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REPRODUCTION AND GROWTH OF TEMPERATE-EVOLVED HONEY BEE COLONIES

(APIS MELLIFERA L.)

by

PHILIP CHRISTOPHER LEE

BSc (Honors), Simon Fraser University, 1982

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Biological Sciences

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SIMON FRASER UNIVERSITY

July 1985

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Reproductive and Growth Patterns of Temperate-Evolved Honey Bees

(Apis mellifera L.)

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ABSTRACT

The effects of colony size and reproductive timing on the number, sex, survival, worker weights, and rates of comb building of offspring produced by temperate-evolved honey bees (Apis mellifera ligustica L.) were examined.

Parental colony size as measured by the number of workers in the colony at swarming was correlated with the number of workers invested in offspring colonies and the number of queens produced, but not with drone production or the number of offspring colonies produced. Worker production prior to winter was an important factor in determining the drone production and survival of post-swarming colonies. The offspring queens which inherited the parental nest survived considerably longer than either prime swarm or afterswarm colonies, presumably due to the advantage of inheriting an established nest.

Drone emergence peaked just prior to swarming, the period when most unmated queens were available. The protandry exhibited by honey bee colonies in drone production was probably due to male-male competition for mating opportunities. High drone production by colonies initiated from prime swarms and afterswarms reflected an attempt to reproduce prior to winter, since the probabilities of either a second swarming cycle within the same year and/or survival through the winter were low for swarms.

The number of workers in hived swarms was positively correlated with emergent worker weights from the first brood,

total amount of comb constructed, and the percentage of drone comb built. The tendency of small swarms to produce lighter workers was probably due to poor nutrition caused by a lack of workers to perform nursing and foraging tasks. The rate of total comb production was rapid, with 90% of all comb being built within 44 days of colony founding. Drone comb construction began an average of 22 days after colony founding, with 90% of the drone comb being built within 42 days after the first drone cells were initiated. By rapidly constructing drone comb, swarms were able to produce large numbers of drones before winter.

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In the time spent at Simon Fraser University as an undergraduate and as a graduate student, my view of biology has changed radically. The change has been prompted by several courses and more importantly by the professors teaching those courses; Larry Dill, Bernie Roitberg and Mart Gross. Through their teaching skills the subject of Evolution became more than just a chapter at the end of a first year text. Special appreciation is owed to Dr. Mark Winston who took a chance on an untried undergraduate. His guidance as a senior supervisor and patience as an editor made this thesis possible. I am also grateful to Elizabeth Punnett, Kenna Mackenzie, Craig Martin and Linda Fergusson for field and laboratory assistance throughout this study, and Dr. and Mrs. R. Nielson for use of their property. Also, Dr. Steven Kolmes reviewed the manuscript and made valuable comments. This research was supported by a President's Research Grant from Simon Fraser University and N.S.E.R.C. Canada Operating Grant A7774 (to M.L.W).

I feel a more complete person for having close friends who have acted as sounding board for academic and personal points of view; John Mendes, Brian Pollock, Sandy Allen, David Hunt, Gary Judd, Mike Smirle and Karen Thompson. A special debt of gratitude and affection is owed to Judith Weymark for organizing my personal life. All have provided valuable links to the outside world and were a source of support throughout.

My father Koy, mother Shuilan, sister Carey, brother Nathan and grandmother Toy Ying have provided a firm emotional and financial base. Also, I am indebted to my grandfather to whom this thesis is dedicated, for his foresight, courage and perserverance in a new country.

DEDICATION

To Kepo 'Sam' Lee (1889-1984)

Some 'advanced thinkers' are of the opinion that anyone who differs from the conventional opinion must be in the right. This is a delusion; if it were not, truth would be easier to come by than it is. There are infinite possibilities of error, and more cranks take up unfashionable errors than unfashionable truths.

Bertrand Russell 1950
from Unpopular Essays

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I. INTRODUCTION

Few organisms are as well studied as the honey bee (Apis mellifera L.). It is the sole subject of research for several university departments and research centres and has several journals devoted specifically to it. This is partly due to its economic importance in agricultural systems but also because of its unique biology, and relative ease of access and manipulation for study. One area of intensive research recently has focused on the reproductive biology of honey bees, mainly because of interest in life history patterns. Also, there is economic interest in attempting to breed honey bee stocks (Goncalves and Stort 1978) and in the introduction and rapid spread of the africanized or 'killer bee' (Apis mellifera adansonii) into South and Central America (Taber 1985).

In honey bees, the production and nature of male and female offspring differ widely from each other. Queens (reproductive females) are reared during colony supercedure or swarming. Supercedure is the replacement of old, failing queens and may occur anytime during the growing season (Gary and Morse 1962). The cues causing workers to replace the queen are: a lack of queen substance, her inability to lay viable diploid eggs, or her laying a predominance of male haploid eggs (Butler 1957). Workers remove diploid eggs or larvae younger than 3 days from worker cells and place them into vertical cells called queen cups, or build cups around existing egg or larval-containing

cells. Usually, the first queen to emerge kills all the other queens and becomes the head of the colony. This type of reproduction is unplanned but occurs frequently because of the relatively short average egg laying lifespan of queens, between 2-3 years (Butler 1975).

Swarming is the more common method of producing female offspring. The factors initiating swarming are complex but it is generally agreed that there is a necessary set of primary stimuli which leads to a series of events culminating in swarming (Winston et al. 1980). Swarming usually occurs in spring during or after a period of resource abundance. The collected resources are diverted into brood production leading to a rapid increase in worker population and an increase in the proportion of younger workers. These events decrease the titre of queen substance in the colony and cause workers to build queen cups (Butler 1954; Boch and Lensky 1976; Lensky and Slabezki 1981; Baird and Seeley 1983). The queen lays female diploid eggs or workers move female diploid eggs from worker cells to the queen cups. Laying and movement of eggs into queen cups continues for 1-2 weeks, producing many different-aged queens. As the first larvae pupate, the parent queen leaves with most of the adult workers in a prime swarm and establishes a new colony usually within 100-1000 m. of the old nest (Seeley and Morse 1978; Seeley et al. 1979). The parent queen continues to lay eggs until a couple of days prior to leaving, resulting in much immature brood in the colony when the prime swarm leaves.

Several days later, a daughter queen emerges and may leave in an afterswarm with some of the remaining workers. Afterswarming may occur 0-4 times (Otis 1980; Winston 1980). Eventually, the worker population declines and a queen emerges, kills the other queens and inherits the former parental nest and remaining worker and drones. Afterswarm queens mate several days after settling at a new nest site, while the queen which inherits the former parental colony mates several days after she assumes control of the colony (Laidlaw 1979).

There are three interesting aspects to the production of females. First, the inclusion of workers in the definition of the female offspring is important because without workers a queen probably has no chance of survival. Second, there are two types of females (offspring colonies) produced; afterswarms which disperse and the queen which inherits the former parental nest. Third, the prime swarm contains the parental queen and hence represents the fate of the parent colony after producing females.

Drones do not overwinter but are reared within the first few weeks of foraging in spring. Ruttner (1966) and Gary (1975) provide good reviews of drone mating behaviour. Briefly, mating occurs at congregation areas which are generally located 0-4 km. from the former parental nest. Drones aerially patrol the congregation site, chasing almost any small dark object which passes through the area, even small pebbles thrown by researchers. Eventually, a female flies through the congregation

area and a group of 100-300 drones begin pursuit. Mating occurs when a single drone alights on the queen's dorsal surface, everts his penis, copulates and ejaculates with a loud, audible, 'pop'. After mating, the drone falls to the ground and dies, having eviscerated himself during mating. The queen removes the remnants of the male genitalia from her vagina, and may mate several times during the same nuptial flight or returns to the colony and workers will remove the remnants of the male genitalia (Taber 1954; Triasko 1956; Woyke 1956). Queens mating during a period of bad weather may obtain a small quantity of sperm and are frequently superceded shortly after establishing a colony (Ruttner 1956). Inclement weather (or possibly a lack of drones) can cause up to a 24 day interval between the first and last mating flight (Alber et al. 1955). Witherell (1972) reported drones making 25 mating flights during the average adult lifespan of 21.2 days with a 96.2% probability of a drone returning from a mating flight. Fukuda and Ohtani (1977) found the mean lifespan of drones was 13.9 days in June, 32.1 days in July, 42.6 days in August and 39.7 days in September. The shortness of the lifespan in June was thought to be related to increased flight activity due to better weather or the presence of more unmated queens. The lower survivorship of drones in September is attributed to the rejection of drones from colonies in late fall. (Free and Williams 1975).

There is some controversy over the number of times that a queen mates, with different methods giving different results

(Adams et al. 1977 review various methods of estimation). The best method of estimating the number of matings uses the introduction of unmated queens which are homozygous for a mutant recessive allele into a polymorphic population. The subsequent distribution of phenotypes in surrounding hives can be used to determine the average number of matings. Taber and Wendel (1958) estimated an average 7 to 10 matings per queen from four different populations located in temperate North America. Adams et al. (1977) used a similar method in Brazil and estimated the average number of matings to be 17.3. The lower temperate average was attributed to the greater unpredictability of weather conditions allowing queens mating flights on only 1 or 2 days.

Recent studies on the reproductive biology of honey bees have focused primarily on the adaptive nature of their unusual pattern of reproduction (Seeley 1978; Seeley and Visscher 1985; Otis 1980; Page 1981; Winston et al. 1981). These studies have usually failed to integrate the production of male and female offspring as an overall reproductive strategy by the parent colony. Also, they have not followed the effect of these factors on male and female offspring success. The first part of this thesis examines the effect of colony size and time of year in determining the sex and extent of energy invested in offspring. The offspring and parent were monitored to determine the effects of their initial size and date of issue on drone production and survival. The emergence patterns of drones were also monitored.

throughout the year and integrated with the annual pattern of unmated queens. The second and third sections discuss the growth of swarms after hiving. The amount of worker brood, ratio of brood/worker population and weights of workers in the first brood are examined in section two. The amount, type, and rate of comb building in colonies are examined in the third section.

II. THE EFFECT OF REPRODUCTIVE TIMING AND COLONY SIZE ON THE SURVIVAL, SIZE AND SEX OF OFFSPRING

Introduction

In seasonal temperate climates, both parental size and reproductive timing are critical factors in determining the extent and sex of offspring produced. In part this is because winter weather is a major source of mortality, and many life histories and reproductive cycles are adapted to accumulating enough resources to survive the winter. Offspring born too early may be small in size and do poorly because the parent was not fully mature at reproduction. Offspring born too late may also do poorly because they lack sufficient time to mature and accumulate resources prior to winter. The actual timing of reproduction and the extent and sex of offspring produced are the result of complex trade-offs and interactions between parental size, offspring size, time of year, cost of offspring, parent and offspring growth rates and chances of surviving the winter.

The adaptive qualities of honey bee colony size and reproductive timing are revealed when we examine closely the swarming and drone rearing cycle in temperate climates. Swarming usually occurs in the spring and is initiated by parental colonies when resources are abundant, but in order for colonies

to swarm in spring, they must begin to rear workers in mid-winter so that they can reach sufficient population to swarm. Colonies which swarm early in spring are better able to recover, survive the following winter and swarm earlier the next year (Seeley and Visscher 1985). Similarly, colonies produce drones and drone comb throughout the growing season, but spring and early summer is the peak production period (Free and Williams 1975), due to the high incidence of swarming and unmated queen availability in early May and June (Page 1981). A colony's success in mating its drones is probably largely determined by the number of drones reared, rather than by diverting energy into producing a larger-sized drone. Free and Williams (1975) reported that the proportion of drone brood reared in colonies increased with colony size until above a worker population of 10,000-20,000 adults, then the proportion remained relatively constant, at 8-29% depending on the colony (Allen 1965; Free and Williams 1975; Page and Metcalf 1984).

Past studies of honey bee life history have focused on either swarming or drone production without integrating them into an overall strategy of male and female reproduction. For example, studies on drone production have been performed while swarm prevention techniques were applied to colonies (Allen 1965; Free and Williams 1975; Page 1981; Page and Metcalf 1984). Also, the effect of reproduction on parent colonies has not been well-studied. The objectives of this study were to relate offspring production and parent and offspring success to

reproductive timing and colony size in unmanaged honey bee colonies, concentrating on three specific topics:

1. The effect of colony worker population on the number, size, and sex of offspring produced.
2. The effect of the date of swarm issue and swarm size on drone and worker production and colony survival.
3. Seasonal emergence patterns of drones relative to the availability of unmated queens.

Materials and Methods

In 1982 and 1983 a total of 14 colonies (7 colonies each year) located at an apiary in Fort Langley B.C., Canada (lat. 49° 10' N, long. 122° 35' W) were monitored for swarm production. During both years captured swarms were hived at a second site 2 km from the first site.

To initiate colonies, overwintered hives were reduced to a single 42 L Langstroth hive box in March of each year. This colony size was chosen because it is the modal size of feral colonies (Seeley and Morse 1976; Winston et al. 1981). Each colony contained approximately 6-8000 worker bees, its original queen, 7 frames of brood, and 3 frames of pollen and honey. Colonies had a mean of 7.8 % drone comb (range 4.4 - 15.9 %). Since there were always more drone cells in each colony than were used during the maximum amount of drone brood rearing, the amount of drone comb was not a limiting factor for drone production. All bees used in this study were originally imported from California.

Colonies were inspected weekly throughout the season and more frequently during the swarming period. The numbers of queen eggs, larvae, pupae and emerged adults were recorded prior to and during swarming.

Both prime swarms and afterswarms were captured using a double-layered nylon mesh bag, and when possible queens were placed in a small cage for the queen's protection during

handling. Each swarm was weighed and hived into a standard 10 frame Langstroth hive. Frames had 2-4 cm strips of wax along the top which guided comb building, otherwise workers constructed all the comb. A subsample of 10-20 workers was removed from the swarm, weighed, and the average worker weight calculated. The number of workers in a swarm was calculated by dividing the swarm weight by the average worker weight. Queens were released from cages within two days after swarms were hived. At the end of the swarming period the number of adult workers and drones remaining in the former parental colony was determined by shaking adults from the hive into a small screened box and a subsample of bees was removed, killed, and separated into workers and drones. The queen was placed in a small cage and hung on the inside of the box. The bees which took flight were allowed time to cluster on the outside of the box. The subsample and box were weighed and the density and percentage of drones and workers in the colony calculated. The numbers of immature workers and drones were estimated (described below) and the values for adults and immatures summed to estimate the colony population. The former parental colony population after swarming was calculated only in 1983.

To estimate the cumulative worker and drone production and emergence patterns for a colony, the area of sealed brood for each caste was measured throughout the season. This was done by placing a clear plastic grid marked out in 5 x 5 cm squares over the brood on one side of each frame, estimating the number of

sealed cells in each quadrat, and doubling that value to determine the colony total. Sealed worker brood were measured in both years for all colonies, while the drone cells were measured in 1982 for swarms only and in 1983 for all colonies. By setting the interval between brood measurements equal to the sealed brood period (13 days for workers and 14 days for drones), it was possible to determine the number of workers or drones emerged during a season. Sealed brood survivorship factors were used to adjust for mortality during that stage, .985 and .936 for workers and drones respectively (Fukuda and Sakagami 1968; Fukuda and Ohtani 1977).

All colonies were inspected weekly through the fall and winter to determine mortality dates. Colony mortality was determined at queen death because colonies have no eggs to rear replacement queens with in the fall and winter. The mid-point between the queen death date and the previous inspection date was used as the date of colony death.

Virgin queens in afterswarms were considered available for mating from the time they were released into their new hive until 2 days before the first eggs were observed in the colony (Laidlaw 1979). The queen which inherited the former parental nest was considered available for mating from when the other virgin queens were killed until two days before the first eggs appeared in the colony. The number of drones available for mating was determined from emergence data.

T-tests were performed on the means of the various parameters measured in 1982 and 1983. No statistical differences could be found between years for any of the parameters measured, hence data for 1982 and 1983 were pooled for the remainder of the analysis.

Results

A total of 30 swarms were produced in the 2 years of study, 12 in 1982 and 18 in 1983. Of these, 14 were prime swarms, 10 were 1st afterswarms, 4 were 2nd afterswarms and 2 were 3rd afterswarms. The average numbers of offspring colonies produced were 1.86 and 2.57 per parental colony in 1982 and 1983 respectively, and over the two years averaged 2.2 offspring colonies per parental colony annually (Table I). All of the original colonies swarmed at least once during the year except for a single colony in 1982. One of the hived prime swarms in each of 1982 and 1983 swarmed a second time that season.

Worker, Queen, and Drone Production in Pre-Swarming Colonies

The mean number of eggs reared to adult virgin queens during a swarming cycle was 10.2 per colony (Table I). The survivorship of queens to the end of each developmental stage was 0.911 (egg), 0.749 (larval), and 0.534 (pupal). Of the queens reared to adulthood, 21.6% inherited an afterswarm or the former parental colony, and the rest were killed by the new queen or workers.

There was a positive correlation between the number of queens reared and the worker population at swarming ($P < 0.05$, Fig. 1). However, there was no correlation between the number of queens reared and the number of drones produced prior to swarming ($P > 0.25$, Fig. 1) nor with the number of offspring

Table I; Summary of Colony Reproductive Characteristics

Characteristic	$x \pm S.E.$	Range
Reproductive rate per colony	$2.2 \pm .3$	0 - 4
No. of adult queens reared during swarming	10.2 ± 1.6	4 - 20
No. of drones produced prior to swarming, including immatures	$2,400 \pm 450$	660 - 3,960
No. of workers produced prior to swarming, including immatures	$42,100 \pm 4,300$	28,300 - 61,300
Swarm and Offspring Sizes (no. of workers)		
Prime swarms	$19,930 \pm 2,860$	6,500 - 34,300
Afterswarm	$9,250 \pm 1,060$	4,300 - 15,700
Remaining afterswarms	$11,030 \pm 2,620$	4,800 - 26,700
All offspring colonies	$21,930 \pm 4,900$	12,500 - 47,300
No. of workers produced after swarming		
Prime swarm	$55,530 \pm 7,600$	19,540 - 86,400
Afterswarm	$38,760 \pm 9,720$	1,600 - 109,200
New queen in original colony	$70,320 \pm 6,810$	24,980 - 109,800
No. of drones produced after swarming		
Prime swarm	$3,690 \pm 850$	0 - 8,200
Afterswarm	830 ± 470	0 - 6,600
New queen in original colony	550 ± 220	0 - 1,600
Survival following swarming, days		
Prime swarm	160.0 ± 11.5	88 - 204
Afterswarm	132.9 ± 15.4	51 - 216
New queen in original colony	195.2 ± 15.7	113 - 312

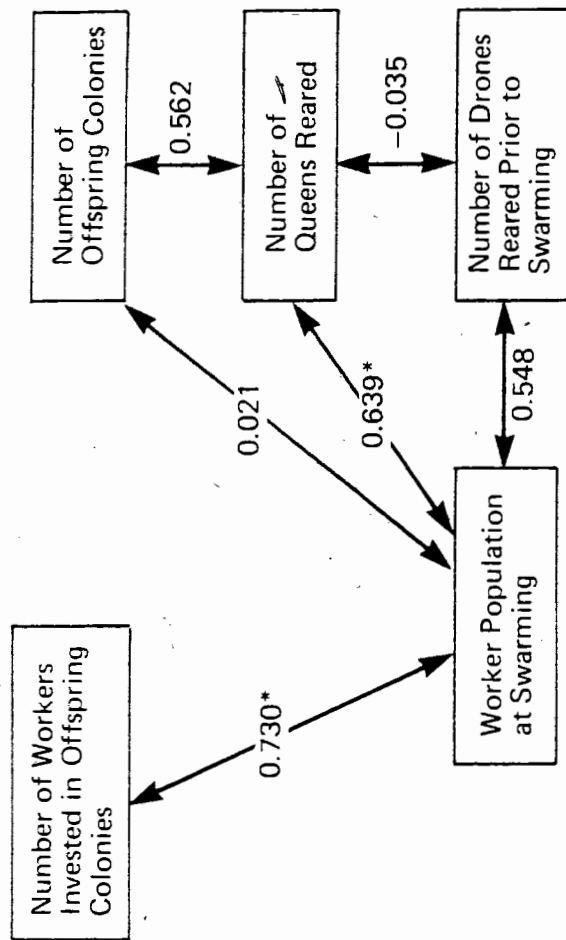
colonies produced ($P>0.09$, Fig. 1). The average worker and drone population sizes reared prior to swarming were 42,100 and 2,400, respectively, and the average number of workers which went to offspring colonies was 21,930 (Table I). The worker population at swarming was not correlated with the number of drones produced prior to swarming ($P>0.10$, Fig. 1) nor with the number of offspring colonies produced ($P>0.25$, Fig. 1), but was positively correlated with the number of workers in offspring colonies ($P<0.05$, Fig. 1).

Swarm Size, Drone and Worker Production, and Survival Time

There was a significant difference between the number of workers in prime and afterswarms (t-test, $P<0.05$). The mean prime swarm size was 19,930 workers while the mean first afterswarm size was 9,250 workers. The average size of second and third afterswarms was 11,030 workers (Table I). The earliest swarm issue dates were 1 May, 1982 and 17 April, 1983, while the latest swarm issue dates were 6 July, 1982 and 15 June, 1983. The median dates for prime swarm issue were 10 and 21 May, in 1982 and 1983 respectively, while the median afterswarm issue dates were 14 and 18 May, 1982 and 1983, respectively.

The mean cumulative worker production at the end of the season by prime swarms, afterswarms and the virgin queens which inherited the original colony were 55,530, 38,760, and 70,320 workers, respectively (Table I); differences between afterswarms and the inherited colonies were significant ($P<0.05$, ANOVA and

Figure 1: Correlations between worker population (including brood and adults) at swarming, the number of workers in offspring colonies, the number of queens and drones reared, and the number of offspring produced. R-values are given for each correlation; $P < 0.05$ confidence levels are denoted with an asterisk.

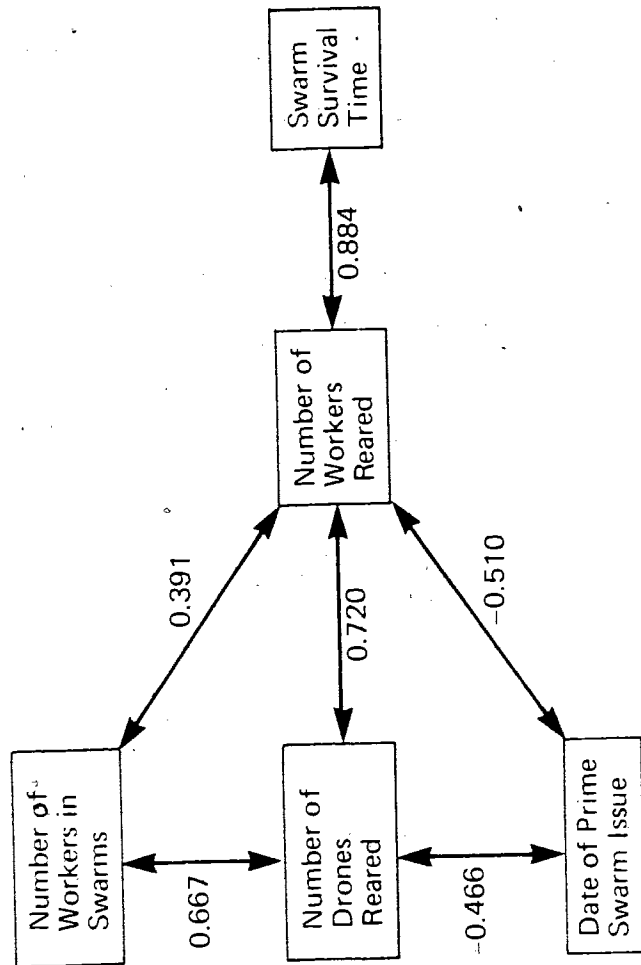


subsequent Neuman-Keuls test). The mean drone production by prime swarms, afterswarms and the queens which inherited the original colonies were 3,690, 830 and 550 drones, respectively (Table I); differences between prime swarm and both afterswarm and the inherited colony productions were significant ($P < 0.05$, ANOVA and subsequent Neuman-Keuls test). No other combinations of either cumulative worker production or drone production after swarming were significantly different ($P > 0.05$).

The average survival times following swarming were 132.9, 160.0 and 195.2 days for afterswarms, prime swarms and the original colony with a new queen, respectively. There was a significant difference between afterswarm survival and the survival of the daughter which inherited the former parental colony ($P < 0.05$, ANOVA and subsequent Neuman-Keuls test, Table I). There were no other significantly different pairs of survival means.

Correlation path analysis was performed to derive a model of interaction between the effects of swarm size, date of swarm issue, drone production and worker production on swarm survival (Sokal and Rohlf 1969). Only the number of workers reared was correlated with swarm survival ($P < 0.005$, Fig. 2). However, swarm size and date of swarm issue were indirectly related to swarm survival, since these factors were correlated with worker number. Drone rearing was not correlated with swarm survival ($P > 0.25$). Swarm size and worker production were positively correlated with drone production, while date of issue was

Figure 2: Correlations between swarm size, date of swarm issue, worker production, drone production, and survival of colonies initiated from swarms. All r-values are $P < 0.05$.



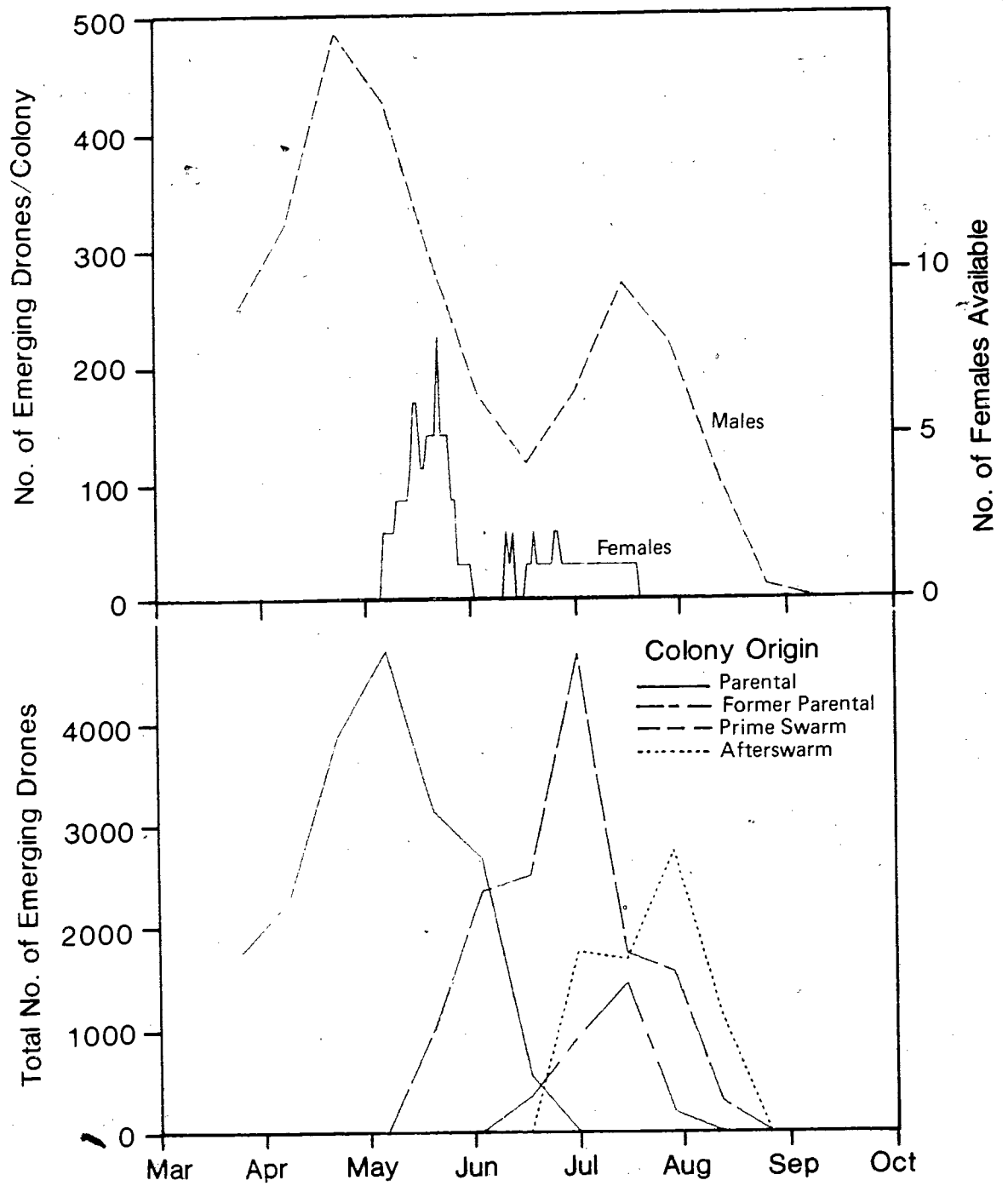
negatively correlated ($P < 0.05$, Fig. 2).

Drone and Virgin Queen Emergence Patterns

Drone emergence was protandrous, preceding female emergence (Fig. 3, top). The first peak of drone emergence occurred on 21 April, 1983, 2 days prior to the first availability of virgin queens for mating. This peak was composed entirely of drones produced by the pre-swarmed parental colonies. A depression in drone emergence then occurred as offspring queens mated and afterswarms and prime swarms constructed nests and began worker production. The second major peak of drone emergence occurred on 14 July and was due to drone production by offspring colonies (afterswarms and the inherited original colony) and the colony established by the prime swarm (Fig. 3, bottom). The greatest number of drones was produced during this period by prime swarms, followed by afterswarms and the inherited original colony (Fig. 3, bottom; Table I).

Figure 3: Top: Temporal emergence pattern of drones per colony compared to the number of unmated reproductive females in the population.

Bottom: The total number of drones emerging daily in pre-swarmed colonies, colonies initiated from prime swarms and afterswarms, and the post-swarmed inherited parental colony.



Discussion

This study has demonstrated that colony reproductive characteristics affect the parental colony size, timing of reproduction, initial offspring and prime swarm colony sizes, and the growth of the worker population prior to winter. Pre-swarmed parental colony size, as measured by the total number of workers in the colonies at swarming, was positively correlated with the number of workers invested in offspring colonies (Fig. 1). The lack of correlation between swarming colony size and number of offspring colonies indicates that large colonies divide into larger swarms rather than producing more smaller-sized swarms. This may be due to the strong positive relationship between swarm size and subsequent worker and drone production and colony survival (Fig. 2).

Colony size at swarming also was positively correlated with the number of queens reared, which was unexpected since the number of colonies produced and requiring new queens did not increase with colony size. This correlation was not due to energetic restrictions on small colonies because the cost of rearing queens is relatively small compared to that of the large number of drones and workers reared (Haydak 1970). The survivorship of immature queens (about 50%) was lower than that found for immature drones and workers (over 90%) by Fukuda and Sakagami (1968) and Fukuda and Ohtani (1977), perhaps indicating an increased sensitivity to mortality factors such as disease,

parasites, temperature, or humidity. Larger colonies may be able to reduce the mortality in immature queens due to these factors. Lower survivorship and overproduction of queens also could be related to the genetic heterogeneity of workers within colonies. Due to polyandry, workers of the same father have a higher degree of relatedness than other patrilineal worker groups (Hamilton 1964). This could result in competition and interference of queen production between worker patrilineal groups in a colony. However, it is not clear why this factor should be expressed more in large colonies than small colonies.

There was no relationship between swarming colony size and drone production, which differs from other studies indicating a strong positive correlation (Allen 1965; Free and Williams 1975; Page and Metcalf 1984). The results may have been due to the limited variability in colony size caused by the use of a single nest size which colonies outgrew prior to swarming. Hence, the range of colony sizes measured may not have included a large enough variation to produce significant correlations with drone production. There is some support for this interpretation, since measurement of more widely varied colonies founded by offspring and prime swarms did yield a significant increase in drone production with worker population.

The second objective of this study was to examine the effect of the date of swarm issue and swarm size on drone and worker production and colony survival. There was a strong difference in survival time between queens in swarms (parental

and offspring) and the daughter which inherited the former parental colony. Presumably, the increased survivorship was due to an advantage gained by inheritance of an already constructed nest and some stored resources, allowing these colonies to place much of the initially collected resources into worker brood rearing (Table I). On the other hand, swarms must devote a great deal of their initial energy to construction of a new nest (see Chapter IV). The survival time of swarms was correlated with the number of workers reared after hiving, which in turn was influenced by the swarm size and date of swarm issue (Fig. 2). Large initial worker populations in colonies result in the nest being constructed more quickly (see Chapter IV), better colony thermoregulation, increased foraging, better brood care, and more effective colony defence, thereby increasing colony growth and enhancing swarm survival. Similarly, colonies swarming early in the season had more time to collect and store resources and rear brood prior to winter. This is particularly important in Southwestern British Columbia because the major nectar flows occur in late April and May. There were no direct correlations of either swarm size or date of swarm issue with swarm-initiated colony survival, possibly because colony mortality usually occurred in late fall to early spring, when the workers from the initial swarm had perished.

Honey bees are protandrous, with males emerging prior to queens and the peak of male emergence preceding the first queens becoming available for mating (Fig. 3). The unmated queen

population curve was characterized by a high initial peak and low flat tail; the discontinuities in the distribution were due to the small sample size rather than to gaps in queen availability. Two proximal factors influenced the female availability curve. First, the majority of colonies began swarming in May, so most females were available for mating in May and June. Second, there were several periods of bad weather during June which prolonged the time unmated females were available.

The population of emerging drones was divided into two subpopulations, early drones originating from pre-swarmed parental colonies and later drones produced by colonies initiated from prime swarms and offspring colonies (Fig. 3; Page 1981). The timing of the first drone emergence peak so as to precede the first emergence of unmated queens by two days was not surprising, since all pre-swarmed colonies initiated drone production prior to queen rearing and subsequent swarming. During the post-swarmed period, the drone emergence patterns of the prime swarm and offspring colonies were more dispersed and asynchronous (Fig. 3) with larger swarms producing more drones (Fig. 2). Colonies initiated from prime swarms produced the first drones, since they contained larger initial worker populations. The former parental nests were the second group to peak in drone production during the post-swarmed period. The late drone production by afterswarms relative to prime swarms and the inherited colonies can be attributed to their smaller

worker populations and construction of nests relatively late in the season.

The availability of females early in the season was related to the timing of colony initiation and its effects on colony success. As we have shown, the survival of offspring colonies increases if they are initiated early, which strongly favours spring queen production and swarming. For drones, male - male competition is the most likely explanation for their emergence peak preceding queen emergence. First, in honey bees, there is fierce competition among drones to mate females (Gary 1963), and protandry is favoured since early - emerging drones have more opportunities to mate than those which emerge after the first queens become available. Second, male emergence should precede female emergence when male lifespan is shorter than the length of female availability (Wiklund and Fagerstrom 1977). In such cases, drones which emerge too early may not survive until the majority of females become available, hence, the peak of male emergence should precede the appearance of available females. The average adult lifespan of drones is 21 - 43 days (Witherell 1972; Fukuda and Ohtani 1977), and in this study unmated females were available for 74 days, from 5 May to 18 July, and the first females appeared 2 days after the peak in drone emergence. Third, if post-emergent mortality of males is greater than pre-emergent mortality, then colonies should produce drones prior to the time of female availability (Iwasa et al. 1983). Fukuda and Ohtani (1977) found pre-emergent mortality to be

lower than post-emergent mortality in drones, and again this study confirmed that colonies initiated spring drone production so that emergence preceeded female availability for mating.

During the post-swarmling period, the amount of drone rearing per colony decreased, but the total drone production in the population was greater than during the pre-swarmling period (Fig. 3). The increased number of colonies partly explains the increase in total drone production but does not explain why colonies rear so many drones when there is a decrease in female availability. One possible explanation is that colonies cannot predict the degree of male competition because of variance and unpredictability in the number and size of other offspring colonies. Also, if winter survival for most colonies is unlikely, then resources stored and used for worker production might be put into drone production in an attempt to reproduce prior to the onset of winter. While these males may not mate with swarm-related females, there would be some females available due to established colonies superceding failing queens (Gary and Morse 1962; Allen 1965).

The importance of colony size and reproductive timing in temperate climates is demonstrated by the general trend of increasing reproductive rates with decreasing latitude; 2.2 colonies/year in Fort Langley, B.C. (lat. 49° 10'N), and 3.6 colonies/year in Lawrence, Kansas (lat. 38° 57'N) (Winston 1980) for european-derived bees, and 8.4 - 11.5 colonies/year for tropically-evolved africanized honey bees in French Guiana,

South America (lat. 10 43'N) (Winston et al. 1981). Data from Ithaca, New York (lat. 43° 20'N) also support this conclusion for temperate bees, although only the frequency of colonies swarming annually (0.92) was recorded and not the total reproductive rate (Seeley 1978). The higher reproductive rates in Kansas and French Guiana were due to increases in the number of afterswarms and swarming events per year. The longer length of the growing season and the increase in diversity and availability of flowering plants with decreasing latitude (Fischer 1960) probably explains the trend in reproductive rates for temperate-evolved bee races. For tropically-evolved bee races, both climate and predation are the major factors which influence their life history patterns. Lack of a severe winter reduces the need for large nests and storage of copious quantities of honey in tropically-evolved bees, resulting in smaller colonies which swarm more frequently. Similarly, vertebrate and invertebrate predation and competition influence colony size, reproductive rates, timing of reproduction, and nest site location in tropical bee races (Winston et al. 1981, 1983; Seeley et al. 1982).

In conclusion, the shortness of the foraging period and the severity of winters allow only a brief period in spring when swarm production is successful. Drone production is linked closely to the swarm cycle because the majority of new queens are produced at that time. Drone production and survival of post-swarmed colonies depends on worker production and in turn

the size of swarms and the timing of swarm issue play an important role in determining the extent of drone and worker production.

Future studies should involve the integration of ultimate causation factors with the present populational and behavioural data. Of particular interest would be to study the role of kin selection and intra-colony genetic relatedness in determining overall reproductive patterns.

III. THE INITIAL BROOD REARING PATTERNS IN NEWLY FOUNDED COLONIES

Introduction

In this chapter I examine the influence of swarm size on initial brood rearing characteristics of newly-founded colonies. Studies done in a beekeeping context, using established, managed colonies, suggest two ways that the size of the worker population might affect new colonies. First, colony size is positively correlated with total brood production and appears to be negatively correlated with the ratio of brood to workers (Farrar 1932; Free and Racey 1968; Moeller 1961; Nelson and Jay 1972; Smirl and Jay 1972). Second, worker weights appear to be influenced by colony size, with heavier workers being produced in mid-summer when colonies are largest (Levin and Haydak 1951).

The objective of this chapter was to determine the effects of swarm size on brood production, brood/worker ratio, and worker weight in newly-founded colonies.

Materials and Methods

Prime swarms and afterswarms used in this section originated from colonies located in Fort Langely, B.C. In 1982, 7 colonies produced 7 prime swarms and 6 afterswarms (2 prime swarms were not caught). In 1983, 10 colonies produced 10 prime swarms and 11 afterswarms (4 prime swarms and 2 afterswarms were not caught). All of the prime swarm queens were Italian stock (A. m. ligustica) imported from California the previous spring. Swarms were caught, hived and their size estimated using the same method as described in the previous chapter. Newly hived swarms were frequently inspected and the progress of egg laying and larval development noted. The area of sealed worker brood was estimated as previously described. The sealed brood per worker ratio was determined by dividing the sealed brood area when the first workers emerged by the size of the swarm population.

We were able to predict the emergence of the first worker brood, which occurred 25-35 days after the swarm was hived. At that time, frames of sealed brood about to emerge were placed in an incubator at 32° C and 50% relative humidity. Emerged bees were removed every hour and placed in a cooled jar for 10 minutes, slowing movement and allowing easier weighing. Fifteen workers from each hive were weighed individually on a Mettler H 20T balance. Workers with physical defects (such as damaged wings, deformed abdomens, poorly developed legs, etc. were

discarded.

Cell size was determined by measuring the width of 10 cells in a row. Comb was categorized as dark or light, corresponding to old or new comb respectively. Sample locations for comb measurements were determined using a random number generator. A pair of random coordinates was plotted on a frame grid with half-centimeter squares. Once located, the nearest cell and the next nine cells to its right were measured. Fifteen measurements were recorded in each colony for each type of comb. Cell sizes were recorded only for colonies in 1982.

Results

In 1982, swarming occurred from 1 May to 6 July. The mean prime swarm population was 20,400 workers (S.D.=9,100, range 6,600-34,300 workers) while afterswarms had a mean of 7,400 workers (S.D.=2,720, range 3,200-11,300 workers). In 1983, swarming occurred from 17 April to 15 June. The mean swarm size was 19,700 workers for prime swarms (S.D.=8,020, range 9,400-33,100) and 12,800 workers for afterswarms. (S.D.=7,600, range 5,700-15,700).

Over the two years, individual worker weights were 87.6 to 150.5 mg. Emergence weights of the first brood were correlated with the initial swarm population in 1982 ($r=0.624$), 1983 ($r=0.374$) and both years pooled ($r=0.511$) ($P<0.01$ in all cases, Fig. 4). The amount of sealed brood present when the first workers emerged was also correlated with the swarm size in 1982 ($r=0.689$, $P<0.05$), 1983 ($r=0.638$, $P<0.01$) and both years pooled ($r=0.641$, $P<0.01$) (Fig. 4). The total sealed brood weight (sealed brood x mean worker weight) was positively correlated with swarm size for 1982, 1983 and both years pooled ($r=0.760$, 0.623 and 0.658 respectively, $P<0.05$). However, the sealed brood area/worker ratio and swarm size showed no correlations in 1982, 1983 or both years pooled ($r=0.278$, -0.068 and -0.186 , respectively, $P>.05$, Fig. 5). An arcsine transformation was performed on the brood/worker ratios prior to analysis (Sokal and Rohlf 1969).

Figure 4: Top: The relationship between the mean emergent weight of workers from the initial broods of newly founded colonies and the number of workers in the founding swarm.

Bottom: The relationship between the amount of sealed brood present in colonies at the time of first worker emergence and the number of workers in the founding swarm.

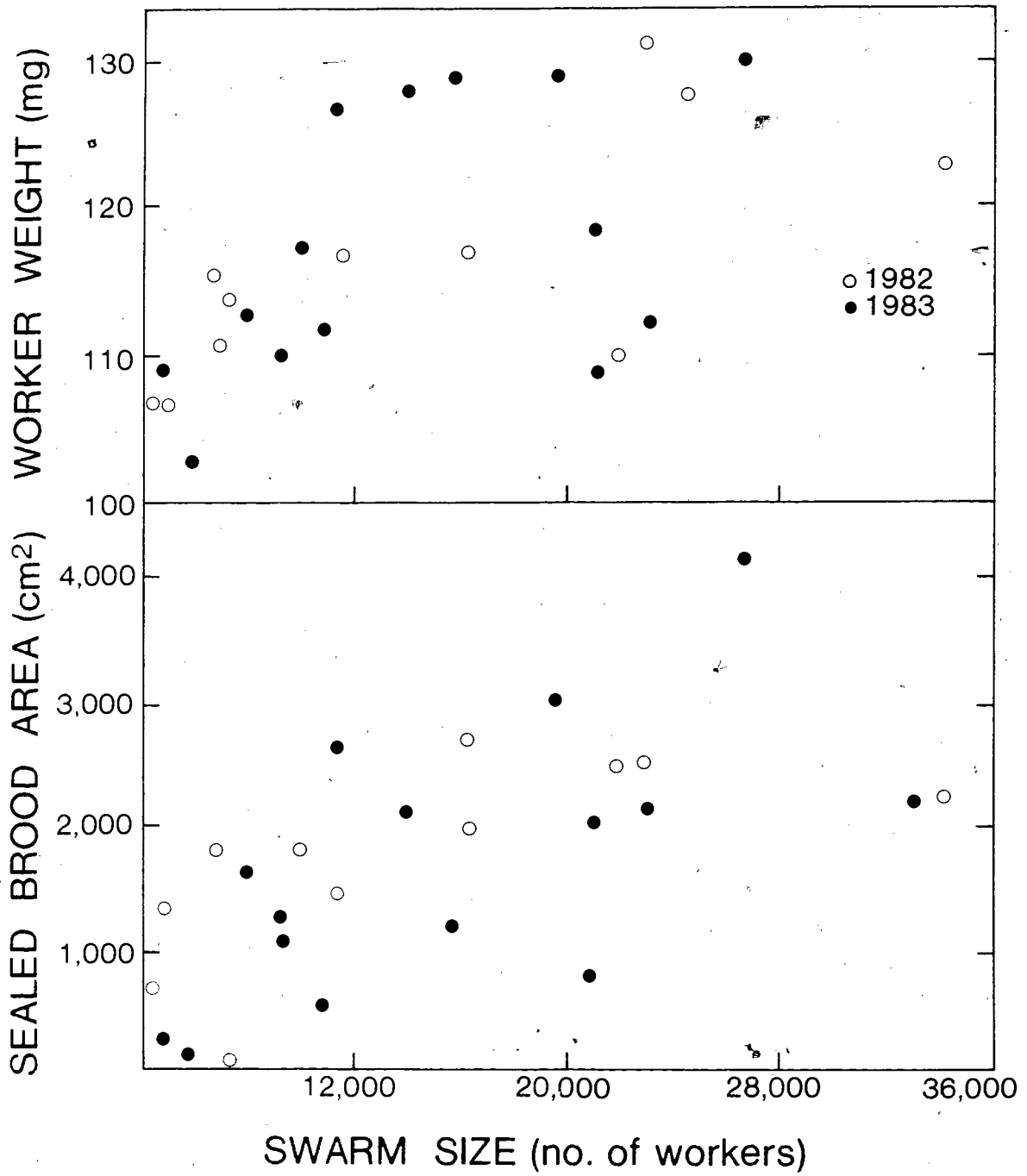
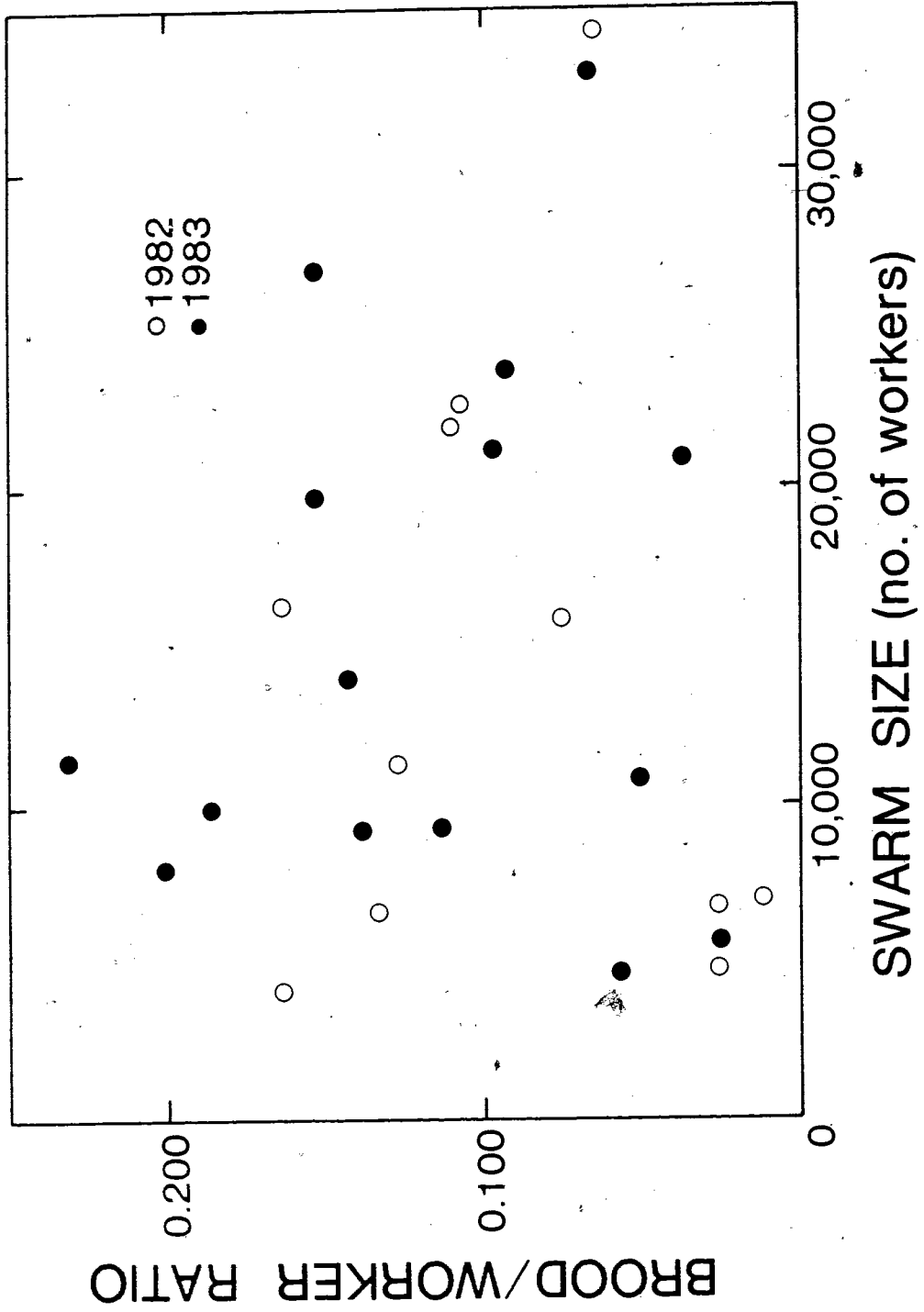


Figure 5: The relationship between the sealed brood per worker ratio at the time of first worker emergence and the number of workers in the founding swarm.



The brood areas and emergent worker weights were compared for prime and afterswarms of comparable sizes ($n=6$, 6,600-16,300 and $n=12$, 4,300 to 15,700 respectively). There were no significant differences in worker weights or brood areas between prime and afterswarms ($P>0.10$, Mann Whitney test).

An ANOVA detected no significant differences for cell size between new and old combs within a colony ($P>0.10$) nor between colonies ($P>0.10$). The mean width of 10 cells for old and new comb for all colonies was 5.25 cm (S.D.=0.046 cm).

Discussion

The results demonstrated that colonies founded by more populous swarms produced more brood (Figs. 2,3,4) which agrees with other studies showing a positive relationship between colony size and brood production (Farrar 1932; Free and Racey 1968; Moeller 1961; Nelson and Jay 1972; Smirl and Jay 1972). Those studies also imply that less populous colonies compensate for their relatively low brood production by increasing the brood/worker ratio, and suggest that brood to worker ratios are negatively correlated with colony population. Michener (1964) suggested that higher brood rearing efficiency per female in less populous colonies may be a feature of other social Hymenoptera as well. However, my results from colonies founded by swarms showed no relationship between swarm size and the brood/worker ratio.

The difference between my results and those of previous studies may have been due to differences in temporal caste structure and the tasks required for swarms and managed colonies. Established colonies have an older age distribution of workers (Winston et al. 1981), and contain drawn comb and stored honey. In contrast, swarms have a very distinct age structure skewed towards younger workers (Butler 1940; Meyer 1956; Winston and Otis 1978), and need to construct comb and collect nectar and pollen. In swarms, younger workers which would normally rear brood may change to comb building and foraging tasks; this may

explain the lack of a relationship between swarm size and worker brood rearing efficiency.

The weight of the first workers to emerge in newly founded colonies was positively correlated with the size of the swarm (Fig. 4). Worker weight in honey bees can be influenced by a number of factors including nurse bee number and age, colony size, cell size, availability of nectar and pollen, interruption of food supply, disease, and time of year (reviewed by Jay 1963 and Levin and Haydak 1951). In my experiment only nurse bee characteristics, colony size, nutrition, and cell size might have been important, since the other factors were either similar for all colonies or did not occur, such as disease.

Cell size was not influenced by swarm population and did not affect worker weights. This result is unique for cell-building social insects, since other examples of worker weight differences in young colonies have been correlated with cell size differences. These include the bumblebee Bombus ruderatus (Pomeroy 1979), the wasps Vespula vulgaris and V. germanica (Archer 1972) and possibly tropically evolved Africanized honey bees recently introduced to South America from Africa (unpublished observations, Winston; Winston et al. 1983).

The worker population and possibly the number of nurse bees in incipient colonies may have influenced worker weight by providing better nutrition and care to brood in larger colonies. Colonies founded by more populous swarms would have more workers available for all tasks including foraging, thermoregulation,

and brood care, resulting in more brood and heavier workers. The number of nurse bees may be especially important in colonies founded by small swarms because such swarms have fewer young workers of the ages typically associated with brood care. Consequently, brood rearing tasks in less populous colonies may be performed by older workers, resulting in decreased weight and longevity of the newly-emerged workers (Haydak 1963).

The production of lighter workers in colonies founded by small swarms could be explained by two hypotheses. First, this pattern could be due to energetic constraints under which less populous swarms are operating. This is supported by our results showing that the total weight of brood produced by larger colonies (sealed brood x average worker weight) was positively correlated with founding swarm size.

Colonies founded by less populous swarms could produce lighter workers not due to energetic constraints but because lighter workers were adaptive in that situation. There is some evidence that light workers might affect caste structure and provide for more nurse bees. Kerr and Hebling (1964) suggested that lighter workers perform in-hive tasks while heavier workers mature faster to perform outside tasks. This is the case for some Bombus species (Alford 1970; Cumber 1949; Garofalo 1978; Richards 1946). Also, Oster and Wilson (1978) proposed that small colonies are more sensitive to energy loss through predation. Smaller workers are less conspicuous and, even if captured, represent a lower energy loss than large workers.

Larger colonies may be less sensitive to the loss of workers and can produce heavier workers which might be more efficient foragers.

At this point constraint factors on worker weight, such as worker population and the number of nurse bees, cannot be separated from the potential advantages of lighter worker production. Further experiments manipulating swarm size and worker age distribution are needed to investigate the relationship between colony population structure and worker weights.

IV. COMB CONSTRUCTION BY NEWLY FOUNDED COLONIES

Introduction

Many social insects build nests which are integral to the colony's survival, growth and reproduction. These nests may be elaborate and often represent a considerable investment in resource collection and metabolic energy from secretions of insect-produced construction materials. Two aspects of nest architecture are particularly important in determining a colony's reproductive success, nest size and cell structure. Large colonies generally produce a higher proportion of reproductives, and may change from worker to reproductive brood rearing earlier than small colonies (Oster and Wilson 1978). Also, in some cell-building social insects, nest architecture partially determines caste structure and the sex ratio of reproductives, since workers and both male and female reproductives generally are reared in different-sized cells (Michener 1974).

In perennial colonies such as those of the honey bee (Apis mellifera L.), a nest may survive for many years. However, most of the nest construction takes place during a colony's first year, and characteristics of founding swarms which affect nest architecture will influence subsequent growth and reproduction for a colony's lifetime. Factors such as swarm size, date of

issue, worker age distribution, genetic relatedness, and engorgement with nectar could be important in determining both nest size and the ratio of worker and male cell types.

Honey bee nests are often found in cavities such as hollow logs, and are composed of a series of vertically hanging wax combs produced by glands in the abdomens of workers. Two sizes of hexagonal cells are constructed in the comb; workers are reared in the smaller cells and drones are reared in the larger cells. Queen rearing is performed in 10-20 vertical, conical cells which are destroyed when queen rearing is completed. Recent studies of nest architecture have examined cavity characteristics by which swarms choose nesting sites (Jaycox and Parise 1980; Rinderer et al. 1981, 1982; Seeley 1977; Seeley and Morse 1976, 1978), the density of feral nests (Avitabile et al. 1978; Taber 1979), nest characteristics involved in predator avoidance (Seeley et al. 1982), comb building patterns in semi-managed colonies (Allen 1965; Free 1967; Free and Williams 1975; Owens and Taber 1973; Simpson 1969; Taber and Owens 1970) and the influence of nest size on reproduction (Otis 1980; Winston and Taylor 1980; Winston et al. 1981).

The objectives of this chapter were to investigate the influence of swarm size and date of issue on total comb production and the ratio of worker to drone cells in colonies founded by swarms.

Materials and Methods

Prime swarms and afterswarms were collected upon emergence from unmanaged colonies located in Fort Langley, B.C., Canada. Swarms were caught, hived and their size estimated using the technique described in Chapter II. The arithmetic mean number of workers in swarms and the dates of issue are presented in Chapter III.

Measurements of comb area were made in mid-October to mid-November each year, after comb building had ceased for the season. Each side of a frame was traced onto a clear plastic sheet of mylar, and the areas of drone and worker comb were measured with a planimeter. In 1983, the pattern of comb building was recorded every 10 - 14 days throughout the season by placing a clear plexiglass sheet marked out in 5x5 cm quadrats over the frame and estimating the drone and total comb present. These figures were divided by the final amount of comb at the end of the year to calculate the relative amount of comb built throughout the year.

There were no statistically significant differences between 1982 and 1983 for the size of swarms, the amount of comb constructed or the percentage of drone comb built (Mann-Whitney U test, $P > 0.10$ in all cases). Therefore, the 1982 and 1983 data were pooled for the remainder of the analyses. Prior to statistical analysis an arcsine transformation was performed on the percentage of drone comb constructed (Sokal and Rohlf 1969).

The dates of swarm issue for 1982 and 1983 were combined by placing them on a similar scale. The earliest swarm to emerge (April 17, 1983) was used as the first date of this scale and all other swarm dates were placed relative to this date.

Results

During 1982 and 1983, the total amount of comb constructed by colonies varied from 1,460 cm² to 15,940 cm², with a mean of 9,480 cm² (S.D. 4,552 cm²). A significant positive correlation was found between swarm size and the total amount of comb constructed ($r=0.590$, $P<0.01$, Fig. 6, top). A significant negative correlation was found between date of swarm issue and the total amount of comb produced ($r=-0.484$, $P<0.05$, Fig. 7, top). A multiple correlation using swarm size and date of swarm issue as independent variables and total amount of comb constructed as the dependent variable increased the correlation coefficient to $r=0.793$ ($P<0.01$). There was no significant correlation between the sizes of swarms and the date of swarm issue ($r=0.121$, $P>>0.05$).

In 1982 and 1983, colonies constructed from 0 - 34.7 percent drone comb with a geometric mean of 8.1 percent. The percentage of drone comb was positively correlated with swarm size ($r=0.499$, $P<0.05$, Fig. 6, bottom) and was negatively correlated with the date of swarming ($r=-0.456$, $P<0.05$, Fig. 7, bottom). A multiple correlation using swarm size and date of issue as independent variables increased the r-value to 0.796 ($P<0.01$).

Generally, drone comb was constructed in the lower corners of the combs. Less frequently, it was located in the center of outer combs. During the two study years, seven colonies built no

Figure 6: Top: The relationship between the total amount of comb constructed and the swarm size (number of workers).

Bottom: The relationship between the percentage of drone comb constructed and the swarm size (number of workers).

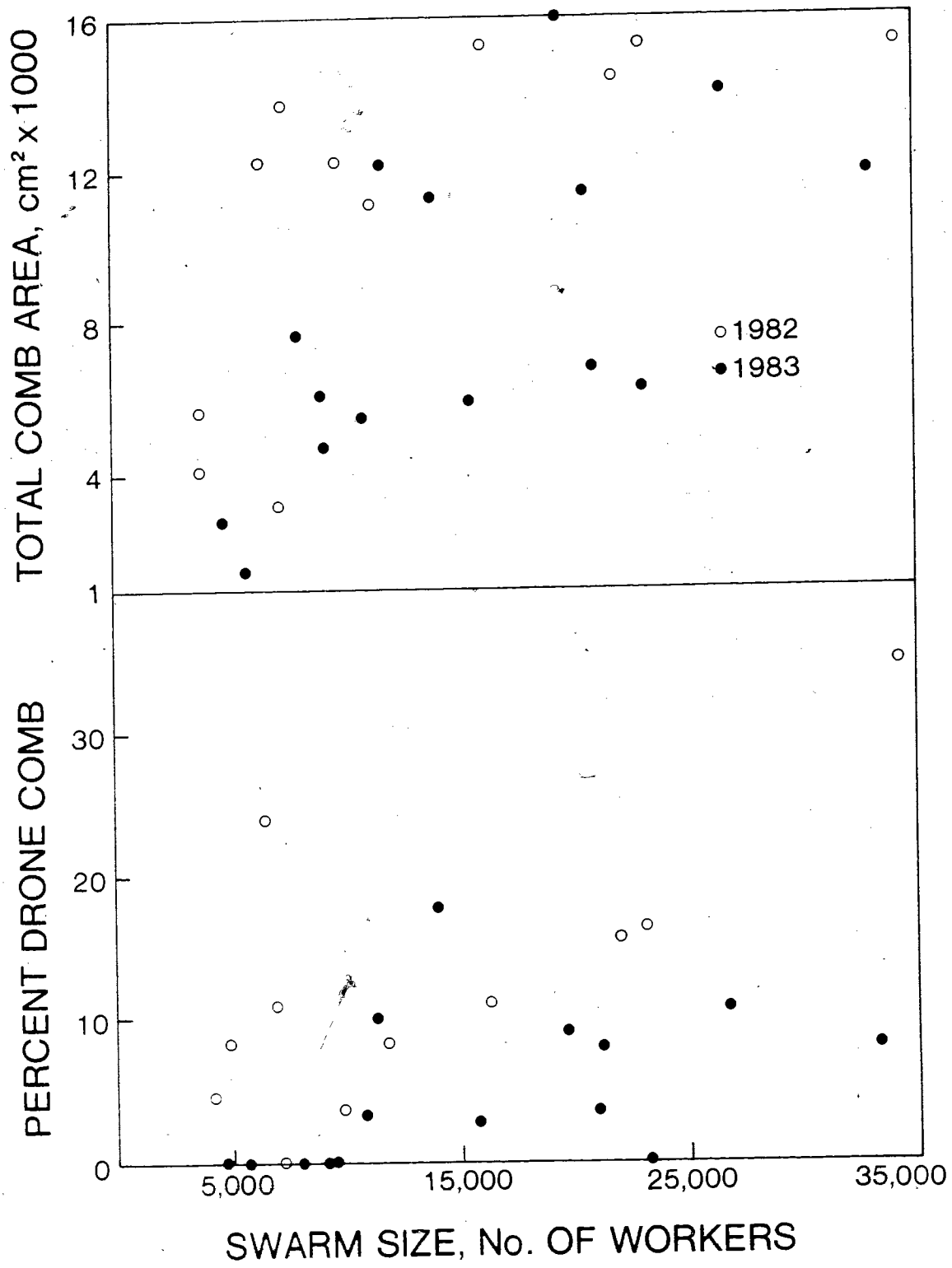
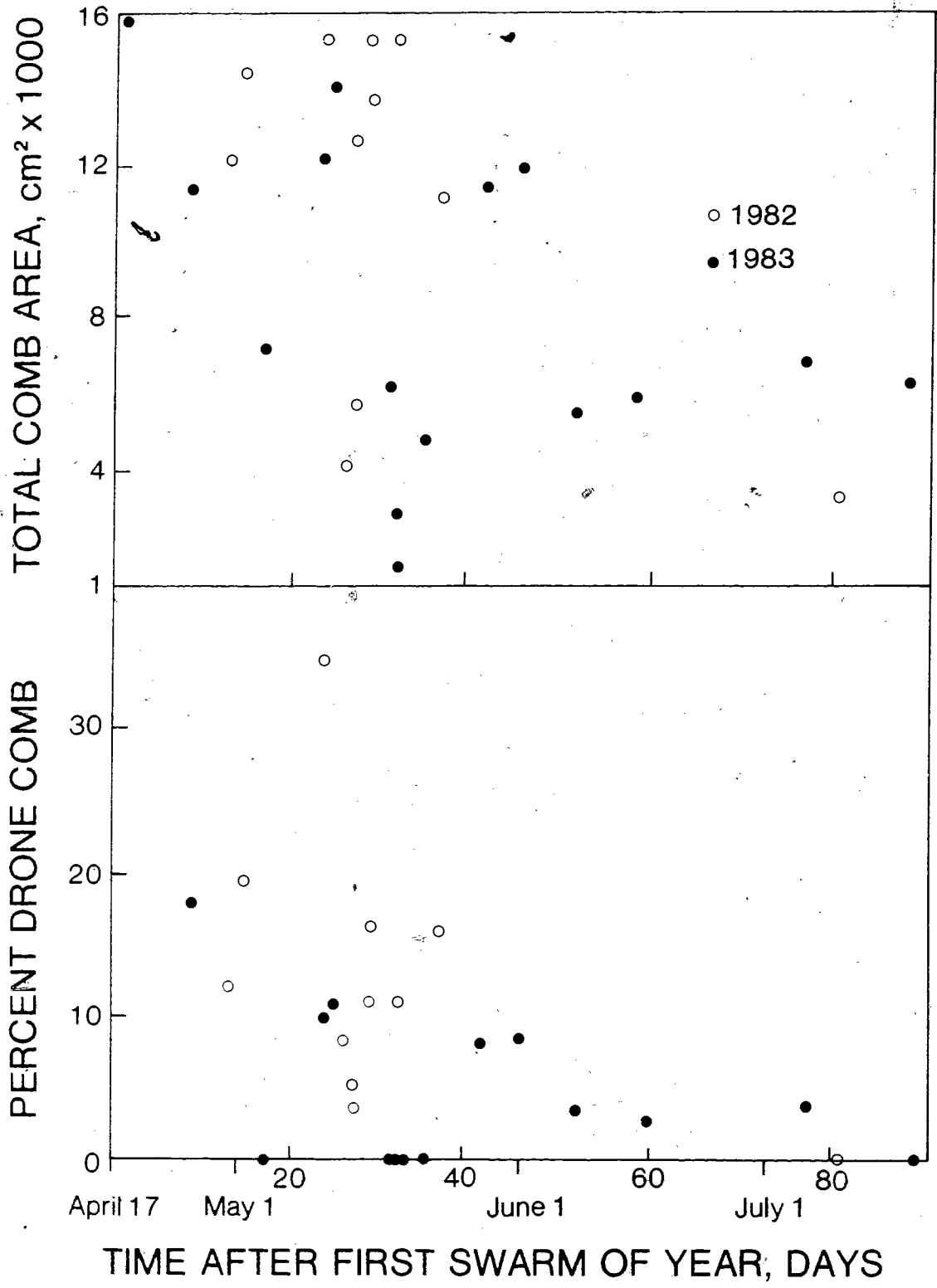


Figure 7: Top: The relationship between the total amount of comb constructed and the relative time of swarm issue.

Bottom: The relationship between the percentage of drone comb constructed and the relative time of swarm issue.

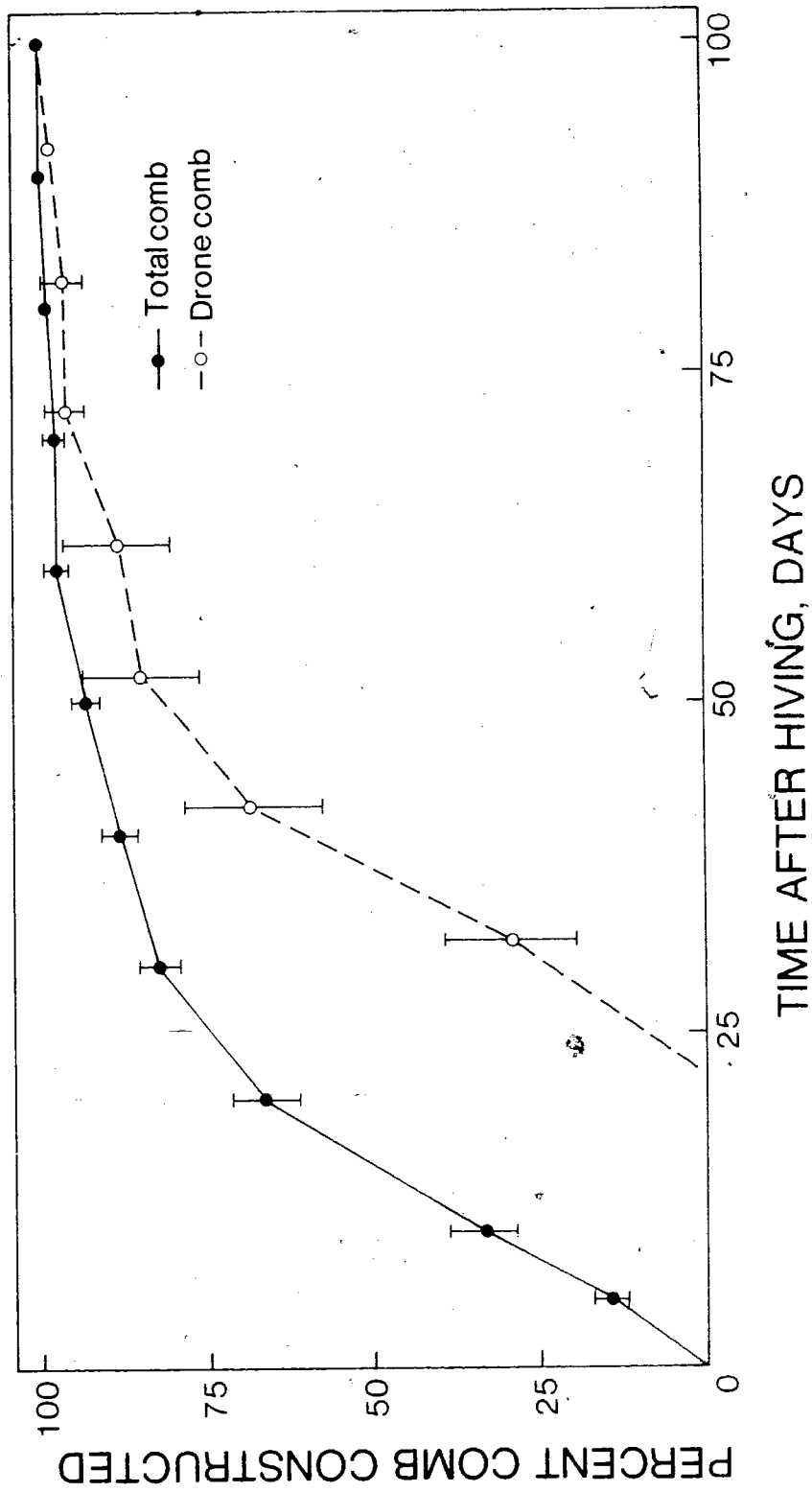


drone comb at all (1 in 1982, 6 in 1983). The average swarm size of the colonies which constructed no drone comb was 9,600 workers, while the average swarm size of colonies which constructed drone comb was 16,200 workers ($P < 0.05$, rank sum test). Colonies which built drone comb originated from swarms emerging earlier in the season than colonies which built no drone comb; the average dates of issue were 12 and 28 May respectively, ($P < 0.05$, rank sum test).

Colonies initially showed high rates of comb construction, with 90% of all comb being built within 44 days after hiving (Fig. 8). Drone comb construction began a mean of 22 days after hiving (range 4-52 days), with 90% of drone comb being built within 42 days after the first drone cells appeared (Fig. 8).

The percentage of drone comb was plotted against the total amount of comb constructed and analyzed with a least squares regression ($P < 0.001$, Fig. 9). Similar data from Otis (1980) for Africanized bees (*A. m. scutellata*) in South America were also analyzed with a least squares regression ($P < 0.001$, Fig. 9). A t-test comparison of the slopes showed the relationship for European-derived bees to have a significantly greater slope than that for Africanized bees ($P < 0.001$).

Figure 8: The mean percentage of total comb constructed weekly by colonies after swarms were hived in 1983 (solid line), and the mean percentage of drone comb constructed following the appearance of the first drone cells in colonies (dotted line).




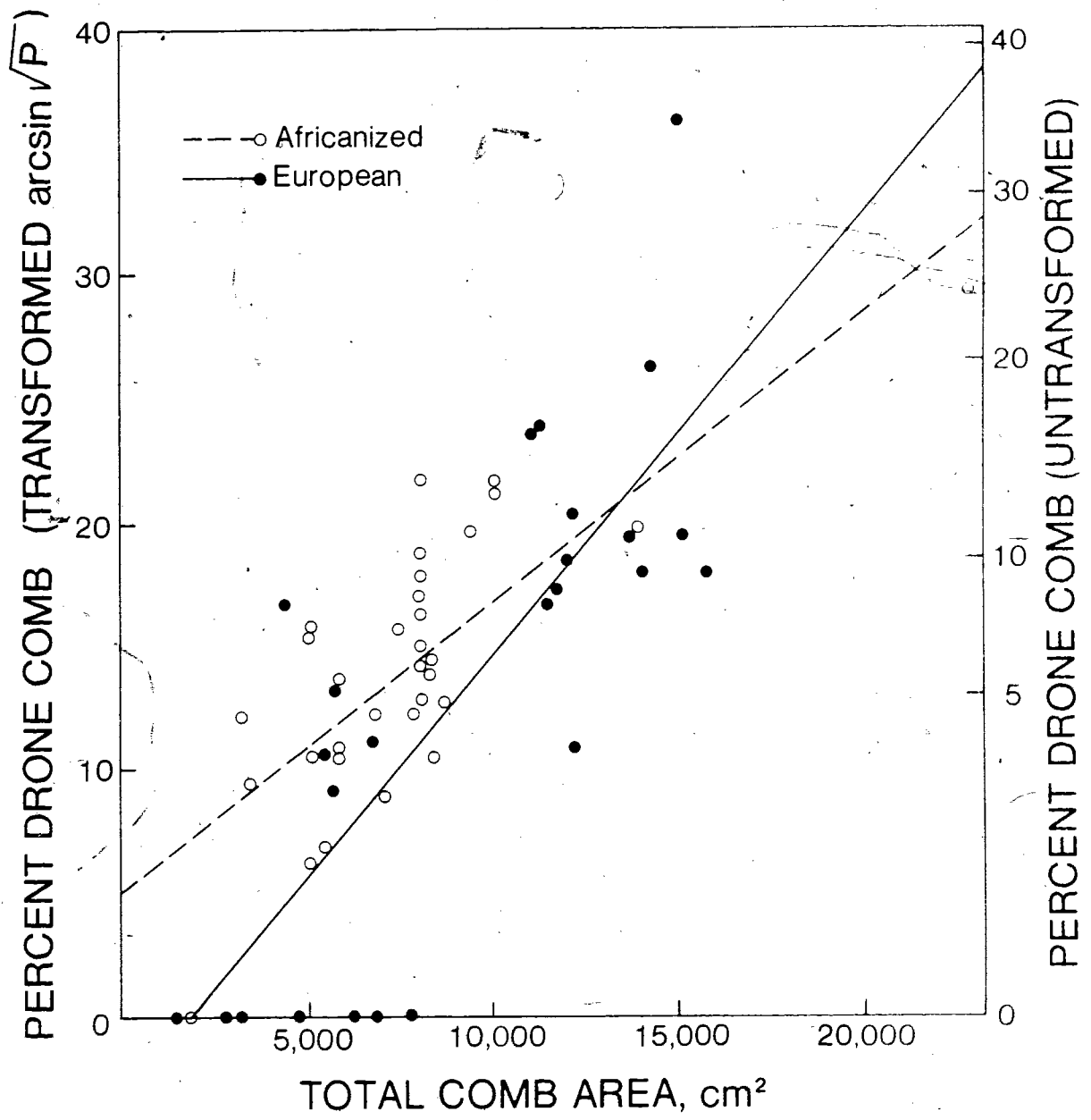


Figure 9: The relationship between the percentage of drone comb and the total amount of comb constructed by colonies of tropically-evolved africanized bees in South America (Otis 1980) and temperate-evolved european bees in British Columbia. Data were plotted and analyzed on the transformed scale shown on the left axis; for comparison the untransformed scale is shown on the right.



Discussion

Swarm size and date of issue were important factors in determining the total amount of comb constructed by colonies founded by natural swarms. Swarm size showed a significant, positive correlation with total comb construction, while date of issue showed a significant negative correlation (Figs. 6, top, 7, top). Large swarms have more workers to perform colony tasks necessary for comb building, such as nectar collection and wax production. This effect is particularly important during the initial phase of comb production, since new workers do not eclose and mature to comb building age until 35 - 40 days after colony founding, by which time almost all the comb has been constructed (Fig. 8). This rapid rate of comb construction is critical to colony growth and survival, since comb is required for brood rearing, food storage, and thermoregulation, and serves as a communication medium for foraging dances (von Frisch 1967), dorso-ventral vibrations (Fletcher 1978a), and queen footprint pheromone (Lensky and Slabezki 1981).

The importance of the swarming date to comb construction was likely due to the greater availability of nectar in the field during the earlier part of the season, which workers could utilize for wax production. This date effect was not due to colonies having insufficient time to construct comb before the winter, since 90% of comb was constructed within 45 days of colony founding, and the median swarming dates were 4 and 1 June

in 1982 and 1983, respectively.

There was also a significant positive correlation between swarm size and the percentage of drone comb constructed, and a significant negative correlation between percent drone comb production and the date of issue (Figs. 6, bottom, 7, bottom). Colonies founded from small swarms of less than 10,000 workers often produced no drone comb at all. Taber and Owens (1970) and Free and Williams (1975) found similar relationships between colony size and drone comb production in experimentally manipulated honey bee colonies. The diminished or complete absence of drone comb construction in colonies founded by smaller swarms could be explained by a colony's resource allocation priorities. Small colonies collect less nectar and construct less comb than large colonies, and since drones do no work and consume colony resources, they are a liability to colony growth. Thus, small colonies would not be expected to produce drone comb until they were larger and had sufficient resources for comb construction. Similarly, the 22-day delay in the initiation of drone comb production was probably due to the priority of worker comb.

The effect of swarm issue date on drone comb construction could have been due to nectar availability in the field and/or a seasonal influence. A rapid decrease or cessation of nectar input decreases the tolerance of colonies to adult and immature drones and stops drone comb production (Free and Williams 1975). This would have affected late-swarving colonies the most, since

their drone comb was constructed from late July to September, when nectar was not available in the Fort Langley area. Managed colonies in the northern hemisphere build most of their drone comb from mid-April to late May (Free 1967), preceding drone brood rearing and emergence which occurs a few weeks later (Allen 1965; Free and Williams 1975; Chapter II). By producing drone comb and rearing drones in the spring, adult drone emergence precedes the peak of reproductive swarming and availability of virgin queens (Page 1981; Chapter II).

Temperate and tropically-evolved honey bee races differed in the percentage of drone comb constructed at similar colony sizes (Fig. 9). Tropical Africanized honey bees in South America produced a larger percentage of drone comb at small colony sizes than temperate-evolved European races. These differences were likely due to different selective factors in their respective habitats (Winston et al. 1983; Fletcher 1978b). In general, colony mortality is higher in the tropics, and the greater percentage of drone comb built by small tropical colonies may reflect an effort to produce some reproductives before the colony is lost to predation. In contrast, temperate-evolved honey bees suffer less predation but must have a large worker population and plentiful stores to survive the winter. Therefore, small colonies of temperate-evolved races do not initially allocate as much resource to drone comb production, but rather emphasize worker comb more than Africanized colonies. At comb areas above 14,000 cm², large temperate-evolved colonies

placed more emphasis on drone comb production. Since Otis (1980) only recorded two tropical colonies above this size, it is not clear whether larger tropical colonies might also increase investment in drone comb.

V. CONCLUSION

The results of this study raise several interesting questions concerning the adaptiveness and evolution of honey bee reproduction. In general, the long winters and short foraging seasons seem to be limiting factors for the survival of feral honey bee colonies in temperate climates (Seeley 1978, Seeley and Visscher 1985, Winston 1979). Ideally, a parental colony should reproduce early with a large investment to ensure the success of its offspring. Despite a relatively early initiation of the swarming cycle and a large investment by parent colonies into offspring colonies, the low rate of colony reproduction and survival indicates that Southwestern British Columbia may be approaching the northern limit of the feral honey bee range. In most areas, the feral population is composed of swarms escaped from managed colonies. Each spring and summer the number of feral colonies will increase greatly because of swarming by overwintered feral and managed colonies. However, since few will survive the winter, their reproductive success depends primarily on drone production and mating prior to winter. Further, these drones must mate with queens from managed colonies or strong feral colonies which are likely to survive the winter.

There are two sources of queens available for mating; swarm-related queens and those produced due to supercedure. The large peak of drone production preceding and during swarming

can be explained by the availability of swarm-related queens. However, the majority of post-swarmed drones, particularly those produced late in the season, could only mate with supercedure queens. The stronger emphasis on supercedure queens would increase the variability when queens would be available because queen replacement can occur at any time of the year. Also, beekeepers use a variety of swarm control methods on managed colonies with varying efficacy which disperses swarming more evenly throughout the season. Both supercedure and availability of swarm queens from managed colonies would favour post-swarmed drone production in feral colonies.

Alternatively, there is some question whether the behaviour of the colonies used in this study was adaptive. The reproductive patterns observed could be adapted to the longer growing season of California where the bees were imported from. Initially, it was thought that California and British Columbia were similar enough to assume that California-imported bees were adapted to British Columbia's climate. Honey bees have been imported to British Columbia from California since 1858 (Turnbull, undated). Subsequently, imported colonies have had swarms escape which have successfully survived, producing a small viable feral population. However, the bees used in this study were not previously exposed to local conditions and had not undergone local selection pressures and may not have been adapted to local conditions. Adaptation to a more southern latitude would cause colonies to produce drones over a longer

period because swarming would occur over a longer period in California. Colonies may have been unable to adjust drone production to the lack of queens caused by the shorter season in British Columbia. Also, the late emerging and smaller sized afterswarms may have survived in milder climates. Unfortunately, this study does not contain the data to address this topic.

The problem of adaptation can be extended to all honey bee populations. At the crux of the problem is the close association between managed and feral colonies. Briefly, adaptation can be defined as, 'the solution to a problem set by nature', (Dunbar 1982). The concept requires that organisms acquire, usually through selection, characters that make them suited to a particular environment. A particular character can only be considered adaptive when shown to be better suited to the environment than an alternative character. The involvement of man in the biology of an organism does not necessarily negate the possibility of adaptation. Organisms can adjust to man as they would any other element in the environment. The major problem in assessing honey bee adaptations is determining whether management practices have remained constant enough from the point of view of the bee for selection to operate. Historically, honey bees have been 'kept' by man since before the primitive Egyptians, and were introduced into North America in 1622 (Crane 1975). The question of adaptation in Southwestern British Columbia depends on whether a significant portion of the genes carried by swarming colonies find their way back into the

managed population prior to winter. If drones produced by swarming colonies are able to successfully mate, then the reproductive patterns observed in this study may be evolutionarily stable. However, if the drones are unable to successfully mate then the behaviour observed in this study may be geographically misplaced or selection cannot produce adaptations fast enough to keep up with management practices. To test between these possibilities will require data on drone mating success and the subsequent success of the queens they mate with.

Whether the behaviour of feral honeybees is adaptive or not, the evolution of honey bees is of interest because it contains two subpopulations which interact, a feral and managed population. The general pattern of this interaction is that swarms are produced in the spring and summer by strong feral and managed colonies. These colonies grow, produce drones, and possibly mate back into the managed population. Thus, the production of drones late in the season may be advantageous in that those drones may mate with managed queens which are likely to survive the winter. The dependence of feral colonies on the managed population increases with an increase in latitude because the longer winters result in a decrease in feral colony survival. In tropical areas such as South America and Africa, the effect of managed colonies on feral colonies would be considerably less because of the higher survival of feral colonies (Otis 1980, Winston et al. 1980) and the less advanced

forms of management (Crane 1975).

By contrasting the 'big-bang' reproductive strategy of temperate-evolved eusocial Hymenoptera such as bumblebees (Bombus spp.), it is possible to further demonstrate limitations of the colony fission strategy utilized by honeybees. Bumblebee colonies sacrifice all colony resources in the late fall and switch from producing worker to male and female reproductives. As these reproductives emerge they mate and the female reproductives diapause through the winter alone. They emerge in the following spring and start a new colony which will repeat the cycle the following year. The queens and the colonies are annual and are destroyed during the winter. In such a strategy, the relative effects of colony size and timing of reproduction are reduced because there is no direct investment of workers into reproductives as in swarming. The release of reproductives at the end of colony growth allows for maximum output without having to save resources for the future. Also, by not maintaining a large worker population and nest, bumblebee populations place a greater portion of the energy collected each year into producing reproductives. This strategy has probably allowed Bombus spp. to extend its range further into colder climates than honey bees (Wilson 1971).

LITERATURE CITED

- Adams, J., Rothman, E.D., Kerr, W.E. and Paulino, Z.L. 1977. Estimation of the number of sex alleles and queen matings from diploid male frequencies in a population of Apis mellifera. *Genetics* 86:583-596.
- Alber, M., Jordan, R., Ruttner, F. and Ruttner, H. 1955. The mating of the honey bee. *Z. Bienenforsch* 3:1-28.
- Alford, D.V. 1970. The production of adults in incipient colonies of Bombus agrorum. *Proc. R. Entomol. Soc. Lond. Ser. A Gen. Entomol.* 45: 6-13.
- Allen, M., 1965. The effect of a plentiful supply of drone comb on colonies of honey bees. *J. Apic. Res.* 4:109-119.
- Archer, M.E. 1972. The significance of worker size in the seasonal development of the wasps Vespula vulgaris (L.) and Vespula germanica (F.). *J. Entomol. Ser. A Gen. Entomol.* 46: 175-183.
- Avitabile, A., Stafstrom, D.P. and Donovan, K.J. 1978. Natural nest sites of honey bee colonies in trees in Connecticut, U.S.A. *J. Apic. Res.* 17:222-226.
- Baird, D.H. and Seeley, T.D. 1983. An equilibrium theory of queen production in honey bee colonies preparing to swarm. *Behav. Ecol. Sociobiol.* 13:221-228.
- Boch, R. and Lensky, Y. 1976. Pheromonal control of queen rearing in honey bee colonies. *J. Apic. Res.* 15:59-62.
- Butler, C.G. 1940. The ages of bees in a swarm. *Bee World* 21:9-10.
- 1954. The method and importance of the recognition by a colony of honey bees (A. mellifera) of the presence of its queen. *Trans. R. Entomol. Soc. Lond.* 105:11-29.
- 1957. The process of queen supercedure in colonies of honey bees (Apis mellifera L.). *Insectes Soc.* 4:211-223.
- 1975. The honey bee colony-life history. In: *The Hive and the Honeybee*. 39-74p. Dadant and sons (eds). Dadant and Sons publ. Hamilton, Ill.
- Crane, E. 1975. History of honey. In: *Honey: A Comprehensive Survey*. 439-438p. E. Crane (ed). W. Heinemann Ltd. publ.

London, England.

- Cumber, R.A. 1949. The biology of humble-bees with special reference to the production of the worker caste. Trans. R. Entomol. Soc. Lond. 100: 1-45.
- Dunbar, R.I.M. 1982. Adaptation, fitness and the evolutionary tautology. In: Current Problems in Sociobiology. 9-28p. King's College Sociobiology Group (eds). Cambridge University Press publ. Cambridge, England.
- Farrar, C.L. 1932. The influence of the colony's strength on brood rearing. Ont. Dep. Agric. Rep. Prov. Apiarist and Ont. Beekprs. Ass. 1930-1931. 126-130p.
- Fischer, A.G. 1960. Latitudinal variations in organic diversity. Evolution 14:64-81.
- Fletcher, D.J.C. 1978a. Vibration of queen cells by worker honey bees and its relation to the issue of swarms with virgin queens. J. Apic. Res. 17:14-26.
- 1978b. The african bee, Apis mellifera adansonii, in Africa. Annu. Rev. Entomol. 23:151-171.
- Free, J.B., 1967. The production of comb by honey bee colonies. J. Apic. Res. 6:29-36.
- Free, J.B. and Racey, P.A. 1968. The effect of the size of honeybee colonies on food consumption, brood rearing and the longevity of the bees during the winter. Entomol. Exp. Appl. 11:241-299.
- Free, J.B. and Williams, I.H. 1975. Factors determining the rearing and rejection of drones by the honey bee colony. Anim. Behav. 23:650-675.
- Frisch, K. von, . 1967. The Dance Language and Orientation of Bees. Harvard University Press, Cambridge, Mass. 566p.
- Fukuda, H. and Ohtani, T. 1977. Survival and lifespan of drone honey bees. Res. Popul. Ecol. 19:51-68.
- Fukuda, H. and Sakagami, S. 1968. Worker brood survival in honey bees. Res. Popul. Ecol. 10:31-39.
- Garofalo, C.A. 1978. Bionomics of Bombus fervidobombus (Mario) 2. Body size and length of life of workers. J. Apic. Res. 17:130-136.
- Gary, N.E. 1963. Observations of mating behaviour in the honey bee. J. Apic. Res. 2:3-13.

- 1975. Activities and behavior of honey bees. In: The Hive and the Honeybee. 185-264p. Dadant & Sons (eds). Dadant and Sons publ. Hamilton, Ill.
- Gary, N.E. and Morse, R.A. 1962. The events following queen cell construction in honey bee colonies. J. Apic. Res. 1:3-5.
- Goncalves, S. and Stort, A.C. 1978. Honeybee improvement through behavioral genetics. Annu. Rev. Entomol. 1:97-214.
- Hamilton, W.D. 1964. The genetical evolution of social behaviour I and II. J. Theor. Biol. 7:1-52
- Haydak, M.H. 1963. Age of nurse bees and brood rearing. J. Apic. Res. 2:101-103.
- Haydak, M.H. 1970. Honey bee nutrition. Annu. Rev. Entomol. 15:143-156.
- Iwasa, Y., Odendaal, F.J., Murphy, D., Ehrlich, P.R. and Launer, A.E. 1983. Emergence patterns in male butterflies: a hypothesis and test. Theor. Popul. Biol. 23:363-379.
- Jay, S.C. 1963. The development of honeybees in their cells. J. Apic. Res. 2:117-134.
- Jaycox, E.R. and Parise, S.G. 1980. Homesite selection by Italian honey bee swarms, Apis mellifera ligustica L. J. Kans. Entomol. Soc. 53:171-178.
- Kerr, W.E. and Hebling, N.J. 1964. Influence of the weight of worker bees on division of labour. Evolution 18:267-270.
- Laidlaw, H. 1979. Contemporary Queen Rearing. Dadant and Sons., Hamilton, Illinois. 199p.
- Lensky, Y. and Y. Slabezki 1981. The inhibiting effect of the queen bee (Apis mellifera L.) footprint pheromone on the construction of swarming queen cups. J. Insect Physiol. 27:313-323.
- Levin, M.D. and Haydak, M.H. 1951. Seasonal variations in weight and ovarian development in worker honeybees. J. Econ. Entomol. 44:54-57.
- Meyer, W. 1956. Arbeitsteilung im bienenschwarm. Insectes Soc. 3:303-324.
- Michener, C.D. 1964. Reproductive efficiency in relation to colony size in hymenopterous societies. Insectes Soc. 11:317-341.
- Michener, C.D. 1974. The Social Behavior of the Bees: A

Comparative Study. Harvard University Press, Cambridge.
352p.

- Moeller, F.E. 1961. The relationship between colony populations and honey production as affected by honeybee stock lines. Prod. Res. Rep. U.S. Dep. Agric. No. 55. 20p.
- Nelson, D.L. and Jay, S.C. 1972. Population growth and honey yield studies of package bee colonies in Manitoba. II. Colonies initiated with four package sizes on one date. Manit. Entomol. 6:17-22.
- Oster, G.F. and Wilson, E.O. 1978. Caste and Ecology in the Social Insects. Princeton University Press, Princeton, New Jersey, 352p.
- Otis, G.W. 1980. The Swarming Biology and Population Dynamics of the Africanized Honey Bee. Ph.D thesis, University of Kansas, Lawrence, Kansas. 197p.
- Owens, C.D., and Taber, S. 1973. Size and shape of comb constructed by honey bees in a 1.2 m box during one season. J. Econ. Entomol. 66:1234-1236.
- Page, R.E. 1981. Protandrous reproduction in honey bees. Environ. Entomol. 10:359-362.
- Page, R.E. and Metcalf, R.A. 1984. A population investment sex ratio for the honey bee (Apis mellifera L.) Am. Nat. 124:680-702.
- Pomeroy N. 1979. Brood bionomics of Bombus ruderatus in New Zealand. Can. Entomol. 111:865-874.
- Richards, O.W. 1946. Observations on Bombus agrorum (F.) (Hymen. Bombidae). Proc. R. Entomol. Soc. Lond. Ser. A. Gen. Entomol. 21:66-71.
- Rinderer, T.E., Collins, A.M., Bolten, A.B. and Harbo, J.R. 1981. Size of nest cavities selected by swarms of africanized honey bees in Venezuela. J. Apic. Res. 20:160-164.
- Rinderer, T.E., Tucker, K.W. and Collins, A.M. 1982. Nest cavity selection by swarms of european and africanized honey bees. J. Apic. Res. 21:98-103.
- Ruttner, F. 1956. The mating of the honey bee. Bee World 37:3-15, 23-24.
- 1966. The life and flight acitvity of drones. Bee World 47:93-100.

- Seeley, T.D. 1977. Measurement of nest cavity volume by the honey bee (Apis mellifera). Behav. Ecol. Sociobiol. 2:201-227.
- 1978. Life history strategy of the honey bee, Apis mellifera. Oecologia (Berl.). 32:109-118.
- Seeley, T.D. and Morse, R.A. 1976. The nest of the honey bee, Apis mellifera. Insectes Soc. 23:495-512.
- 1978. Nest site selection by the honey bee (Apis mellifera L.). Insectes Soc. 25:323-337.
- Seeley, T.D. and Visscher, P.K. 1985. Survival of honey bees in cold climates: the critical timing of colony growth and reproduction. Ecol. Entomol 10:81-88.
- Seeley, T.D., Morse, R.A. and Visscher, P.K. 1979. The natural history of the flight of honey bee swarms. Psyche (Camb. Mass.) 86:103-113.
- Seeley, T.D., Seeley, R.H. and Akwatanakul, P. 1982. Colony defense strategies of the honey bees in Thailand. Ecol. Monogr. 52:43-63.
- Simpson, J. 1969. The amounts of hive-space needed by colonies of european Apis mellifera. J. Apic. Res. 8:3-8.
- Smirl, C.B. and Jay, S.C. 1972. Population growth and honey yield studies of package bee colonies in Manitoba. I. Colonies initiated with two package sizes on three dates. Manit. Entomol. 6:9-16.
- Sokal, R.R. and Rohlf, F.J. 1969. Biometry, 2nd ed. W.H. Freeman and Company, San Fransisco. 860p.
- Taber, S. 1954. The frequency of multiple mating of queen honey bees. J. Econ. Entomol. 47:995-998.
- 1979. A population of feral honey bee colonies. Am. Bee J. 119:842-847.
- 1985. Government plans to deal with the africanized bees. Am. Bee J. 125:181-182.
- Taber, S. and Wendell, J. 1958. Concerning the number of times queen bees mate. J. Econ. Entomol. 51:786-789.
- Taber, S. and Owens, C.D. 1970. Colony founding and initial nest design of honey bees (Apis mellifera L.) Anim. Behav. 18:625-632.
- Triasko, V.V. 1956. The mating sign of the queen and its

characteristics. Pchelovodstvo 33:43-50.

Turnbull, W.H. undated. One Hundred Years of Beekeeping in British Columbia 1858-1958. B.C. Honey Producers Association, Vernon, British Columbia.

Wiklund, C. and Fagerstrom, T. 1977. Why do males emerge before females? Oecologia (Berl.) 31:153-158.

Winston, M.L. 1980. Swarming, afterswarming, and reproductive rate of unmanaged honey bee colonies (Apis mellifera). Insectes Soc. 27:391-398.

Winston, M.L. and Otis, G.W. 1978. Ages of bees in swarms and afterswarms of the africanized honeybee. J. Apic. Res. 17:123-129.

Winston, M.L. and Taylor, O.R. 1980. Factors preceding queen rearing in the africanized honeybee (Apis mellifera) in South America. Insectes Soc. 27:289-304.

Winston, M.L., Taylor, O.R. and Otis, G.W. 1980. Swarming, colony growth patterns, and bee management. Am. Bee J. 120:826-830.

----1983. Some differences between temperate european and tropical african and South American honey bees. Bee World 64:12-21.

Winston, M.L., Dropkin, J.A. and Taylor, O.R. 1981. Demography and life history characteristics of two honey bee races (Apis mellifera). Oecologia (Berl.) 48:407-413.

Withrell, P.C. 1972. Flight activity and natural mortality of normal and mutant drone honey bees. J. Apic. Res. 11:65-75.

Woyke, J. 1956. Mnogokratnoe Sparivanie Pchelinoimatki vo vremie odnogo brachnogo vyleta. Pchelovodstvo 33:32-39.