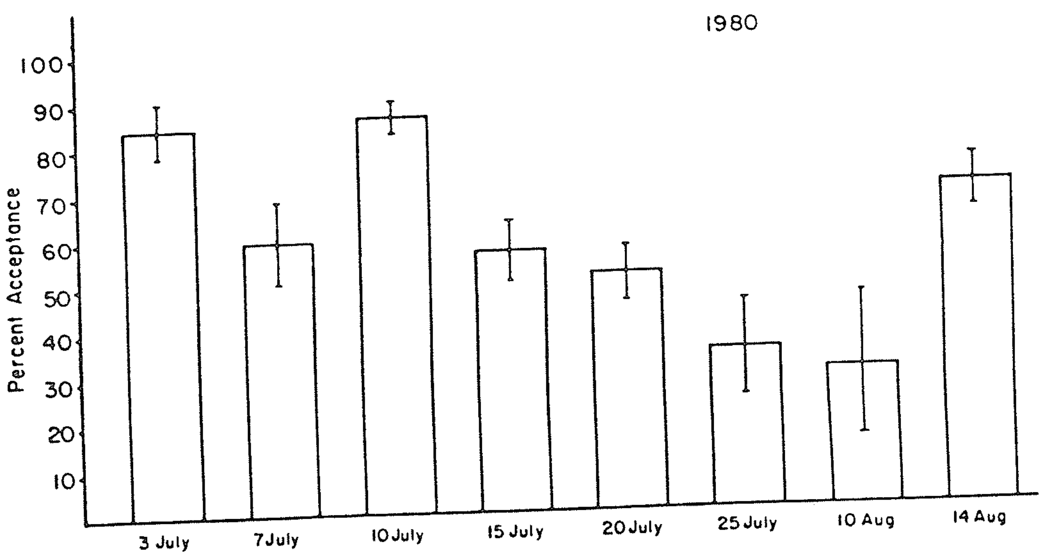
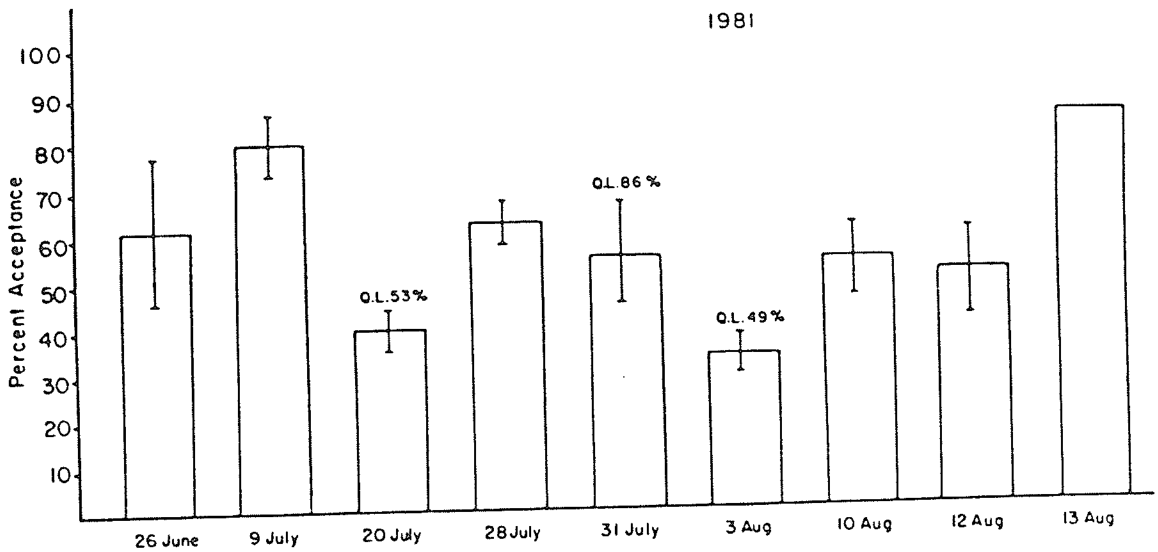

1980
Percent Acceptance
100
90
80
70
60
50
40
30
20
10
3 July
7 July
10 July
15 July
20 July
25 July
10 Aug
14 Aug

Figure 14. The mean acceptance of drones introduced into colonies on the day following introduction for specified dates during 1981. The vertical bars indicate standard errors and Q.L. indicates acceptance into queenless colonies.

Figure 15. The mean acceptance of drones introduced into colonies (when drones were 6 days old) for specified dates during 1981. The vertical bars indicate standard errors and Q.L. indicates acceptance into queenless colonies.


1981
100
90
80
70
60
50
40
30
20
10
Percent Acceptance
Q.L.53%
Q.L.86%
Q.L.49%
26 June
9 July
20 July
28July
31 July
3 Aug
10 Aug
12 Aug
13 Aug

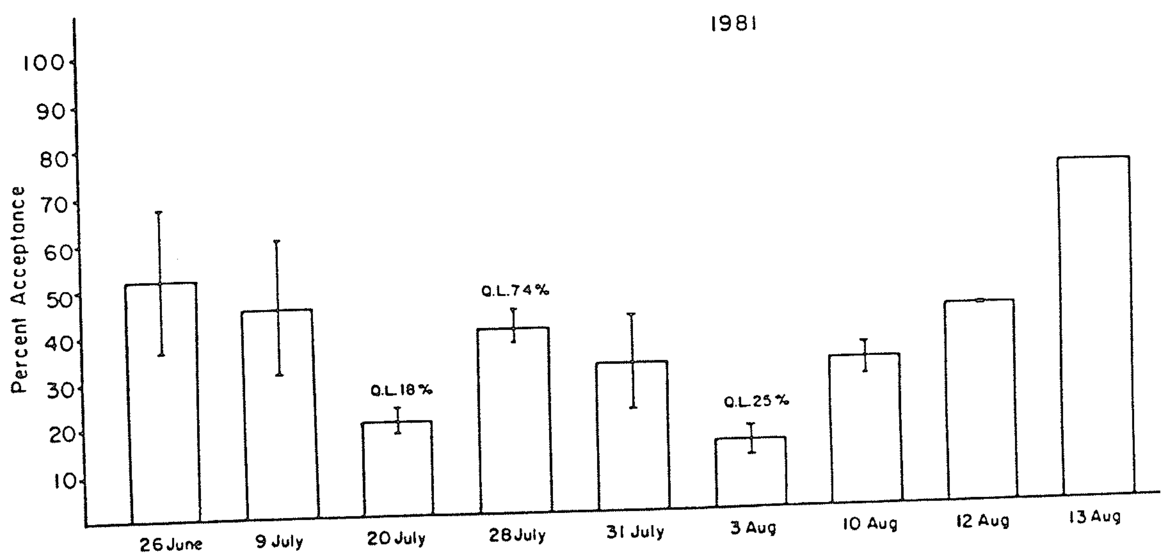
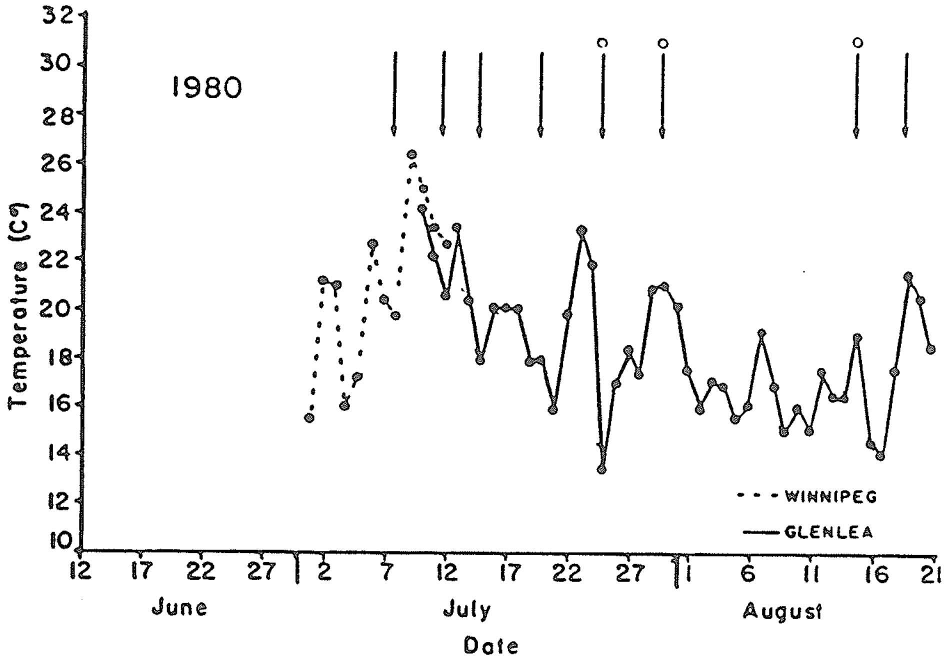
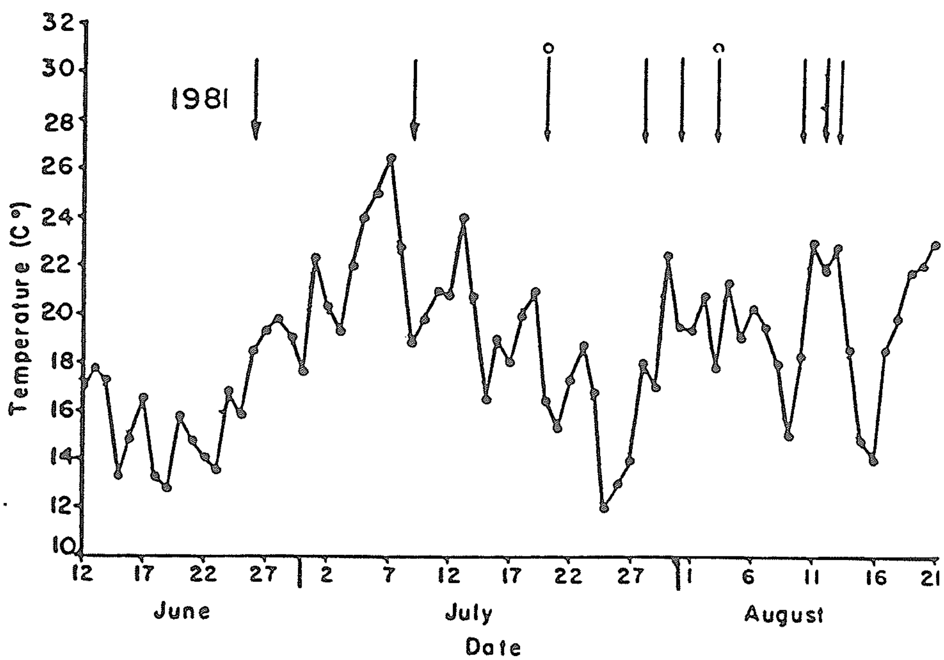

1981
100
90
80
70
60
50
40
30
20
10
Percent Acceptance
Q.L.18%
Q.L.74%
Q.L.25%
26June
9 July
20 July
28July
31 July
3 Aug
10 Aug
12 Aug
13 Aug

Figure 16 . The mean daily temperature throughout the summer in 1980. The dates on which drones were introduced are indicated with arrows. Dates with poor drone acceptance are indicated by a "0".

Figure 17 . The mean daily temperature throughout the summer in 1981. The dates on which drones were introduced are indicated with arrows. Dates with poor drone acceptance are indicated by a "0".



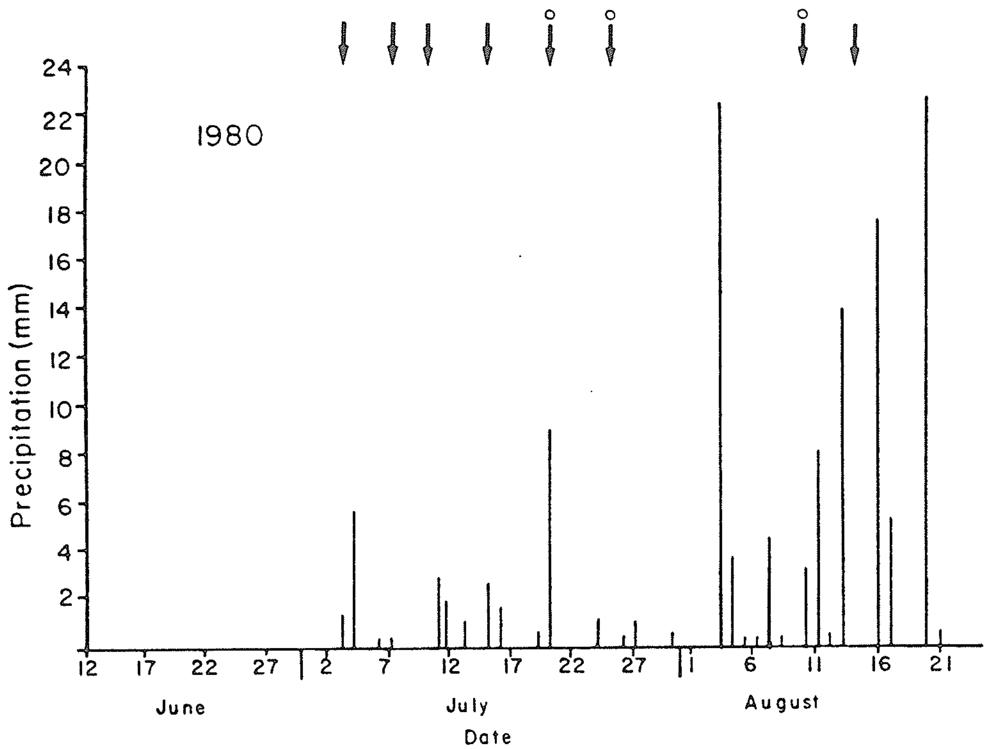
1980
32
30
28
26
24
22
20
18
16
14
12
10
Temperature (C°)
12
17
22
27
2
7
12
17
22
27
1
6
11
16
21
June
July
August
Date
WINNIPEG
GLENLEA



1981
32
30
28
26
24
22
20
18
16
14
12
10
Temperature (C°)
12
17
22
27
2
7
12
17
22
27
1
6
11
16
21
June
July
August
Date

Figure 18. The daily preciptation throughout the summer of 1980. The dates on which drones were introduced are indicated with arrows. Dates with poor drone acceptance are indicated by a "0".

Figure 19. The daily preciptation throughout the summer of 1981. The dates on which drones were introduced are indicated with arrows. Dates with poor drone acceptance are indicated by a "0".


1980
Precipitation (mm)
June
July
August
Date

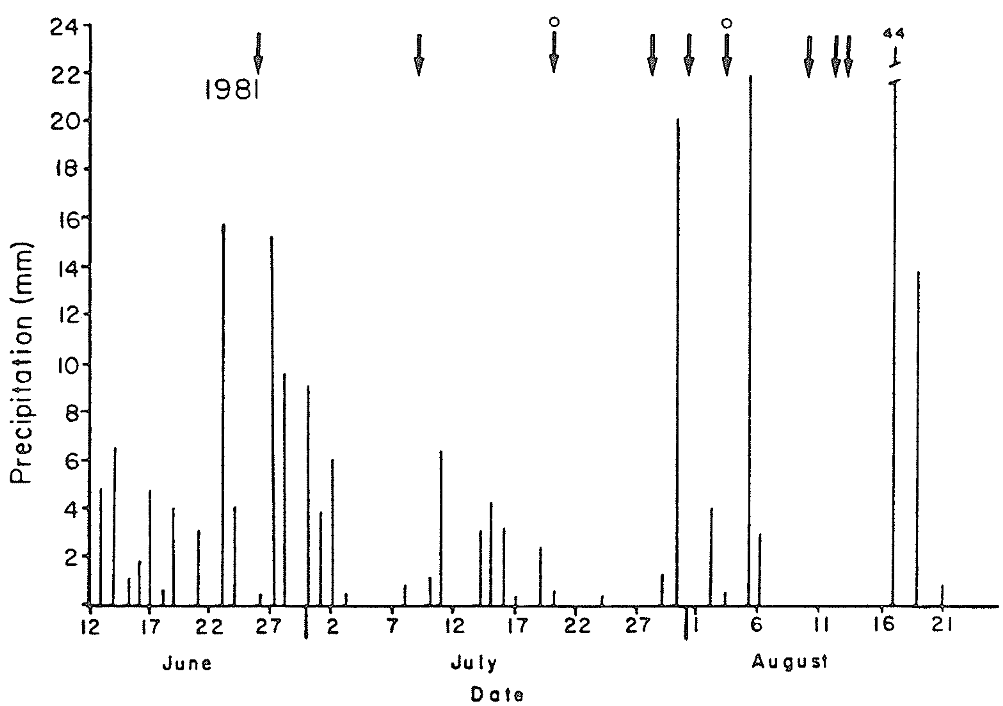
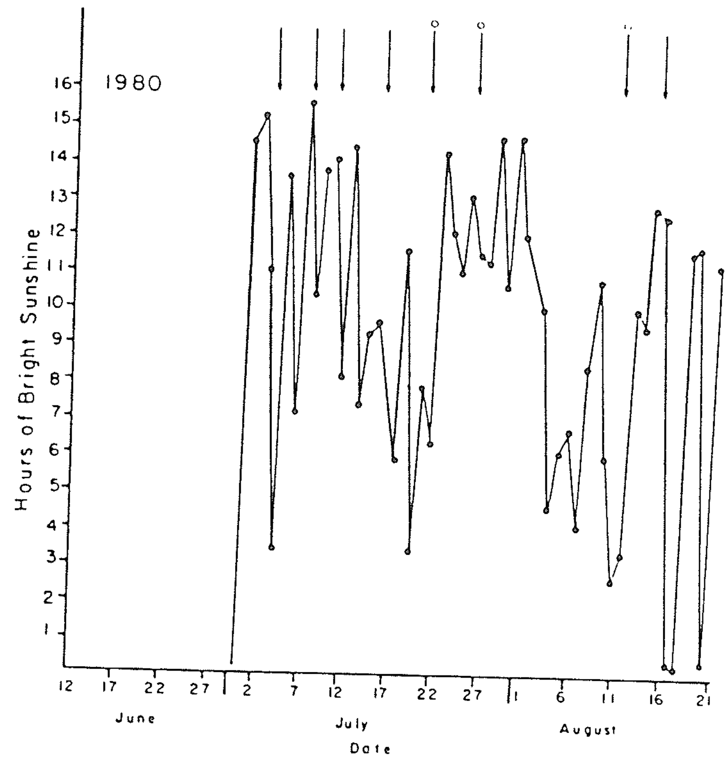

1981
44
Precipitation (mm)
June
July
August
Date

Figure 20. The hours of bright sunshine throughout the summer in 1980. The dates on which drones were introduced are indicated with arrows. Dates with poor drone acceptance are indicated by a "0".

Figure 21. The hours of bright sunshine throughout the summer in 1981. The dates on which drones were introduced are indicated with arrows. Dates with poor drone acceptance are indicated by a "0".


1980
Hours of Bright Sunshine
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
12
17
22
27
2
7
12
17
22
27
1
6
11
16
21
June
July
August
Date

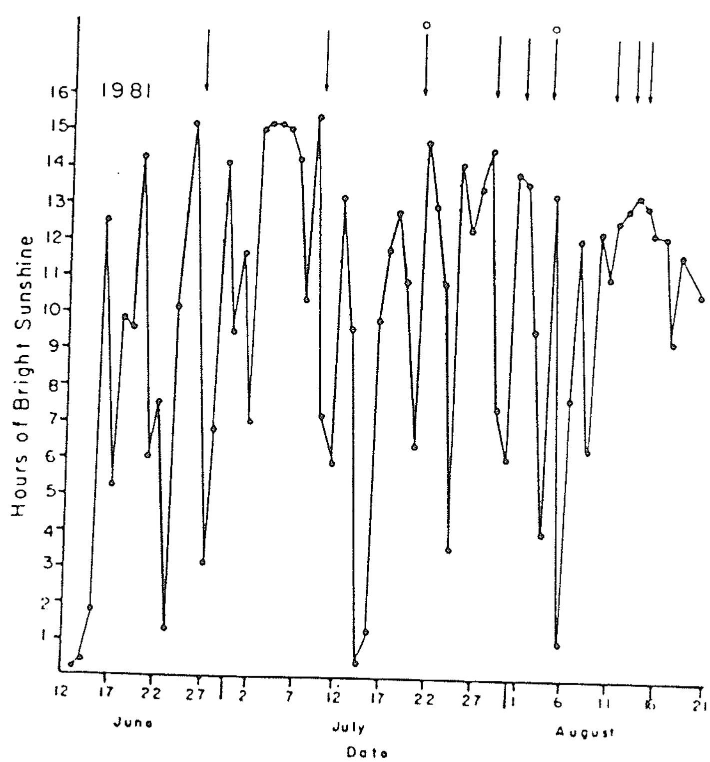
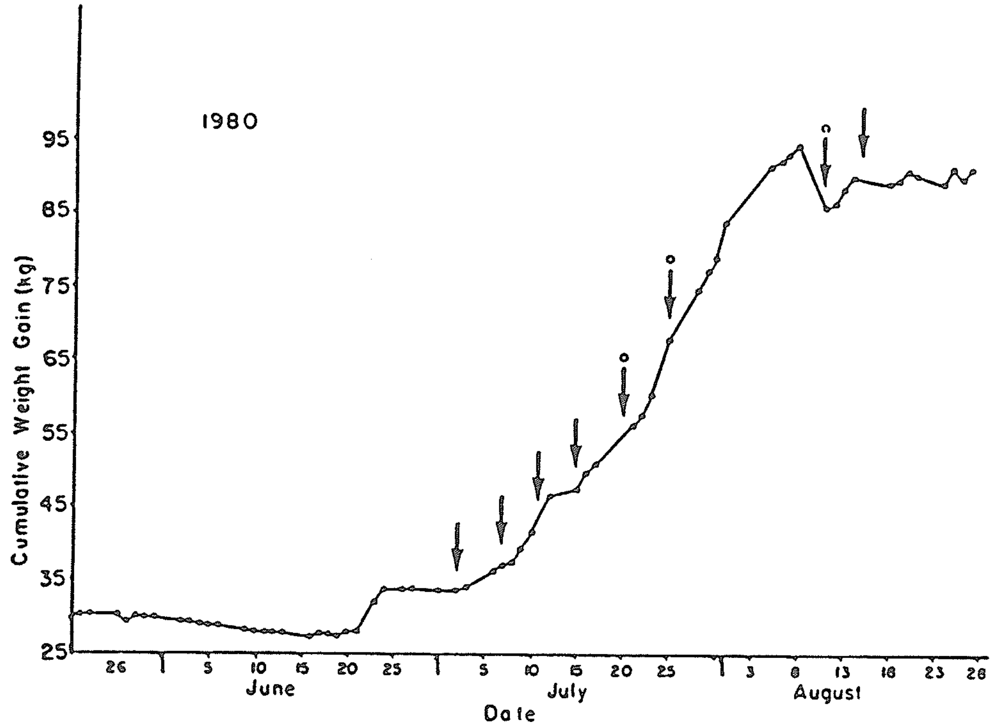

1981
Hours of Bright Sunshine
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
12
17
22
27
2
7
12
17
22
27
1
6
11
21
June
July
August
Date

Figure 22. Cumulative weight gain of scale colonies during the summer of 1980. The dates on which drones were introduced are indicated with arrows. Dates with poor drone acceptance are indicated by a "0".

Figure 23. Cumulative weight gain of scale colonies during the summer of 1981. The dates on which drones were introduced are indicated with arrows. Dates with poor drone acceptance are indicated by a "0".


1980
Cumulative Weight Gain (kg)
95
85
75
65
55
45
35
25
26
5
10
15
20
25
5
10
15
20
25
3
8
13
18
23
28
June
July
August
Date

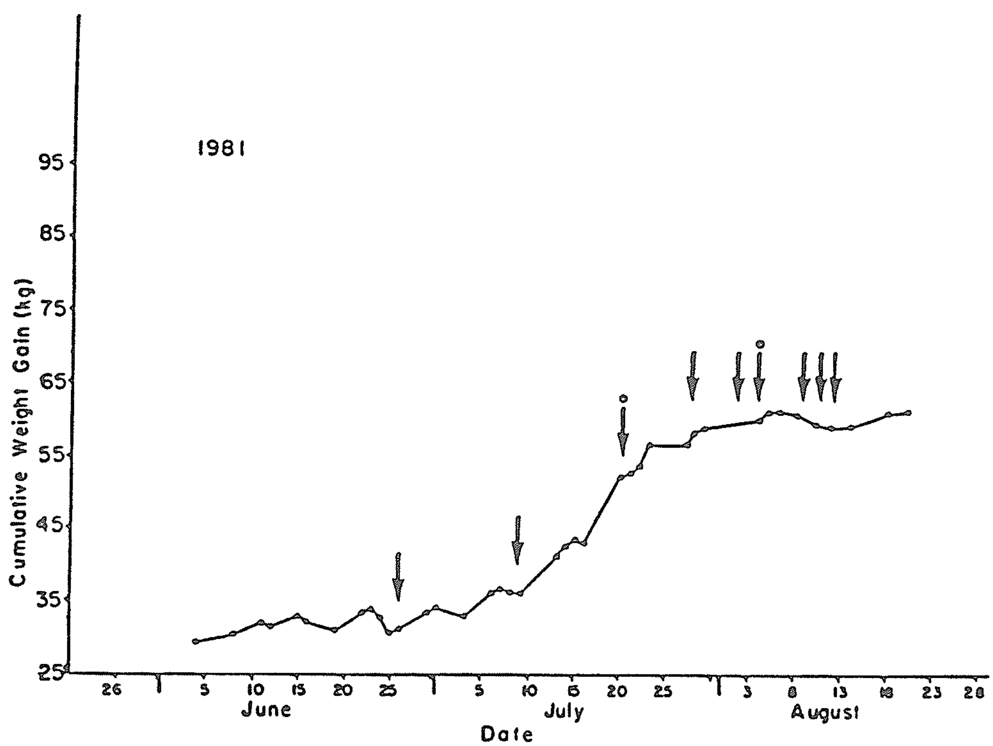
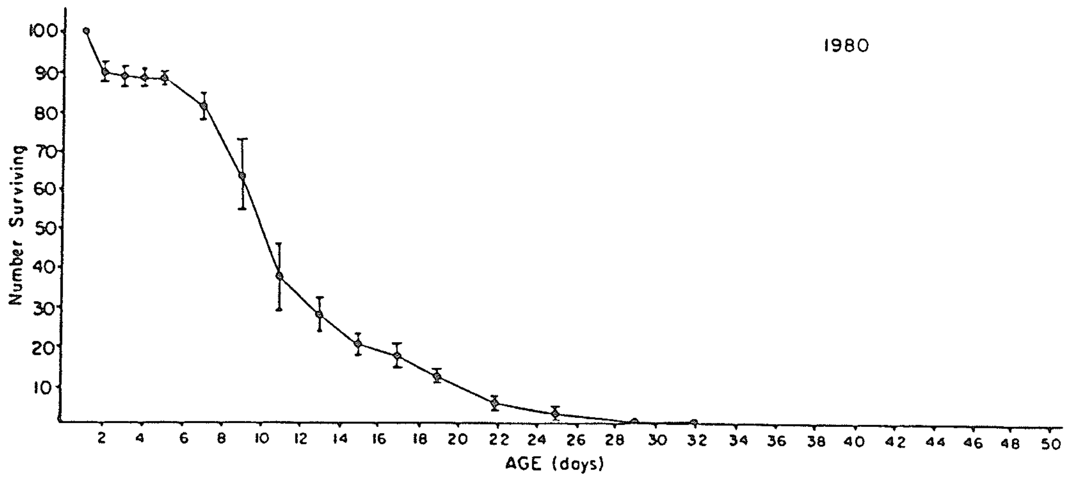
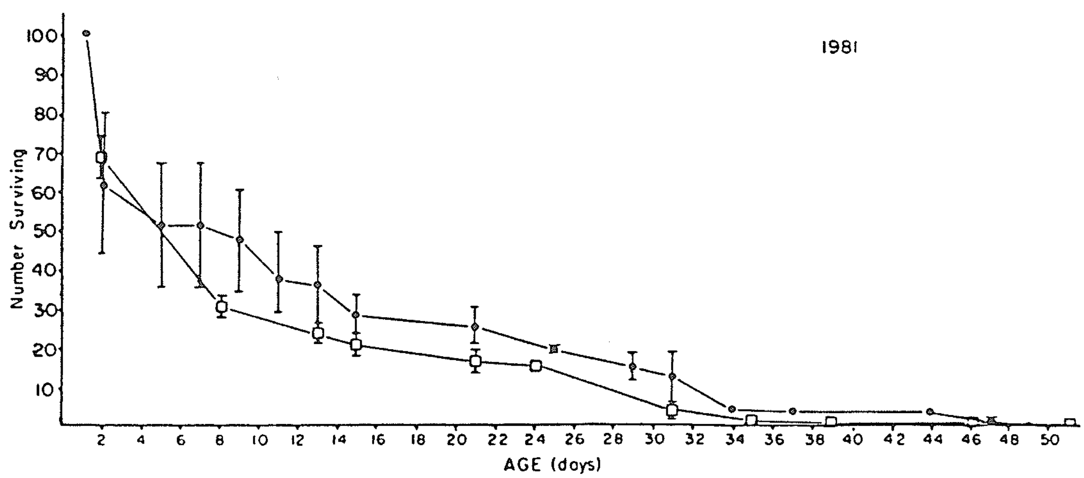

1981
Cumulative Weight Gain (kg)
95
85
75
65
55
45
35
25
26
5
10
15
20
25
5
10
15
20
25
3
8
13
18
23
28
June
July
August
Date

Figure 24. Survival curve of adult drone honey bees on 3 July, 1980 (from 3 colonies).

Figure 25. Survival curves of adult drone honey bees on 26 June, 1981 (——□—— from 3 colonies) and on 9 July, 1981 (——●—— from 2 colonies).

Figure 26. Survival curves of adult drone honey bees on 12 August, 1981 (——●—— from one colony).


1980
Number Surviving
AGE (days)


1981
Number Surviving
AGE (days)

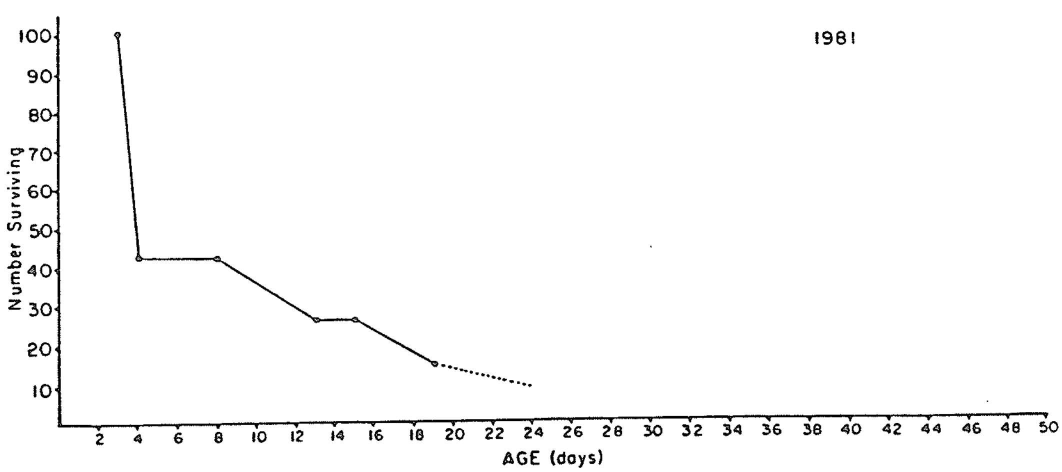
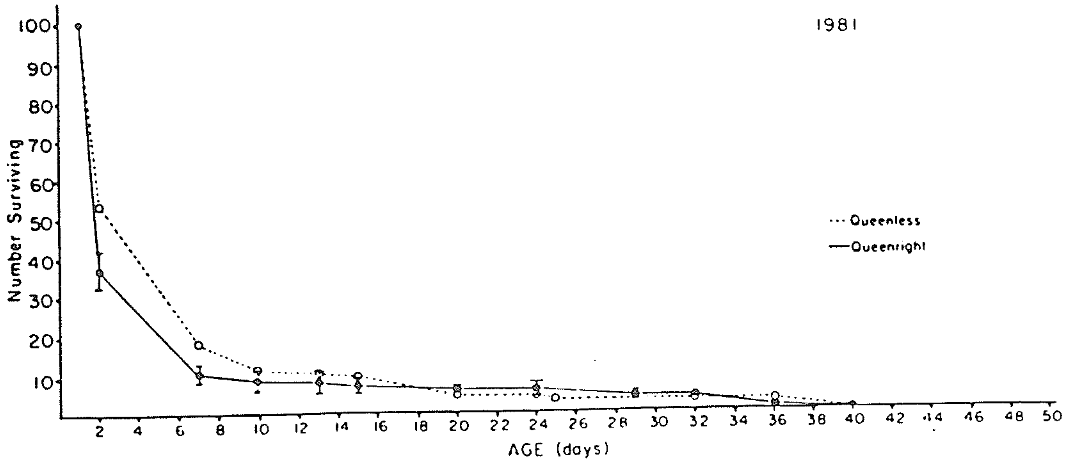
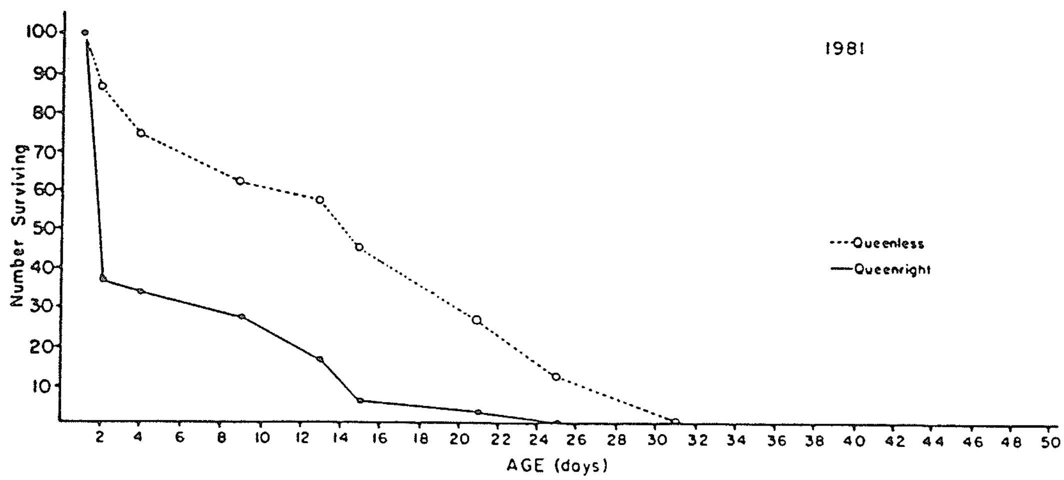

1981
Number Surviving
AGE (days)

Figure 27. Survival curves of drones from four queenright colonies
(——●——) and from one queenless colony
(——○——) (20 July, 1981).

Figure 28. Survival curves of drones from one queenright colony
(——●——) and from one queenless colony
(——○——) (31 July, 1981).

Figure 29. Survival curves of drones from six queenright colonies
(——●——) and from one queenless colony
(——○——) (3 August, 1981).


1981
··· Queenless
— Queenright
Number Surviving
AGE (days)


1981
--- Queenless
— Queenright
Number Surviving
AGE (days)

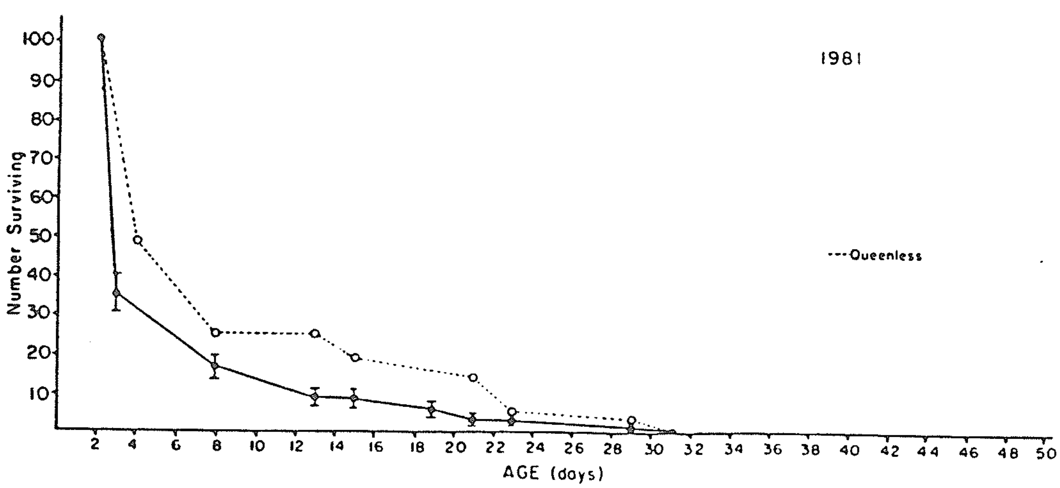
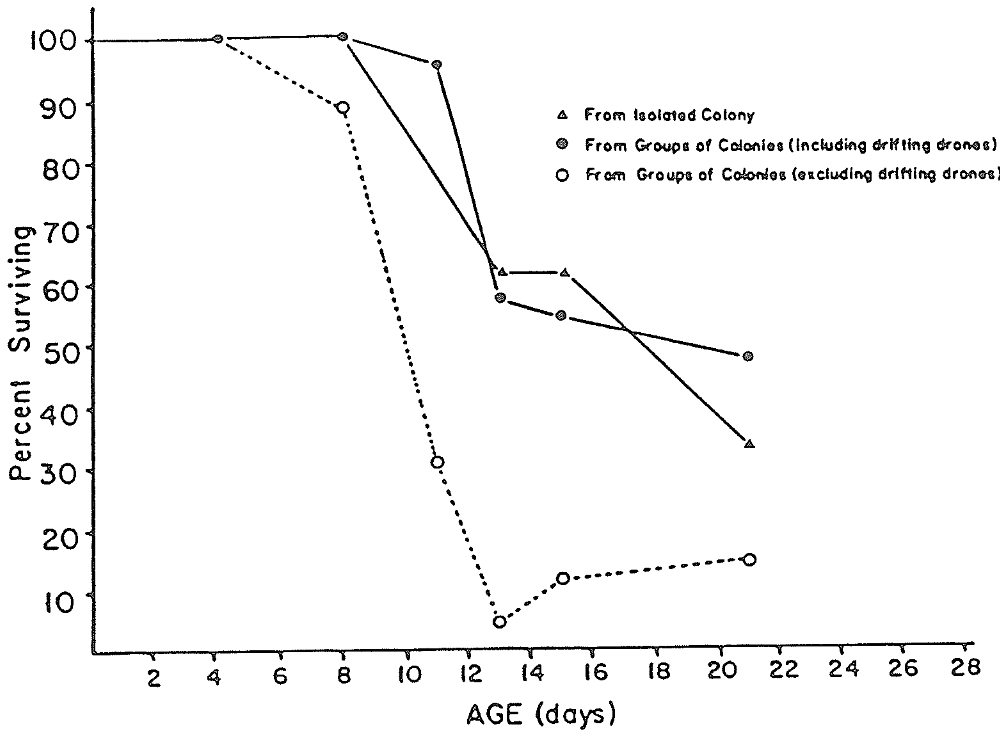

1981
--- Queenless
Number Surviving
AGE (days)

Figure 30. Survival curves of drones from groups of colonies where drifting occurred (1m. experiment) and from isolated colonies where drones did not drift.

Figure 31. Survival curves of drones from groups of colonies where drifting occurred (5m. experiment) and from isolated colonies where drones did not drift.


100
90
80
70
60
50
40
30
20
10
Percent Surviving
2 4 6 8 10 12 14 16 18 20 22 24 26 28
AGE (days)
From Isolated Colony
From Groups of Colonies (including drifting drones)
From Groups of Colonies (excluding drifting drones)

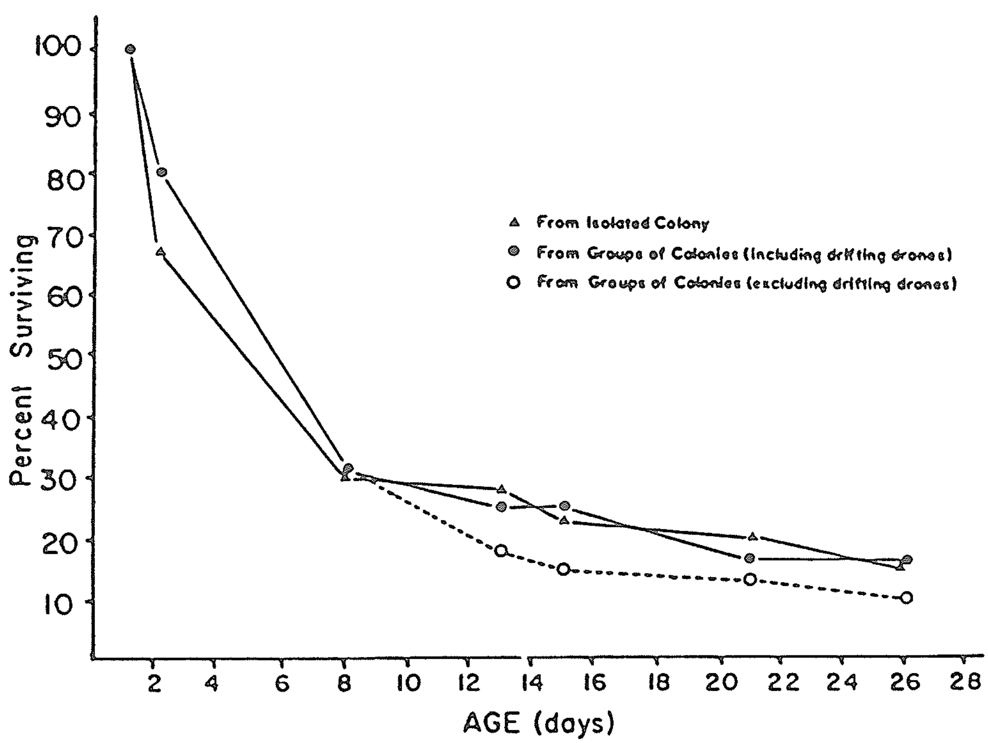
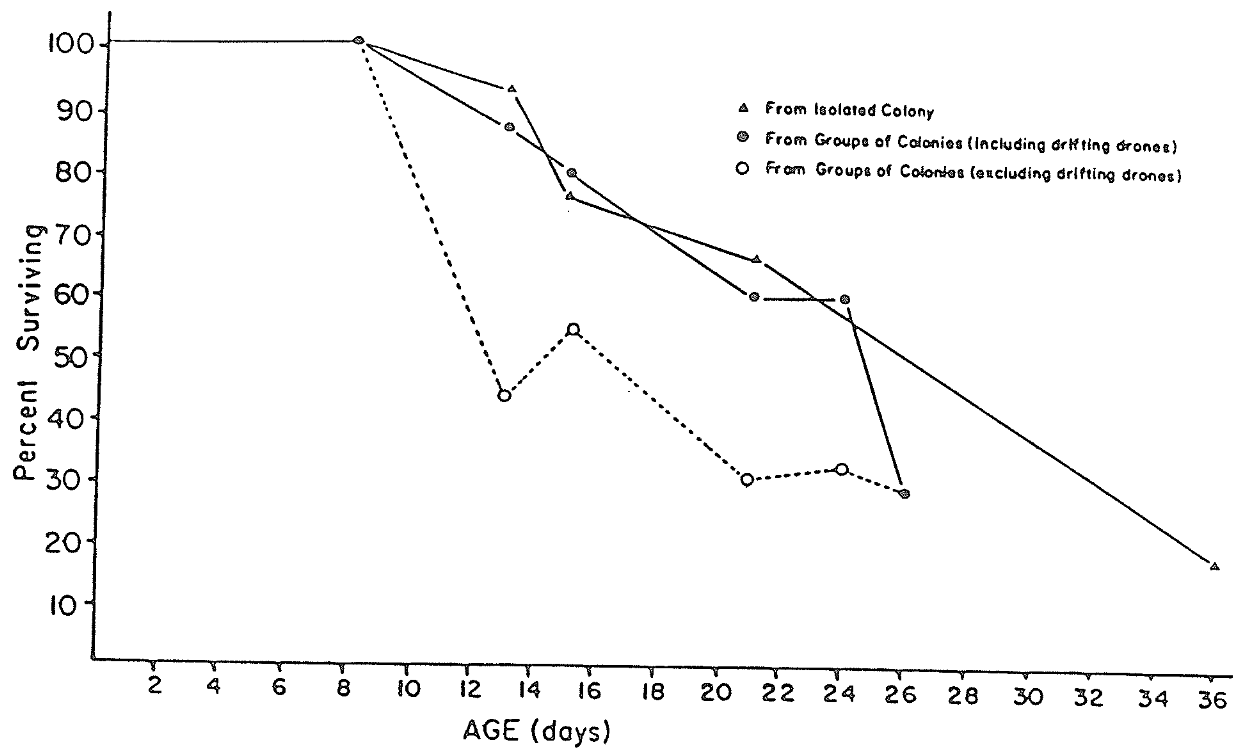

100
90
80
70
60
50
40
30
20
10
Percent Surviving
2 4 6 8 10 12 14 16 18 20 22 24 26 28
AGE (days)
From Isolated Colony
From Groups of Colonies (including drifting drones)
From Groups of Colonies (excluding drifting drones)

Figure 32. Survival curves of drones from groups of colonies where drifting occurred (5m. experiment) and from isolated colonies where drones did not drift.

Figure 33. Survival curves of drones from groups of colonies where drifting occurred (50m. experiment) and from isolated colonies where drones did not drift.


100
90
80
70
60
50
40
30
20
10
Percent Surviving
From Isolated Colony
From Groups of Colonies (including drifting drones)
From Groups of Colonies (excluding drifting drones)
2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36
AGE (days)

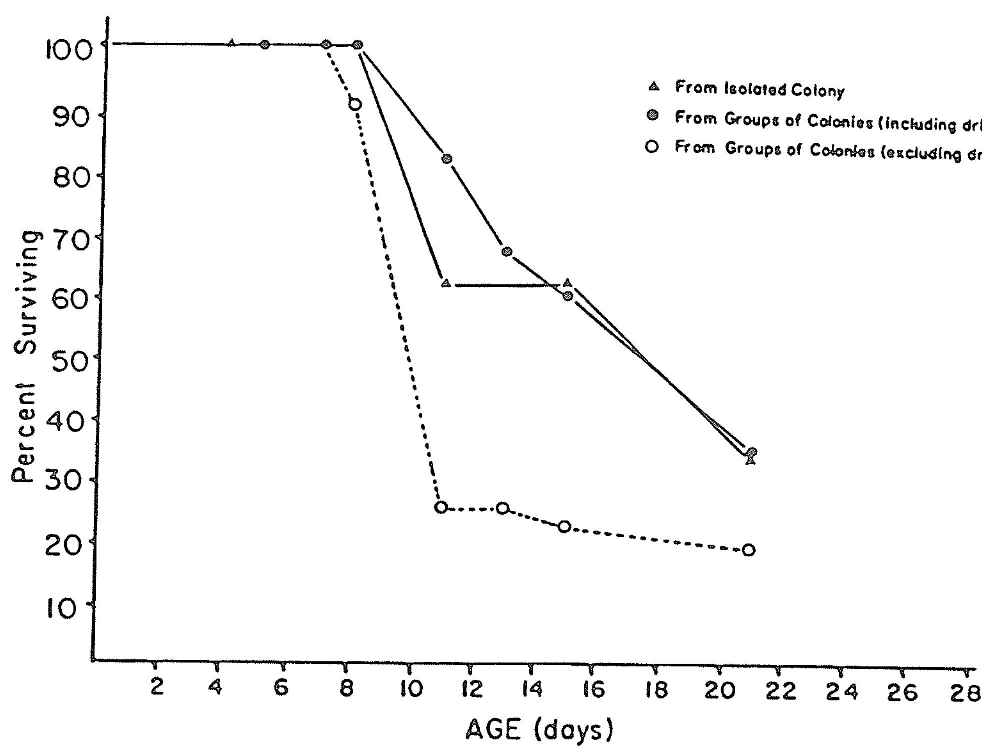
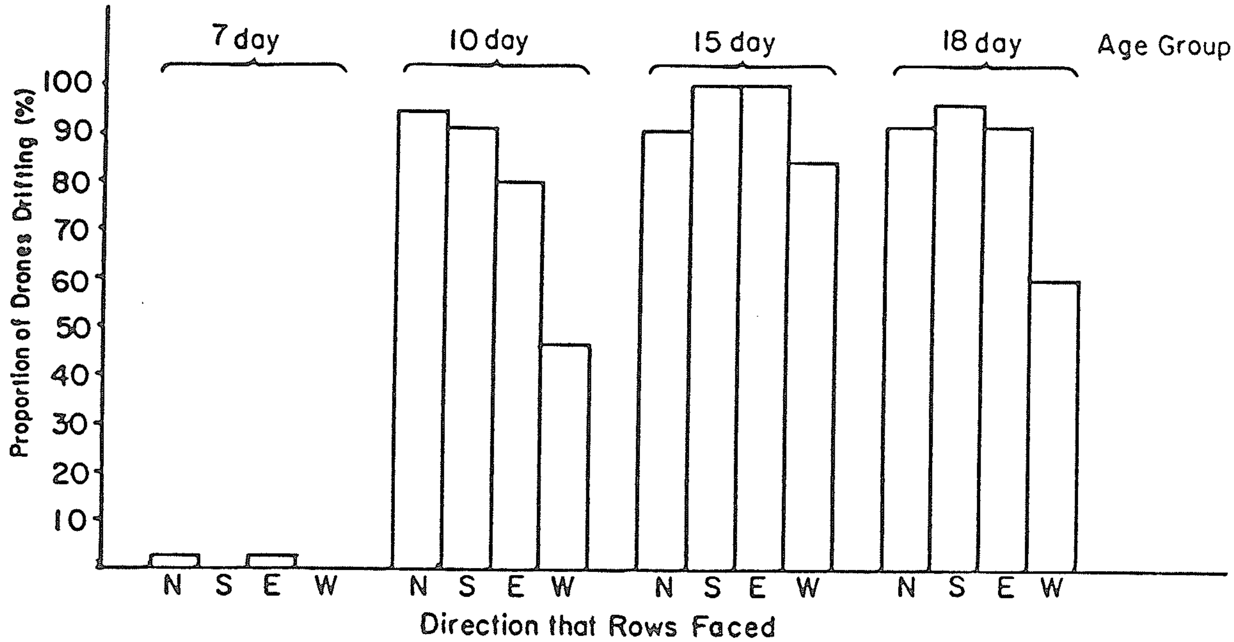
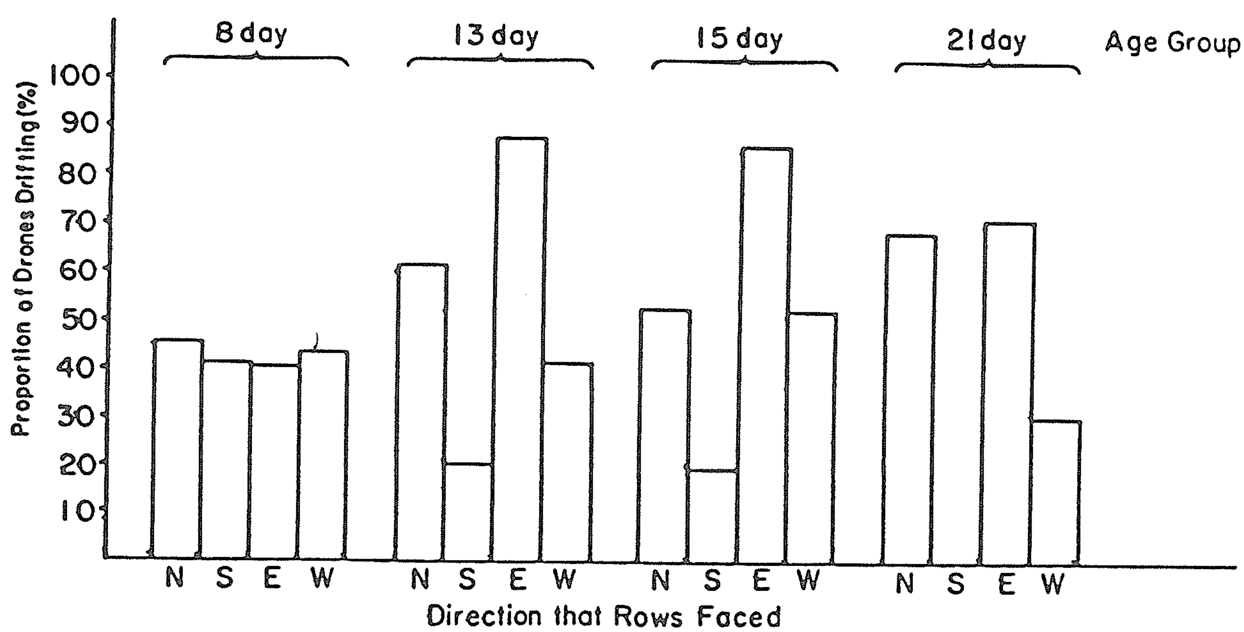

100
90
80
70
60
50
40
30
20
10
Percent Surviving
From Isolated Colony
From Groups of Colonies (including drifting drones)
From Groups of Colonies (excluding drifting drones)
2 4 6 8 10 12 14 16 18 20 22 24 26 28
AGE (days)

Figure 34. Proportions of drones drifting from each of four rows of hives that faced the cardinal points of the compass (large square experiment) in 1980.

Figure 35. Proportions of drones drifting from each of four rows of hives that faced the cardinal points of the compass (large square experiment) in 1981.



7 day
10 day
15 day
18 day
Age Group
100
90
80
70
60
50
40
30
20
10
Proportion of Drones Drifting (%)
N S E W
N S E W
N S E W
N S E W
Direction that Rows Faced



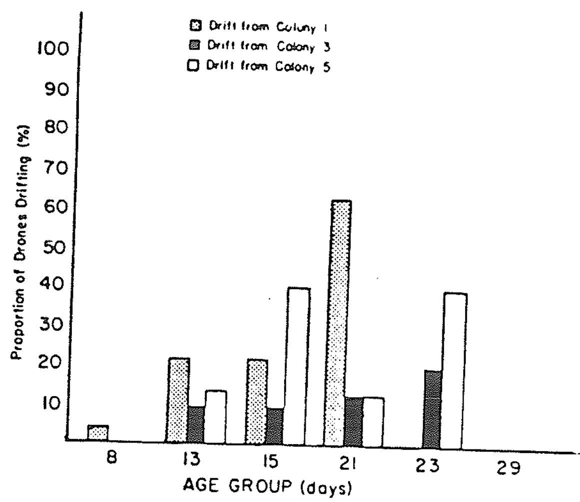
8 day
13 day
15 day
21 day
Age Group
100
90
80
70
60
50
40
30
20
10
Proportion of Drones Drifting (%)
N S E W
N S E W
N S E W
N S E W
Direction that Rows Faced

Figure 36. The difference in the proportion of drones drifting from the centre colony and the end colonies of straight rows (3 July 1980).

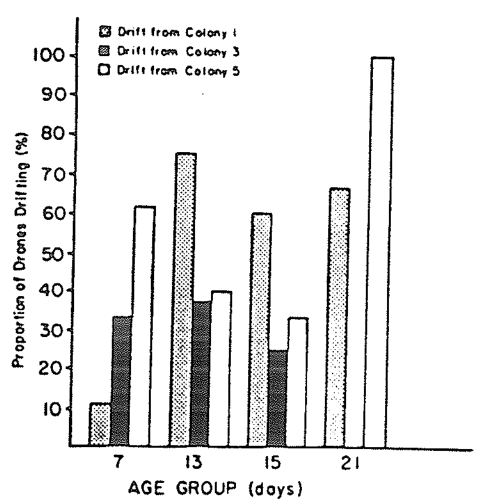
Figure 37. The difference in the proportion of drones drifting from the centre colony and the end colonies of straight rows (3 August 1981).

Figure 38. The difference in the proportion of drones drifting from the centre colony and the end colonies of straight rows (10 August 1981).

Drift from Colony 1
Drift from Colony 3
Drift from Colony 5
Proportion of Drones Drifting (%)
100
90
80
70
60
50
40
30
20
10
7
9
11
13
15
17
19
22
25
27
AGE GROUP (days)



Drift from Colony 1
Drift from Colony 3
Drift from Colony 5
Proportion of Drones Drifting (%)
100
90
80
70
60
50
40
30
20
10
8
13
15
21
23
29
AGE GROUP (days)



Drift from Colony 1
Drift from Colony 3
Drift from Colony 5
Proportion of Drones Drifting (%)
100
90
80
70
60
50
40
30
20
10
7
13
15
21
AGE GROUP (days)

Table 1. Mean longevity of adult drones introduced into colonies (including drifting drones).

Date trial began	Number of colonies	Mean longevity of adult drones**
26 June	2	17.8 ± 1.45
9 July	3	12.4 ± 1.07
20 July	4	9.2 ± 1.40
*20 July	1	7.7
31 July	1	11.8
*31 July	1	15.4
3 August	5	10.0 ± 0.93
*3 August	1	12.4
12 August	1	16.3
Seasonal mean		12.8 ± 3.25

* Queenless colonies
** Age in days, with standard errors

Table 2 . Effect of age of drones on the proportion drifting from their parent colonies.

Age (days)	Total number found *	Number and percent drifting from parent colony
2	269	0 (0%)
3	266	0 (0)
4	266	0 (0)
5	266	0 (0)
7	258	6 (2)
9	206	61 (30)
11	113	58 (51)
13	84	43 (51)
15	62	41 (66)
17	53	31 (61)
19	38	26 (68)
22	14	13 (93)
25	8	7 (88)
29	1	1 (100)

* Drones introduced into three colonies

Table 3. Number of times individual drones changed hives.

Trial	Number of examinations	Age of drones (days)	Number of hives visited			
			0*	1	2	3
A	0	1	40 (100%)	0 (0%)	0 (0%)	0 (0%)
	1	2	35 (100%)	0 (0%)	0 (0%)	0 (0%)
	2	8	18 (78%)	5 (22%)	0 (0%)	0 (0%)
	3	13	9 (47%)	7 (37%)	3 (16%)	0 (0%)
	4	15	5 (36%)	3 (21%)	4 (29%)	2 (14%)
	5	20	1 (10%)	5 (50%)	1 (10%)	3 (30%)
	Total		21 (52%)	9 (23%)	6 (15%)	4 (10%)
	Number of examinations	Age of drones (days)	Number of hives visited			
			0 *	1	2	3
B	0	5	13 (100%)	0 (0%)	0 (0%)	0
	1	8	11 (85%)	2 (15%)	0 (0%)	0
	2	13	10 (77%)	2 (15%)	1 (8%)	0
	3	15	9 (69%)	3 (23%)	1 (8%)	0
	4	21	8 (62%)	4 (31%)	1 (8%)	0
	5	24	1 (17%)	3 (50%)	2 (33%)	0
	Total		7 (54%)	4 (31%)	2 (15%)	0

* Number (and percent) of drones drifting at each age interval.

Table 4. Number of drones that changed hives between examinations.

Trial	Number of examinations	Age of drones (days)	Number and percentage of drones in same hives	Number and percentage of drones that changed hives
A	0	1	40 (100%)	0 (0%)
	1	2	35 (100%)	0 (0%)
	2	8	18 (78%)	5 (22%)
	3	13	11 (58%)	8 (42%)
	4	15	8 (62%)	5 (38%)
	5	20	4 (40%)	6 (60%)
B	0	5	13 (100%)	0 (0%)
	1	8	11 (85%)	2 (15%)
	2	13	11 (85%)	2 (15%)
	3	15	11 (85%)	2 (15%)
	4	21	10 (77%)	3 (23%)
	5	24	5 (83%)	1 (17%)

Table 5. The number of drones drifting to colonies placed at distances of 1 m., 5 m., 50 m., 100 m. and 200 m.

Age (days)	Number and Percentage Drifting from Parent colony				
	1m*	5m**	50m***	100m*	200m*
8	0 (0%)	4 (5%)	0 (0%)	0 (0%)	0
13	31 (49)	15 (41)	20 (63)	4 (17)	0
15	18 (31)	15 (46)	10 (61)	4 (17)	0
21	20 (57)	6 (29)	11 (55)	3 (15)	0

* One replicate
** Three replicates
*** two replicates

Table 6. Direction of hives to which drones drifted when colonies were placed at equal distances from a central colony.

Experiment	Age (days)	Total Number Found	Direction of Hives (number drifting)							
			N	NE	E	SE	S	SW	W	NW
1m*	15	58	1	-	8	-	2	-	7	-
5m(a)*	15	25	0	1	3	1	1	0	4	0
5m(b)**	15	25	0	0	2	0	0	0	1	0
5m(c)**	15	43	2	2	4	0	0	2	0	16
50m(a)*	9	9	5	-	0	-	0	-	0	-
50m(b)*	15	23	2	-	0	-	12	-	0	-
100m*	15	23	0	-	0	-	4	-	0	-

* hive entrances facing south

** hive entrances facing north

Table 7. The daily direction and speed of the prevailing winds for the periods in which the 50 m. and 100 m. experiments were conducted.

Experiment	Date	Average Wind Speed	Prevailing Wind Direction
	8	18.0	N
	9	13.7	NNE
	10	7.7	SSW
50 m.(a)	11	10.9	WSW
	12	11.3	ENE
	13	12.8	S
	14	15.2	N
	17	13.3	S
	18	13.1	S
50 m.(b)	19	22.2	S
and	20	15.2	SSE
100 m.	21	19.2	S,SSE
	22	6.7	S,SSE
	23	13.3	S,SSE

Table 8 . Drifting of drones between three apiary layouts placed in a north- south line (spaced 40 m. apart).

Group drifted from	Age (days)	Total marked drones found	Number (%) drifted to other patterns	Number (%) drifted to pattern 40m. north	Number (%) drifted to pattern 80m. north
1	9	208	10 (5%)	8 (4%)	2 (1%)
	13	95	14 (15%)	12 (13%)	2 (2%)
	15	64	7 (11%)	5 (8%)	2 (2%)
	19	38	6 (16%)	6 (16%)	0 (0%)
	22	17	7 (41%)	6 (35%)	1 (6%)
	Age (days)	**Total marked drones found**	**Number (%) drifted to other patterns**	**Number (%) drifted to pattern 40m. south**	**Number (%) drifted to pattern 80m. south**
2	6	183	2 (1%)	2 (1%)	0 (0%)
	12	88	5 (6%)	3 (3%)	2 (2%)
	14	60	7 (12%)	2 (3%)	5 (8%)
	17	30	8 (27%)	4 (13%)	4 (13%)
	20	30	1 (3%)	1 (3%)	0 (0%)
	Age (days)	**Total marked drones found**	**Number (%) drifted to other patterns**	**Number (%) drifted to pattern 40m. north**	**Number (%) drifted to pattern 80m. south**
3	6	273	3 (1%)	2 (1%)	1 (0%)
	8	247	8 (3%)	1 (0%)	7 (3%)
	10	145	3 (2%)	2 (1%)	1 (1%)
	14	88	6 (7%)	0 (0%)	6 (7%)
	18	75	9 (12%)	0 (0%)	9 (12%)

Table 9. Drifting of drones between five apiary layouts placed in an east-west line (spaced 100 to 150 m. apart).

			Number of drones drifting to other groups of hives				
Group drifted from	Age (days)	Total drones found	Total drifted	To pattern 150 m. east	To pattern 250 m. east	To pattern 350 m. east	To pattern 450 m. east
	7	132	16 (12%)	5 (4%)	9 (7%)	0	2 (2%)
1	11	96	17 (18)	13 (14)	2 (2)	0	2 (2)
	14	57	14 (25)	13 (23)	0 (0)	0	1 (2)
Group drifted from	Age (days)	Total drones found	Total drifted	To pattern 150 m. west	To pattern 100 m. east	To pattern 200 m. east	To pattern 300 m. east
	10	50	14 (28%)	3 (6%)	7 (14%)	3 (6%)	1 (2%)
2	15	50	24 (48%)	7 (14)	4 (8)	6 (12)	7 (14)
	18	30	16 (32%)	4 (8)	5 (10)	3 (6)	4 (8)
Group drifted from	Age (days)	Total drones found	Total drifted	To pattern 250 m. west	To pattern 100 m. west	To pattern 100 m. east	To pattern 200 m. east
	11	36	13 (36%)	3 (8%)	6 (17%)	2 (5%)	2 (5%)
3	15	32	8 (25)	2 (6)	3 (9)	0 (0)	3 (9)
	18	32	17 (53)	1 (3)	13 (41)	0 (0)	3 (9)
Group drifted from	Age (days)	Total drones found	Total drifted	To pattern 350 m. west	To pattern 200 m. west	To pattern 100 m. west	To pattern 100 m. east
	11	37	22 (60%)	2 (5%)	13 (35%)	2 (5%)	5 (14%)
4	15	37	26 (70)	3 (8)	13 (35)	6 (16)	4 (11)
	18	18	12 (67)	2 (11)	5 (28)	0 (0)	5 (28)
Group drifted from	Age (days)	Total drones found	Total drifted	To pattern 450 m. west	To pattern 300 m. west	To pattern 100 m. west	To pattern 100 m. west
	6	85	11 (13%)	3 (4%)	4 (5%)	3 (4%)	1 (1%)
5	9	62	1 (2)	1 (2)	0 (0)	0 (0)	0 (0)
	11	50	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

Table 10. Direction of drift in four rows of hives facing the cardinal points of the compass (large square experiment).

Replicate	Age (days) of drones when hives were examined	Direction hives faced: North A	North B	North C	North D	North E	South A	South B	South C	South D	South E
1	7	38	0	1	W	none	67	0	0	-	none
	10	15	0	4	W	$p < .05$	11	7	1	W	$p < .05$
	15	12	2	8	W	$p < .025$	5	2	1	W	none
	18	6	2	3	W	none	5	4	0	W	$p < .05$
2	8	33	9	2	E	$p < .025$	21	7	0	W	$p < .01$
	13	24	7	5	E	none	12	0	0	-	none
	15	16	6	1	E	$p < .05$	10	0	0	-	none
	21	13	6	1	E	$p < .05$	7	0	0	-	none

Replicate	Age (days) of drones when hives were examined	Direction hives faced: East A	East B	East C	East D	East E	West A	West B	West C	West D	West E
1	7	37	0	0	-	none	26	0	0	-	none
	10	10	5	0	S	$p < .05$	11	1	3	S	none
	15	4	3	1	S	none	10	6	1	N	none
	18	3	2	0	S	none	5	3	0	N	none
2	8	39	7	7	-	none	39	9	5	N	none
	13	24	14	5	S	$p < .05$	33	3	9	S	none
	15	17	8	7	S	none	21	3	7	S	none
	21	13	6	3	S	none	9	1	1	-	none

A Total number found in row
B Number drifted left of centre
C Number drifted right of centre
D Direction of drift in row
E Degree of significance

Table 11. Drifting of drones between the four rows of the large square.

Replicate	Age (days) of drones when hives were examined	North: Total found	North: S*	North: E	North: W	South: Total found	South: N*	South: E	South: W
1	10	25	0	2	10	31	0	2	18
	15	21	0	0	9	29	3	0	21
	18	12	0	2	5	26	2	2	17
2	8	38	2	3	2	24	1	0	1
	13	31	1	2	4	14	0	0	1
	15	19	0	1	2	11	0	0	1

Replicate	Age (days) of drones when hives were examined	East: Total found	East: N*	East: S	East: W	West: Total found	West: N*	West: S	West: E
1	10	24	4	0	10	13	0	2	0
	15	21	7	3	7	13	3	0	0
	18	12	0	3	6	7	4	0	0
2	8	37	2	0	0	41	2	0	0
	13	25	1	1	0	35	1	3	0
	15	21	2	1	0	25	1	2	0

* The direction rows faced, to which drones drifted.

Table 12. Direction of drift from centre colonies in rows of 5 hives that faced west.

Date*	Age (days)	Total found	Number drifted north	Number drifted south	Direction and significance
3 July 1980	9	77	3 (4%)	21 (27%)	S P<0.001
	11	40	6 (15)	17 (43)	S P<0.025
	13	31	4 (13)	18 (52)	S P<0.005
	15	20	3 (15)	14 (70)	S P<0.01
	17	19	2 (11)	10 (53)	S P<0.025
	19	13	1 (8)	8 (62)	S P<0.025
	22	9	0 (0)	8 (89)	S P<0.005
	25	5	2 (40)	3 (60)	S n.s.**
15 July 1980	8	52	0 (0%)	2 (4%)	S n.s.**
	11	23	1 (4)	3 (13)	S n.s.
	15	15	6 (40)	6 (40)	- n.s.
	18	16	5 (31)	4 (25)	N n.s.
20 July 1981	13	11	0 (0%)	1 (9%)	S n.s.**
	15	11	0 (0)	1 (9)	S n.s.
	21	8	0 (0)	1 (13)	S n.s.
	23	5	0 (0)	1 (20)	S n.s.
3 Aug. 1981	7	31	9 (29%)	1 (3%)	N P<0.025
	13	24	2 (8)	7 (29)	S n.s.**
	15	12	2 (17)	1 (8)	N n.s.
10 Aug. 1981	6	91	1 (1%)	3 (3%)	S n.s.**
	8	87	10 (12)	26 (30)	S P<0.01
	10	54	4 (8)	30 (56)	S P<0.001
	11	30	1 (4)	18 (72)	S P<0.001
	14	30	1 (4)	26 (90)	S P<0.001

* Date on which experiment began.
** Not significant P>0.05.
S More drones drifted south.
N More drones drifted north.

Table 13. Direction of drift from end colonies in rows of 5 hives facing west.

Date*	Age (days)	Drift from hive 1: Total found	Drift from hive 1: Number drifted	Drift from hive 5: Total found	Drift from hive 5: Number drifted	Direction and significance
3 July 1980	9	74	13 (18%)	47	9 (19%)	- n.s.**
	11	39	14 (36)	20	2 (10)	S n.s.
	13	30	7 (23)	20	7 (35)	N n.s.
	15	23	10 (43)	14	7 (57)	N n.s.
	17	14	5 (36)	11	5 (46)	N n.s.
	19	8	6 (75)	11	4 (36)	S n.s.
	21	2	2 (100)	1	1 (100)	S n.s.
20 July 1981	8	26	1 (4%)	21	0 (0%)	S n.s.**
	13	14	3 (21)	15	2 (13)	S n.s.
	15	14	3 (21)	15	6 (40)	N n.s.
	21	8	5 (63)	8	1 (12)	S n.s.
	23	2	0 (0)	5	2 (40)	N n.s.
3 Aug. 1981	7	9	1 (11%)	13	8 (61%)	N n.s.**
	13	8	6 (75)	5	2 (40)	S n.s.
	15	5	3 (60)	3	1 (33)	S n.s.
	21	3	2 (67)	3	3 (100)	N n.s.
10 Aug. 1981	6	91	3 (3%)	91	3 (3%)	- n.s.**
	8	78	28 (36)	73	16 (22)	S n.s.
	10	57	41 (72)	52	20 (39)	S $P<0.05$
	11	23	13 (57)	23	5 (22)	S $P<0.005$
	14	18	15 (83)	14	3 (21)	S $P<0.025$

* Date on which experiment began.
** Not significant $P>0.05$.
S More drones drifted south.
N More drones drifted north.

Table 14. Direction of drift from paired colonies with hive entrances facing south.

Date*	Age (days)	Drift from hive 1 Total found	Number drifted	Drift from hive 2 Total found	Number drifted	Direction and significance
15 Aug. 1980	10	54	2 (4%)	63	0 (0%)	E n.s.**
	13	45	3 (7)	54	18 (33)	W P<0.005
	15	47	5 (11)	50	12 (24)	W P<0.05
20 July 1981	7	29	0 (0%)	6	1 (17%)	W n.s.**
	10	8	0 (0)	5	2 (40)	W n.s.
	13	5	1 (1)	5	3 (60)	W n.s.
	15	5	0 (0)	5	4 (80)	W P<0.05
	20	5	0 (0)	4	2 (50)	W n.s.
28 July 1981	7	26	2 (7%)	40	5 (13%)	W n.s.
	12	26	2 (7)	39	18 (46)	W P<0.01
	15	21	2 (10)	34	17 (50)	W P<0.025
	21	16	1 (6)	27	17 (63)	W P<0.01
	24	15	0 (0)	23	12 (52)	W P<0.005
	28	10	1 (10)	4	4 (100)	W P<0.05

* Date on which experiment began.
** Not significan P>0.05.
E More drones drifted east.
W More drones drifted west.

Table 15. Amount of drone drift from a row of 5 colonies spaced 1 m. apart (by drones 13-15 days old).

Trial	Total found	Number drifted	Percentage drift from parent
1	56	30	54%
2	37	17	46
3	40	10	25
4	57	34	60
5	10	1	10
6	12	4	38
7	15	12	80
8	10	1	10
9	24	9	38
10	57	35	61
11	37	17	46
Total	355	170	48%

Table 16. The amount of drift in offset entrance apiary layouts vs. the amount of drift in controls.

Date*	Experiment	Age (days)	Total found	Number in parent	Number drifted	Drift reduced	Degree of significance
15 July 1980	A	7	263	256	7 (3%)	No	n.s.**
	B	7	161	154	7 (3%)		
	A	11	97	58	39 (40)	No	n.s.
	B	11	117	56	61 (52)		
	A	14	56	26	30 (53)	No	n.s.
	B	14	86	41	45 (52)		
3 Aug. 1981	A	5	63	63	0 (0%)	No	P<0.05
	B	5	114	106	8 (7%)		
	A	7	53	34	19 (36)	No	n.s.
	B	7	91	45	46 (51)		
	A	13	37	20	17 (46)	No	n.s.
	B	13	48	24	24 (50)		
	A	15	20	13	7 (35)	No	n.s.
	B	15	38	10	28 (74)		
	A	21	9	4	5 (56)	No	n.s.
	B	21	21	2	19 (91)		
10 Aug. 1981	A	8	66	65	1 (2%)	No	n.s.
	B	8	35	33	2 (6%)		
	A	13	40	34	6 (15)	No	n.s.
	B	13	19	15	4 (21)		
	A	15	40	30	10 (25)	Yes	n.s.
	B	15	19	16	3 (16)		
	A	21	24	17	7 (29)	Yes	n.s.
	B	21	9	8	1 (5)		

* Date on which experiment began.
** Not significant P>0.05.
A Control layout.
B Offset entrance layout.

Table 17. The amount of drift in apiary layouts with coloured boards (on hives 1, 3, and 5), vs. the amount of drift in controls.

Date*	Experiment	Age (days)	Total found	Number in parent	Number drifted	Drift reduced	Degree of significance
	A	14	56	26	30 (53%)	Yes	n.s.**
	B	14	52	32	20 (39%)		
10 July 1980	A	17	44	23	21 (48)	Yes	P<0.05
	B	17	27	23	4 (15)		
	A	20	32	15	17 (53)	Yes	n.s.
	B	20	28	18	10 (36)		
	A	6	263	256	7 (3%)	Yes	n.s.**
	B	6	74	73	1 (1%)		
15 July 1980	A	9	198	151	47 (24)	Yes	n.s.
	B	9	56	44	12 (21)		
	A	15	56	26	30 (54)	No	n.s.
	B	16	50	20	30 (60)		

* Date on which experiment began.
** Not significant P>0.05.
A Control layout.
B Coloured board layout.

Table 18. The amount of drift in apiary layouts with coloured boards (on hives 1 and 3), vs. the amount of drift in controls.

Date*	Exper-iment	Age (days)	Total found	Number in parent	Number drifted	Drift reduced	Degree of significance
	A	8	19	19	0 (0%)	No	n.s.**
	B	8	2	2	0 (0%)		
3 Aug.	A	13	11	10	1 (10)	Yes	n.s.
1981	B	13	2	2	0 (0)		
	A	15	11	10	1 (40)	Yes	n.s.
	B	15	2	2	o (0)		
	A	5	31	31	0 (0%)	No	n.s.**
	B	5	29	28	1 (4%)		
	A	7	31	21	10 (32%)	Yes	P<0.05
	B	7	13	13	0 (0%)		
10 Aug.	A	13	24	15	9 (38)	Yes	n.s.
1981	B	13	10	8	2 (20)		
	A	15	12	9	4 (33)	Yes	n.s.
	B	15	10	7	3 (30)		
	A	21	3	3	0 (0)	No	n.s.
	B	21	1	0	1 (100)		

* Date on which experiment began.
** Not significant P>0.05.
A Control layout.
B Coloured board layout.

Table 19. The amount of drift in horseshoe apiary layouts vs. the amount of drift in controls.

Date*	Experiment	Age (days)	Total found	Number in parent	Number drifted	Drift reduced	Degree of significance
	A	8	52	50	2 (4%)	Yes	n.s.**
	B	8	54	54	0 (0%)		
15 July 1980	A	11	23	19	4 (17)	No	n.s.
	B	11	15	5	10 (77)		
	A	15	15	3	12 (80)	Yes	n.s.
	B	15	11	5	6 (55)		
	A	18	16	7	9 (56)	No	n.s.
	B	18	6	1	5 (83)		
	A	8	19	19	0 (0%)	No	n.s.**
	B	8	3	3	0 (0%)		
3 July 1981	A	13	11	10	1 (10)	Yes	n.s.
	B	13	2	2	0 (0)		
	A	15	11	10	1 (10)	Yes	n.s.
	B	15	1	1	0 (0)		
	A	7	31	21	10 (32%)	Yes	P<0.005
	B	7	36	36	0 (0%)		
10 July 1981	A	13	24	15	9 (38)	Yes	P<0.001
	B	13	30	30	0 (0)		
	A	15	12	9	3 (25)	Yes	n.s.
	B	15	14	13	1 (7)		

* Date on which experiment began.
** Not significant P>0.05.
A Control layout.
B Horseshoe layout.

Table 20. The amount of drift in paired colony apiary layouts vs. the amount of drift in controls.

Date*	Experiment	Age (days)	Total found	Number in parent	Number drifted	Drift reduced	Degree of significance
15 Aug. 1980	A	7	263	256	7 (3%)	Yes	n.s.**
	B	7	125	125	0 (0%)		
	A	10	198	151	47 (24)	Yes	P<0.001
	B	10	117	115	2 (2)		
	A	13	81	45	36 (44)	Yes	P<0.01
	B	13	99	78	21 (21)		
	A	15	57	22	35 (61)	Yes	P<0.001
	B	15	98	81	17 (17)		
20 July 1981	A	7	53	34	19 (36%)	Yes	n.s.**
	B	7	14	13	1 (7%)		
	A	13	37	20	17 (46)	Yes	n.s.
	B	13	10	6	4 (40)		
	A	15	20	13	7 (35)	No	n.s.
	B	15	10	6	4 (40)		
	A	20	9	4	5 (56)	Yes	n.s.
	B	20	8	6	2 (25)		
28 July 1981	A	7	53	34	19 (36%)	Yes	P<0.01
	B	7	66	59	7 (11%)		
	A	13	37	20	17 (46)	Yes	n.s.
	B	13	65	45	20 (31)		
	A	15	20	13	7 (35)	-	n.s.
	B	15	55	36	19 (35)		
	A	21	9	4	5 (56)	Yes	n.s.
	B	21	43	25	18 (42)		

* Date on which experiment began
** Not significant P>0.05
A Control layout.
B Paired colony layout.

Table 21. The number of drones drifting to each hive within a straight row layout.

Date*	Age (days)	Hives to which drones drifted				
		1	2	3	4	5
		13**	1	4	4	1
03/07/80	15	2	1	3**	5	9
		0	1	1	6	6**
		1	2	3	4	5
15/07/80	15	4	2	3**	4	2
		1	2	3	4	5
		2**	4	0	0	2
03/08/81	15	2	0	9**	0	1
		0	1	0	0	2**
		1	2	3	4	5
		11**	1	2	0	0
10/08/81	15	0	0	10**	0	1
		6	0	0	0	9**

* Date on which trial began.
** Hive into which drones were introduced.

Table 22. The number of drones drifting to each hive within the offset entrance lyout.

Date*	Age (days)	Hives to which drones drifted 1	2	3	4	5
		18**	3	4	4	0
15/07/80	14	15	0	10**	7	1
		6	3	0	2	13**
		1	2	3	4	5
		12**	3	5	1	1
03/08/81	13	0	3	5**	1	3
		1	1	4	1	7
		1	2	3	4	5
		8**	0	0	0	0
10/08/81	15	2	0	5**	1	0
		0	0	0	0	3

* Date on which trial began.
** Hive into which drones were introduced

Table 23. The number of drones drifting to each hive within the coloured board layouts.

Date*	Age (days)	Hives to which drones drifted 1	2	3	4	5
	10	9**	0	13	1	4
10/07/80	10	3	0	28**	1	1
	10	1	2	9	3	13**
		1	2	3	4	5
	9	9**	0	1	0	0
15/07/80	9	2	0	6**	4	4
	9	2	0	0	4	29**
		1	2	3	4	5
03/08/81	10	0	0	2**	0	0
		1	2	3	4	5
10/08/81	13	0	1	8**	0	1

* Date on which trial began.
** Hive into which drones were introduced.

Table 24. The number of drones drifting to each hive within a horseshoe layout.

Date*	Age (days)	Hives to which drones drifted 1	2	3	4	5
15/07/80	11	1	7	5**	2	0
03/07/81	15	0	0	13**	1	0
10/07/81	15	0	0	1**	0	0

* Date on which trial began.
** Hive into which drones were introduced.

CHAPTER IV

DISCUSSION AND CONCLUSIONS

Acceptance and Survival of Introduced Drones

The acceptance of drones that were introduced into colonies varied throughout the season in 1980 and 1981 (figures 12 and 14). The number of drones that were accepted by colonies was high early in the season and high in the post honeyflow period in both 1980 and 1981 (figures 12 and 14). The initial loss of marked drones may have resulted from, paint markings falling off, death from injury during marking, introduction or transport and from rejection of drones by the workers of the colony. The rejection of drones by the workers of the colony is probably the most important variable affecting the acceptance of drones into a colony.

Variation in the number of drones accepted on different days appeared to be correlated to the climatic conditions occurring at the time of drone introduction. Temperatures, on introduction dates with poor initial acceptance were below 18^{o}C. (figures 16 and 17). The "hours of bright sunshine" were generally lower on dates with poor acceptance than on dates with "better" acceptance (figures 20 and 21). Precipitation often occurred on the days prior to introduction, or from the time introduction took place until the first examination was conducted (figures 18 and 19). Drone acceptance varied throughout the period when there was a nectar flow (figures 22 and 23). Acceptance of drones by colonies was high on 13 August, 1980 and 19 August, 1981, when the nectar flow had begun to taper off (figures 22 and 23).

Poor drone acceptance caused by weather conditions may result from a reduction in the amount of forage collected by workers (Free 1977) or low temperatures (Morse et al. 1967, Taber 1964) which can cause workers to reject drones. Conditions that prevent workers from foraging are, low hours of bright sunshine, rainfall, and low temperatures all of which occurred on dates with poor acceptance of drones. However, good acceptance of drones was obtained in both years (1980 and 1981) after the main honeyflow was over in August. Although poor weather on days before drones were introduced to colonies may affect the acceptance of drones by preventing worker foraging, the weather conditions from the time of introduction until the first examination of colonies was done were probably more important. Rainfall and low temperatures during this period appeared to greatly reduce the success of introducing marked drones. The environmental conditions occurring at the time of drone introduction are probably more important than the time of year.

Loss of drones did occur between the initial examination and the second examination (at six days of age) before most drones began flying. The number of drones lost during the preflight period (before 6 days of age) was greater (22%) in 1981 than in 1980 (13%). The higher numbers of drones that were rejected by workers in the preflight period in 1981 may have been caused by adverse environmental conditions that caused the workers to expel the drones from the colony.

The survival curves indicate that survival rates of drones during the preflight period can be quite stable (figures 24 and 26). However, in some trials many drones were rejected in the preflight period (figures 25 and 27 to 29). Identical marking and introduction techniques were used in all trials and appeared to cause little drone mortality after the initial examination in the preflight period (figures 24 and 26). Therefore, it is probable that the drone loss observed in the preflight period (figures 25 and 27 to 29) is chiefly a result of the rejection of drones by the workers of the colony.

The number of drones that were successfully introduced into different colonies on the same day also varied. The difference in acceptance may be due to individual colonies' characteristics.

Colonies without queens tended to accept more drones than colonies with queens (figure 14). Queenless colonies have been shown to be more tolerant of drones than queenright ones (Free 1977). The initial acceptance of marked drones into queenless colonies was higher than in queenright colonies (figure 14). However, the acceptance of marked drones by queenless colonies by the time drones were 6 days of age was not consistently higher than the number accepted by queenright colonies (figure 15). Also, the mean longevities of drones in queenless colonies were not consistently higher than in queenright colonies (table 1). It appears therefore, that although the initial introduction of marked drones was more successful in queenless colonies than queenright colonies, the survival rates of drones after their introduction to queenless colonies were not consistently higher (see also figures 27 to 29).

There also appears to be differences in the tolerances of different colonies to drones. Although all colonies were of about equal size and located in the same general area, some colonies retained few drones.

The survival of drones during flight may be influenced by : the amount of food they carry on flights, the age of the drone, predation from natural enemies and death through mating (Oertel 1956). Drone survival during flight may also be related to their ability to relocate their colonies when returning from flights. Drones do not feed while outside the colony (Mindt 1962) so any drones that fail to successfully reorient to a colony die.

The survival rates of drones drop sharply when drones are older than 7 days (figures 24 to 29). This period corresponds to the beginning of flight activity (Witherell 1972, Fukuda and Ohtani 1972).

The longevity of adult drones during the summer of 1981 averaged 13 days (table 1). This is much lawer than the mean longevities reported by: Howell and Usinger (1933), Lavrekhin (1947), Jaycox (1961), Kepena (1963), Drescher (1969), Garofalo (1972) and Witherell (1972), who found that drones lived an average of 21 to 54 days. However, it is close to the mean longevity reported by Fukuda and Ohtani (1977) of 13.89 days during the summer season. (Of interest, is that Fukuda and Ohtani found that the length of life of drones later in the season averaged 32-43 days).

Factors that may have decreased the survival of drones, in this study, include: higher drone rejection by workers as a result of adverse environmental conditions, increased predation, and higher rates of disorientation when locating colonies. The ability of drones to locate their colonies in this study may have been lowered because of the study site. Prairie conditions provide few visual cues to aid drones in locating their colonies when returning from flights.

Many drones that failed to locate their parent colony were found in other colonies. These were included in the calculation of adult longevity. However, drones that drift to other colonies may not survive if they do not "happen to locate" the colonies to which they drift. The survival curves from groups of colonies that included drifted drones were similar to the survival curves of drones from isolated colonies but the number of drones surviving from the parent colony (excluding drifting drones) was much lower than the survival curves from isolated colonies (figures 30 to 33). This indicates that drifting drones should be included in the determination of drone survival because the survival rate of drones was not greater (than in isolated colonies) when the drifting drones were included.

The sharp drop in drone survival after drones are older than 7 days, indicates that few drones survive until they are sexually mature. Drones do not become sexually mature until they are at least 9 days old and the optimal age of sexual maturity is about 14 days old (Zmarliki and Morse 1963b, Woyke and Jasinski 1978). The mean length of life (12.88 days) found in this study was lower than the optimal age of sexual maturity. Thus it may be necessary to rear large numbers of drones in order to obtain successful mating of queens under Manitoba conditions.

The Effect of the Age of Drones on Drifting

The calculations of the percentage of drones drifting from their parent colony are probably lower than they should be because it is not known how many times drones changed positions between readings or how many drones may have drifted back to their parent colony.

Drones first began drifting when they reached 5-7 days of age (tables 2 and 16). This period corresponds to the age when drones first begin to fly from the colony. Drones can fly when four days old (Howell and Usinger 1933) but usually begin to fly at an average of 7.96 days

(Witherell 1972).

Large numbers of drones drift between the time when drones were 7 to 13 days old (table 2). All drones have usually made their first flights when 15-18 days old (Howell and Usinger 1933, Kurennoi 1953c, Drescher 1969). Levenets (1951) stated that drifting of drones generally occurs on their first orientation flight while Free (1958) found that most worker bees drift on their "play" or orientation flights. In this study, large numbers of drones began to drift during the time when drones were making their first flights which may indicate that a large proportion of drones drift on their initial orientation flights. However, the drifting of drones continued past the age by which all drones were supposed to have made their first flights (over 18 days old) (table 4). This indicates that the drifting of drones does not only occur on their first orientation flights.

Levenets (1951) concluded that drones generally remain in the colonies to which they first drift. The results of the individually marked drone experiment (table 3) indicate that although many drones drift only once (23 to 31 percent), drones frequently (15 to 25 percent) drift at least 2 or 3 times. Therefore, drones do not always remain in the colonies to which they first drift.

It appears that when drones begin to fly, large numbers (51 to 66%) drift from the parent colony by 13 to 15 days of age (table 2) but as indicated in table 4, drift continues at a fairly constant rate even as drones get older.

The Distance that Drones Drift

Drones drifted between colonies that were up to 150 m. apart (table

5). The proportion of drones drifting to colonies up to 50 m. away was high (29 to 63%) but fewer drones (17%) drifted to colonies 100 m. away. Drones did not drift between hives that were 200 m. apart. It appears that the amount of drone drifting may decrease with increased distance between hives but only at distances of over 50 m.

Witherell (1956b) also found that drones drifted more readily to a nearby hive than to one which was farther away. He found that 12 percent of marked drones drifted to a colony 30.5cm. west while 0.25 percent of marked drones drifted to a colony 3.8 m. east. The level of drift observed by Witherell and the distances drones drifted appeared to be lower than those found in this study. The differences in the amount and distance of drone drifting found between this study and Witherell's (1965b) may result from, the method of calculating the proportion of drones drifting (discussed below), the number of visual cues present in the two study areas, or the different arrangement of hives used.

This study was conducted under prairie conditions where few visual cues were present to aid drones in orienting to their colonies. Witherell (1965b) conducted his experiment in Massachusetts where there may have been more visual cues. The drones in Witherell's study may have orientated better to their own colonies because more visual cues were present.

However, because of Witherell's experimental design no conclusions about the amount of drifting occurring to hives at either distance can be made. The arrangement of Witherell's hives resembled a paired colony arrangement, which was shown to reduce drift in this study. Also, (in this study) when hives were placed in rows facing south there was a greater tendency for drones to drift towards the west than the east. If this directional tendency is present in Massachusetts (which is at a similar latitude 43^{o} N. to this study site of 49^{o} N.) then there may have been more drift to the far colony if it were placed 3.8 m. west rather than east.

The Direction of Drone Drift

Hives were placed at equal distances around a central hive that contained marked drones. Drones tended to drift more frequently to certain hives. The directions of the hives to which drones drifted appeared to vary with the distance between hives. At short distances (of 1 m.) more drones often drifted to hives in the east and west than to hives in the north and south. When hives were farther apart (between 50 m. to 100 m.) drones drifted only to the hives in the north and south.

In the 50 m. trial A, drift was predominantly to the hive to the north (table 6). In the 50 m. trial B, more drones drifted to the south than the north and in the 100 m. trial, drones only drifted to the south. Drifting to hives 50 to 100 m. away appeared to be correlated to wind data (table 7).

The prevailing winds during the 50 m. experiment trial A (from 6 August, 1981 to 12 August, 1981) were predominantly northerly. The prevailing winds during the 50 m. experiment trial B and the 100 m. experiment, which ran concurrently from 17 August, 1981 to 30 August, 1981, were predominantly southerly. When hives were spaced 50 m. and 100 m. apart drones drifted only to the colonies that were downwind or upwind. However, more drones drifted to colonies upwind than downwind.

Wind can affect the drifting of worker bees (Jay 1965), but workers generally drifted to hives that were downwind. Butler and Fairey (1964) found that drones fly upwind when they detect the queen's sex pheromones and they suggested that queens may fly upwind on nuptial flights. As more drones drifted to the hives on the upwind side when returning from flights this may indicate that the preferred direction of flight of outgoing drones is upwind.

The pattern of drone drift changed when the hives were more tightly spaced (when hives were 1 m. and 5 m. apart). When hives were 1 m. apart more drones tended to drift to the colonies to the east and west than to the north and south for unknown reasons (table 6). In the 5 m. trials "A and B" drift was not significantly greater to any hive.

The colony in the north north-west position in the 5 m. experiment trial C (table 6) received large numbers of disoriented drones. This colony had a much larger population size than the other colonies in the pattern. Levenets (1951) found that drone flight occurred chiefly to the strongest hives in the rows. Colonies that have large populations of workers may be able to support more drones and as a result may reject fewer drifting drones.

Direction of drone drift in rows. Marked drones placed in hives in the centres and ends of rows (of 5 hives) consistently drifted more in one direction along a row than in the other direction. The direction, along the row towards which drones drifted, depended on the direction the row faced.

Drones placed in the centre hive of rows facing north or south tended to drift more towards the west than to the east (table 10). The drift in the north row (replicate 2) (table10) was greater towards the east than towards the west. However, both colonies to the west of the centre colony had low worker population sizes that dwindled further as the experiment progressed. These colonies may have been unable to support many drifted drones because the number of drones a colony can support is related to the size of its worker population and conditions of food stores (Free 1977).

Drones from the centre hives of rows facing east or west tended to drift more towards the south than to the north (table 8). Although drift from the west row of the large square was not consistently greater towards the south, results from straight row experiments facing west indicated that drone drifting was predominantly towards the south (table 12). This was indicated not only by drones from the centre colonies of the row but also by drones from the end colonies of rows (table 13). The significance of the directional tendencies of drift observed will be discussed below.

A directional tendency of drone drift was also noted in paired colonies, between the rows (in the large square), and between separate apiary layouts.

When marked drones were placed in paired hives with hive entrances facing south, the drifting of drones was much higher from the east hive to the west one, than from the west hive to the east one (table 14).

Drones within the large square design often drifted between the rows of hives that formed the sides of a square. The drifting of workers in a large square design was studied by Jay (1966 a,b, 1968, 1971) but workers rarely drifted between the rows. Drones usually drifted to the two sides of the square that were perpendicular to the side of the square that the drones originated from, rather than to the row on the opposite side of the square (table 11). However, many drones from the east row (table 11) did drift to the west row. More drones drifted to the west row from the other sides of the square than to other rows in the large square. There did not appear to be any strong tendency of drifting to the south row from the other rows.

Although the proportion of drones drifting from different rows appeared to be lower in the west and south rows there was no significant difference in the numbers of drones drifting from the rows that faced different directions.

Drones also drifted between apiary layouts (groups of hives) even though the groups were widely spaced. Three groups of hives were placed 40 m. apart in a line running north-south (figure 4). More drones from the centre group (group 2) drifted to the group 40 m. south (group 3) than to the group 40 m. north (group 1) (table 8). Drifting of drones between 5 groups of colonies placed in a line running east-west also occurred (figure 5) (table 9). However, it is difficult to conclude anything about the direction of drift from any group in the row except for group 3 because the other four groups of hives consisted of apiary layouts that reduced drone drift. Group 3 was located in the centre of the row of groups and consisted of a row of 5 hives spaced 1 m. apart facing west. More drones from group 3 (figure 39) drifted to groups in the west(groups 1 and 2) than to groups in the east (groups 4 and 5) (table 9).

Jay (1966 a, 1968, 1971) found a strong tendency for worker bees to move towards the south along rows facing east-west and a weak tendency for drones to drift westward along rows facing north or south (in temperate regions)(14° 38′ N., 97° 09′ W.). Jay suggested that the directional preference of drifting workers may have been influenced by the southerly position of the sun in the sky (in Manitoba) and the apparent westward movement of the sun across the sky during the day. This test was repeated by Jay (1971) in Jamaica (18° 00′, 76° 45′W.) where the sun passed directly overhead. Workers drifted more to the west than to the east along rows of the large square and no tendency for drift towards the south was noted.

In this study drones showed a strong tendency for drift towards the south in rows facing east or west. However, drones also showed a very strong tendency of drift towards the west in rows facing north or south. This study was conducted in the same location as Jay's temperate experiments (at 14° 38′ N., 97° 09′W.). It appears that if the sun's position does influence the direction that workers drift in rows it also influences the drifting of drones.

The reason drones may have drifted very strongly in a westerly direction (when workers showed a weak tendency for drift towards the west) may be related to the position of the sun during the time of drone flight. Peak flight activity of drones occurs from 14:00 to 16:00 hours (Taber 1964). During this period in the afternoon the sun's position in the sky was in the west. It appears that the sun's position or the apparent movement of the sun across the sky may influence the direction that drones drift in rows.

If drones do use the sun's position to aid in orientation this may explain why more drones drifted to the west row of the large square and why fewer drones drifted from the west row than from other rows. The westerly position of the sun may have allowed drones in rows that faced west to orient more accurately than the drones from other rows.

Oertel (1956) concluded that drones probably used landmarks rather than the sun in orienting to their colonies. However, it is possible that drones may use a combination of sun and landmark orientation to find their colonies. Under prairie conditions where few landmarks are available drones may be more dependent on sun orientation than landmark orientation.

The Amount of Drone Drift

The amount that drones drift is reported to range from nil to 80 percent (Butler 1939, Free 1958). The amount of drift found in different studies may vary with: the sampling technique used, the method of calculating drift, the age of the drones at the time of sampling, the apiary layout used, the environmental conditions, and the topography of the study area.

Some authors reported that small proportions of drones drift (between 0 and 12 percent) (Butler 1939, Levenets 1951, Witherell 1965), while others have found high proportions of drone drift (30 to 50 percent) (Borchert 1928, Goetz 1954, Free 1958).

Butler (1939) found virtually no drifting of drones occurred in his apiary. However, systematic searches of all colonies at regular intervals were not done. Levenets (1951) found that between .58 to 1.75 percent of drones drifted to other colonies. Free (1958) criticized the method Levenets used to calculate drift because it did not take into account the number of drones left in the parent colony. Thus, the proportion of drones which had drifted could not be ascertained.

Witherell (1965) found more drones drifting (11 to 12 percent) than did Levenets (1951) or Butler (1939). However, Witherell marked drones of unknown ages. Some of these drones may have drifted at least once before (from other colonies), or may not have been of flight age when the colonies were searched for marked drones. Wither 11 calculated the proportions of drones drifting from the total number of drones marked and not from the total number surviving when colonies were searched. This method did not give a true indication of the proportion of drones drifting from the parent colony because many of the originally marked drones would die by the time the colonies were examined. The apiary lay-out Witherell used may also have reduced drone drift. The marked drones were placed in a colony with two colonies placed on either side. One colony was 30.5 cm. away and the other 3.8 m. away. This arrangement is similar to a paired colony arrangement found to reduce drifting of drones in this study.

Goetz (1954) determined that just over half of the population of drones that were present in a colony placed in an apiary were of a different race than that colony and had drifted to that colony. However, this estimate gave no indication of the proportion of drones that drifted to the colony from other colonies.

Free (1958) calculated the proportion of drones that drifted from their parent colonies and found drift ranged from 8.6 to 80 percent. The proportion of drones that drifted in 9 replicates was 21 percent. Free pointed out that this method also underestimates the amount of drift that occurs because it gives no information about drones that drift to other colonies and return, or how much drones drift between hives after they leave the parent colony. Free (1958) examined colonies for marked drones when they were 7 or 14 days old. This study indicated that few 7 day old drones drifted, but by the time drones were 14 days old much of the drift had already occurred (table 2). Unfortunately, Free did not separate his data on the basis of age criteria so it cannot be determined which of the replicates were sampled when drones were 7 days old and which were sampled when they were 14 days old. If Free (1958) had made all of his comparisons using 14 day old drones he may have found that higher proportions of the drones had drifted.

This study also indicated that a high proportion of drones drifted from their parent colonies. Drift was calculated using Free's (1958) method (the proportion of drones drifting from the parent colony) but the age groups of the drones were also considered. The proportions of drones over 21 days old, that drifted from the parent colony could be as high as 100%. However, these high percentages of drift can be misleading because the number of drones surviving over 21 days of age is low. Since most drones appeared to drift by the time drones were 13 to 15 days old, and enough drones were still remaining, the amount of drone drifting was measured between the ages of 13 to 15 days (table 15). The apiary layout in which the amount of drift was measured (a straight row of 5 hives placed 1 m. apart with entrances facing west) was chosen because this was thought to be an apiary layout that did not reduce drifting. The amount of drone drifting ranged from 10 to 80 percent which is quite similar to the range of drone drift found by Free (1958). However, the proportion of drones that drifted over all 12 replicates was much higher (48.7 percent) (table 15) than the amount of drift found by Free (21 percent). The differences in the proportions of drone drifting between this study and Free's may result from, the difference in age groups sampled, the apiary layout, or the topography of the region. All trials in this study were conducted on the prairie where there are few visual orientation cues.

A more accurate determination of drift was done by using individually marked drones. Fifty-two to fifty-four percent of marked drones did not drift (or 46 to 48 percent did drift) during the sampling period (sampling ended when drones were 21 to 24 days old) (table 3). This agrees with the estimate of the proportion of drones that drifted from their parent colony, found in this study (48.7 percent) (table 15).

The proportion of drones drifting varied between trials (table 15). All trials were conducted on different dates throughout 1980 and 1981. Jay (1965) found no seasonal differences in the level of worker drift in the months of May to August, but environmental factors such as wind did influence worker drift. The variation in the proportion of drones drifting, of the same age, in the same apiary layout, examined during June to August may have resulted from differences in the climatic conditions occurring at the specific times that trials were conducted but no seasonal trend was noted.

Free (1958) compared the level of drone drift to the level of worker drift and found that drones drifted 2 to 3 times more than did workers. Jay (1966, 1968) examined the drifting of worker bees in straight rows of 5 hives spaced 1 m. apart facing south. Data from his experiments indicated that the proportion of worker drift ranged from 4.0 to 87 percent. The proportion of workers that drifted during 17 replicates was 43.3 percent. This level of worker drift is only slightly lower than the levels of drone drifting found in this study (49 percent). Although these results seem to indicate that the levels of drone drift are similar to the levels of worker drift, this may only apply in conditions where both workers and drones are provided with few orientation cues. Free (1958) compared drone drifting to worker drifting in a paired apiary layout that can reduce drifting in workers. Workers drift very little between members of a pair (Jay 1966b) but this study indicated that up to 42% of drones do drift between members of a pair. Workers may drift less than do drones in apiary layouts that are designed to reduce drift. This may occur because workers orient to colonies better than do drones. Alternately, the number of orientation errors made by workers may be similar to those made by drones, but errors made by drones are observed because drones may be accepted into foreign colonies more readily than are workers. Drones that make orientation errors would be accepted by foreign colonies and noted when colonies were examined, but workers making orientation errors may be rejected at the entrance and may eventually return back to their colonies.

The Effect of Apiary Layout on the Drifting of Drones

Some apiary layouts that were shown to reduce drifting in worker bees (Jay 1965, 1966a,b, 1968) were tested for their effects on drone drifting.

Straight rows. Drift from the apiary layouts tested were compared to drift from a straight row of 5 hives placed one metre apart. This pattern was used as a "control" because it was an apiary layout in which there was no attempt to control drift through increasing visual cues. This pattern was also used as a "control" in worker drifting experiments by Jay (1966 a,b, 1968).

In straight rows, more workers drifted from hives in the centre of rows than from the hives on the ends of rows (Jay 1968). However, the drifting of drones in this study did not appear to be consistently greater from the centre hives of rows than the drifting of drones from the hives at the ends of rows (figures 36 to 38). Marked workers from the end and centre hives of the rows tended to drift more to the ends of rows than to other hives in the row. There was no apparent tendency for hives at the ends of rows to receive more drones than the hives in the middle of rows (table 21).

Offset hive entrances. Workers can use the sun as a compass to orient (Wilson 1971) and can detect the differences between hives placed at different angles. When hive entrances in rows were angled to face different directions drifting of workers was reduced (Jay 1966b). However, the use of rows of hives with offset entrances did not reduce drifting of drones (table 16).

Drifting in the offset hive entrance pattern was often higher than in the controls (table 16). The poor orientation by drones within the pattern using hives with angled entrances suggests that, if drones do use the sun as a compass to orient to their colonies, their use of the compass may not be as efficient as workers.

The reason that the rate of drone drift was higher in the offset entrance apiary layout than in the controls is unclear. The drones did not appear to drift more to the hives that were angled in the same direction (table 22).

Coloured boards above entrances. Worker bees can recognize colour differences (Wilson 1971). The placement of coloured boards above hive entrances reduced the drifting of worker bees (Jay 1965). Drones placed in rows with coloured boards over hive entrances drifted slightly less than they did in control rows (tables 17 and 18). Although drones oriented slightly better in colonies with coloured boards this does not necessarily mean that drones can recognize differences in colour. Drones may just be detecting differences in shades of grey between the different coloured boards.

When drones were between 7-12 days old a virgin queen emerged in the centre colony of the coloured board experiment (on 10 July, 1980). This colony appeared to attract large numbers of drones (table 23). During one of the 50 m. distance trials, a virgin queen emerged and was present in the colony for a brief period of time before it was noticed and removed. During this period many drones drifted to that colony. It appears that virgin queens may attract drones to the hives in which virgins are found. The attractiveness of drones to the centre colony of the coloured board experiment did not appear to be due to the colour of the board over the entrance (yellow) as other colonies that had yellow boards (hive 5 on 15 July, 1981 and hive 4 on 3 August and 10 August, 1981) did not attract drones (table 23). It appears as though drones may be attracted to virgin queens in colonies. Butler (1939) and Levenets (1951) found that virgin queens in the hive were not attractive to drones. Drifting in the row with coloured boards was slightly lower than the controls after the virgin queen was no longer present.

Horseshoe. Fewer drones drifted in horseshoe patterns than in control patterns (table 19). When drones did drift in the horseshoe layout it was usually only to the colony on either side of the parent colony (table 24). Drift may have been lower in the horseshoe layout because the hives faced different directions or because hives were not placed in a straight line.

Paired colony layout. Fewer drones drifted between paired colonies facing south than in the controls. Most of the drift that occurred between the colonies of a pair was chiefly in one direction (from the east to the west) (table 14). Workers rarely drift between the colonies making up the pair (Free 1958). However, in apiary layouts using rows of paired colonies, workers frequently drifted from one side of a pair to hives on the same side in the other pairs of hives in the row (Jay 1966b). Drones did not drift between different pairs in this study. However, the pairs were not placed in a straight row and were placed 25 m. apart. The paired colonies used by Jay (1966b) were arranged in a straight line and were much closer together. In Jay's experiment the hives were spaced 5 cm. apart and the pairs were spaced 1 m. apart.

Drifting Between Apiary Layouts

Large percentages of drones drifted between different apiary layouts though the groups of colonies were widely separated (tables 8 and 9). In both of these trials the separate groups of colonies were placed in fields in a straight line (figures 4 and 5). Drift occurred between the apiary layouts though the groups of hives were spaced 40-150 m. apart. In 1981, five different apiary layouts were tested in the same field and the distance between hives was much lower (25 m.). The different groups of hives were placed throughout the field so groups were not in line with each other. Few drones drifted between groups of hives arranged in the field in this manner. Fewer drones appeared to drift when groups of hives were not placed in rows though the groups were closer together.

Although paired colonies, rows with coloured boards and horseshoe patterns tended to slightly reduce the drifting of drones, none of these layouts controlled drift completely. Drone drift may be difficult to control because drones are readily accepted into foreign colonies. When drones make orientation errors they may tend to accept the first colony they find.

Drones can disseminate many bee diseases (Moreaux 1953, 1959, Bailey 1972, Bailey and Fernando 1972, and Hanko and Lemakova 1971). This study has shown that high proportions of all age groups of drones drift between colonies; many drones drift more than once; many drones drift between rows facing different directions, including to rows facing the opposite direction; drone drift occurs between hives spaced up to 150 m. apart; many drones drift between apiary layouts; some drones drift up to 450 m. away from their original colony. These aspects of drone behaviour make drones serious potential vectors for the spread of bee diseases in commercial apiaries. Apiary layouts that reduce drone drifting may help to control the spread of bee diseases within or between commercial apiaries.

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