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Original article

The effect of the age of the honey bee (*Apis mellifera* L) queen on worker population, swarming and honey yields in a subtropical climate

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Summary — In a study carried out in the subtropics, we found that brood areas, worker populations and honey yields were higher, and less swarm queen cells were constructed, in colonies headed by 7- to 10-month-old queens than in those headed by up to 20-month-old queens during the nectar flow season. There was a significant effect of seasonal conditions on the number of queen cups constructed but not on that of swarm queen cells. Neither brood area nor worker population affected construction of the 2 kinds of cells in uncongested colonies. The queen's age and the season affect honey yields through the population level of workers.

queen bee / ageing / swarming / population / population dynamics / Israel

INTRODUCTION

It is generally accepted that the longevity of a queen bee in a temperate climate varies between 1 and 4 years (Bodenheimer, 1937b; Seeley, 1968; Butler, 1975), and exceptionally between 5 and 9 years (Bozina, 1961; Butler, 1975). One of the major causes for supersedure seems to be insufficient production of queen pheromones (Butler, 1957; Crane, 1990). The ageing of the queen bee affects her attractiveness to workers (De Hazan *et al*, 1989a) and her capacity to inhibit the construction of queen cups and swarm queen cells (Lensky and Slabezki, 1981; Hyams, 1988). The fine structure of queen mandibular glands (De Hazan *et al*, 1989b) and the chemical composition of mandibular (De Hazan, 1986) and tarsal (Hyams, 1988) gland secretions are also age-dependent (Cassier and Lensky, 1992; Lensky and Cassier, 1992).

In temperate climates of England (Simpson, 1959), New Zealand (Forster, 1969) and Poland (Woyke, 1981), colonies

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headed by 1-year-old queens performed better than those headed by 2-year-old queens . However, Szabo and Lefkovitz (1991) indicate that in Canada 2-year-old queens performed as well as 1-year-old queens. Except for a recommendation to annually requeen bee colonies in a hot climate (Weaver, 1978), there is no quantitative data about the effect of the queen's age on the performance of bee colonies in a subtropical climate.

Due to the mild winter in the subtropics, queen egg-laying activity continues all the year round, but is marked by a pronounced decline during the autumn and at the beginning of winter (Bodenheimer and Ben-Nerya, 1937). The subtropical climate of the coastal plain of Israel is of the Mediterranean type, characterized by a mild rainy winter and a prolonged dry and hot summer. A periodicity of drought years is typical of the whole region, and thus, the annual precipitation may vary greatly from 1 year to the next (Lensky and Golan, 1966). Most of the plants flower between March and May and peak in April.

The irrigated citrus plantations provide bee colonies with the most important and stable source of nectar secretion, which is less affected by drought than other nectariferous plants. Bee colonies are thus managed for a rapid expansion of brood rearing during winter so that the peak of foragers' population will coincide with that of citrus nectar flow (Lensky and Golan, 1966). In these conditions, the population of workers peaks in April and coincides with swarming (Lensky and Slabezki, 1981). The losses of honey due to swarming are about 15 kg/colony (Lensky and Hochberg, 1973; Lensky and Cassier, 1992).

This report examines the effect of the queen's age during 2 successive years on: (i) the population of developing and adult workers; (ii) the construction of queen cups and swarm queen cells; and (iii) the honey yields of bee colonies.

METHODS AND MATERIALS

Bee colonies

We used Italian honey-bee (*Apis mellifera* L var *ligustica* Spin) colonies at the Apiary of the Triwaks Bee Research Center, Rehovot, in field trials, from December to March, 1982–1984. The colonies were housed in Langstroth, 10-frame full-depth (24.6 cm) boxes that were used as brood-chambers and supers.

Queen rearing

We reared all queens in April, June and September–October, from a stock obtained from Park Apiaries, Palo Cedro, CA, USA. The queens were open mated with local drones. At the onset of egg-laying, each queen was marked on her thorax with a non-toxic enamel paint (Humbrol, Hull, UK), using specific colours for each season.

Colony management

Feeding

During the fall and winter all colonies were fed with 60% (w/v) sugar syrup (10 l per season per colony).

Swarming prevention and control

At the beginning of March, and prior to citrus main nectar flow, we placed full-depth (24.6 cm) Langstroth supers containing 9 drawn combs each on the top of a queen excluder above single brood-chambers. Whenever adult workers occupied 6 combs in the first super, a second or a third super was added.

About 1 week after adding the first super and every 2 weeks during the nectar flow season, brood combs were removed from the brood chamber into the supers and were replaced with 6 and 4 wax foundations during the first and the second years, respectively.

Once a week during the spring season queen cups and swarm queen cells were counted and cut.

Brood area

Once a month, from December till the end of April, we measured all surfaces upon a comb containing open and sealed brood. In most cases the brood pattern resembled that of an ellipse and was calculated according to the formula of an ellipse; when the surface was rectangular it was calculated accordingly. In 1982–1983 the measurements were carried out during the third week of each month, and in 1983–1984, during the first week of each month.

Worker population

The evaluation of the number of adult workers during the spring season was made on the basis of brood-area measurements. Since worker lifespans have been studied in temperate and tropical climates, but not in the subtropics, and in order to compare our results with previous research carried out in Israel (Bodenheimer, 1937b; Bodenheimer and Ben-Nerya, 1937), we used the same criteria for evaluation of worker populations. The evaluation was based on the following assumptions made by Bodenheimer (1937a,b): (i) the average life span of a worker is 7 weeks during the spring; (ii) there is no brood mortality; (iii) the duration of development of a worker is 21 d; and (iv) the egg-laying rate of a queen bee changes gradually and is almost linear between 2 consecutive measurements.

The following is an example of an evaluation of the growth of worker population during the season till the beginning of citrus main nectar flow. Workers that were present in colonies at the beginning of citrus nectar flow emerged between February 12 and April 4 in 1983, and between February 4 and March 25 (49 d) in 1984. Since the duration of development of 1 generation of workers is 21 d, there are 2.33 generations in 49 d. The total brood surface from which the workers emerged, till the beginning of main citrus nectar flow, was calculated as the surface that corresponded to this period. The surface was subdivided into several trapezoids (3 for 1983 and 2 for 1984) and the surface of each was calculated according to the trapezoid formula. To calculate the number of workers in a colony at the onset of nectar secretion, the general brood surface was divided by 0.25 (the surface of a single worker cell is 0.25 cm^2). The above method was also used to calculate the populations of workers/colony, 3 and 6 weeks before the onset of the main nectar flow.

Construction of queen cups and swarm queen cells

Queen cups and swarm queen cells in brood chambers of each colony were counted and destroyed once a week, from March 15 in 1983, and from March 5 in 1984. The total number of queen cups and swarm queens cells per colony per season were determined. Of the total number of colonies, we calculated the percentage of those that constructed queen cups and swarm queen cells. We also established the duration of the construction of the 2 types of cells.

Honey yields

Honey was extracted only from supers above queen excluders at the end of the citrus nectar flow (May 5, 1983 and April 18, 1984). Each super was marked and weighed separately. The tare was subtracted and net honey yield (kg/colony) calculated.

Survival of queens

The presence of marked queens in colonies was recorded during each monthly visit and at the end of each season.

Meteorological data

Data for the periods of December–May, 1982–1984 were obtained from the Meteorological Institute at Beit Dagan.

Statistical analyses

Data were analysed by SAS GLM, regression and correlation programs.

RESULTS

Weather conditions and citrus flowering in 1983–1984

December 1982–April 1983

The winter was cool and rainy; the temperature was 1.5–2.5°C lower, precipitation was 276 mm higher, and relative humidity was 2–7% higher, than the annual averages. During the citrus nectar flow, which began on April 5 1983 and lasted 4 weeks, maximum and minimum temperatures ranged between 17–24°C and 6–12°C, respectively (fig 1).

December 1983–April 1984

The winter was relatively warm and dry. Monthly temperatures were close to annual averages, but precipitation was 30% below the annual average and 50% lower than that recorded in 1983. Citrus flowering began on March 25 and lasted 3 weeks, maximum and minimum temperatures were 19–24°C and 8–12°C, respectively (fig 1).

The effect of the age of the queen on colony population

Brood area

The results in figure 2A show that in 1982–1983 the brood area of young queens was 23% higher than that of old queens (significant at $p < 0.01$). However, in 1983–1984 until February (fig 2B) there was no difference between the average brood area of old and young queens, but it was 20% higher in young queens in March and April (significant at $p < 0.05$) (table I).

Population of workers

In February, March and April 1983 the populations of workers in colonies headed by young queens were significantly ($p < 0.05$) higher (20, 31, 47%, respectively) than those headed by old queens. In 1984 until March there was no significant difference between the 2 age-groups. At the end of March, however, colonies headed by young queens had stronger (11%) worker populations than those with old queens ($p < 0.05$). The population of work-

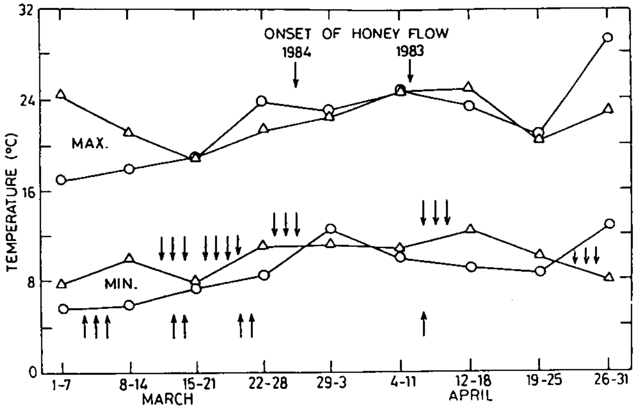

Fig 1. Temperature fluctuations and precipitation before and during the citrus nectar flow in Rehovot: o – 1983; Δ - 1984. Arrows indicate rain: (↓ – 1983) and (↑ – 1984).

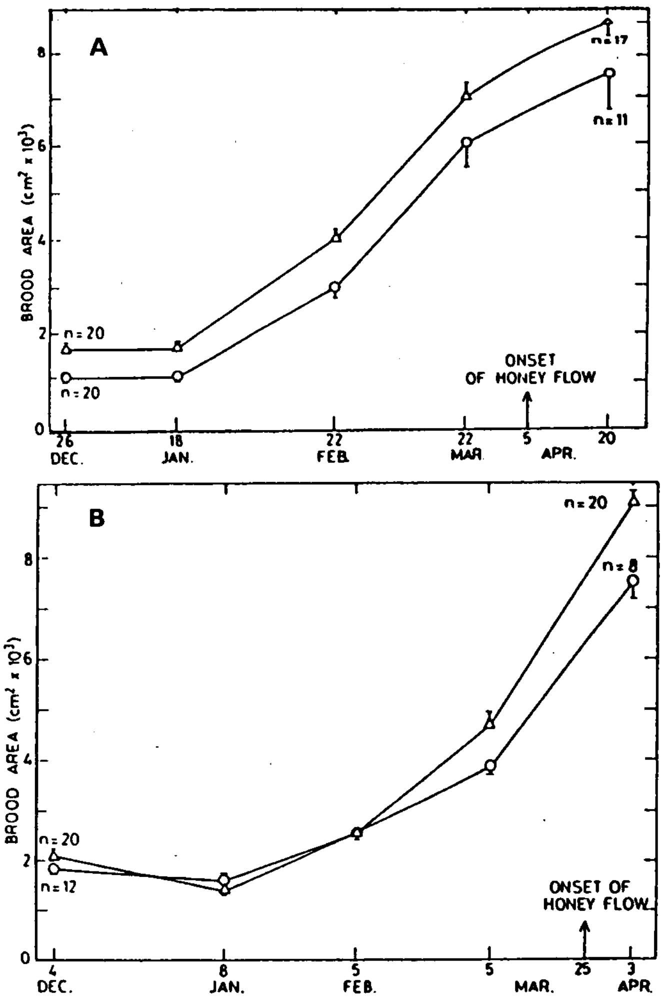

Fig 2. The effect of queen's age on brood area during 1982–1983 **(A)** and 1983–1984 **(B)**. Δ – Young queens; O – old queens.

ers in colonies headed by young and old queens was 26 and 17% higher, respectively, in 1983 than in 1984 (significant at $p < 0.01$) (table I).

In 1983, colonies headed by young queens had about 20 000 workers on February 21 and 65 000 workers on April 5.

The effects of the age of the queen on swarming

Queen cups

The number of queen cups constructed between March 15 and April 15 in colonies

Table I. The effect of queen's age on brood surface, construction of queen cups and cells, and honey yields.

Year	*Queen's age*	*Brood area in April (cm^2/colony)*	*No workers/colony at the nectar flow onset**	*No queen cups/ colony/season*	*No queen cells/ colony/season*	*Honey yields (kg/colony)*
1983	Young queens, $n = 15$	$8\,944 \pm 430^{A}$	$66\,954 \pm 9\,370^{A}$	14.3 ± 2.1^{A}	0.2 ± 0.1^{A}	50.1 ± 3.4^{A}
	Old queens, $n = 11$	$7\,576 \pm 175^{B}$	$55\,767 \pm 14\,607^{B}$	14.9 ± 1.5^{A}	4.7 ± 2.1^{DC}	37.5 ± 5.1^{B}
1984	Young queens, $n = 20$	$9\,071 \pm 246^{A}$	$53\,280 \pm 1\,768^{B}$	34 ± 7.0^{B}	2.3 ± 1.0^{AB}	38.6 ± 2.9^{B}
	Old queens, $n = 8$	$7\,574 \pm 403^{B}$	$4\,782 \pm 2\,272^{C}$	36 ± 5.5^{B}	9.8 ± 7.3^{C}	27.7 ± 3.6^{C}

* The beginning of nectar flow in 1983 was on April 5 and in 1984 on March 25. Averages assigned the same letters do not significantly differ at $p < 0.05$.

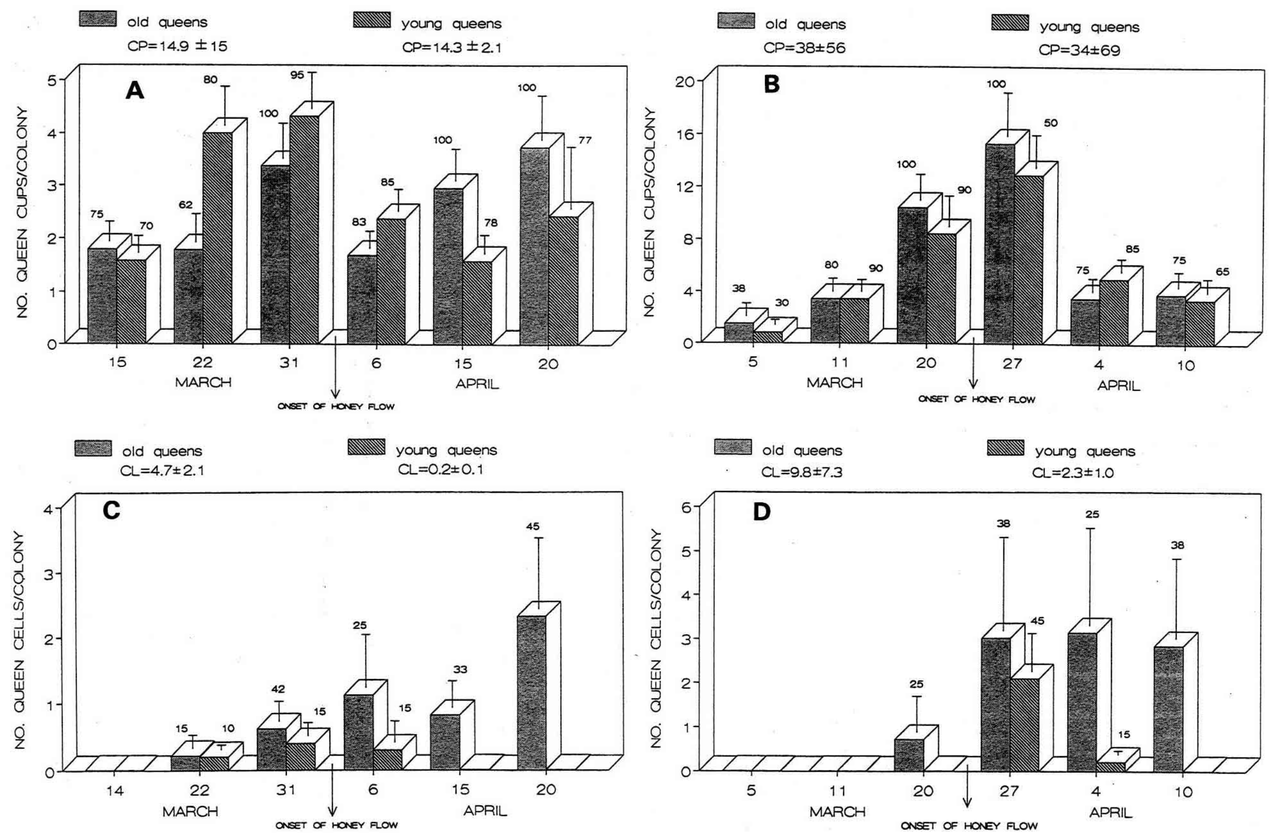

Fig 3. The effect of queen's age on the construction of queen cups (**A** – 1983; **B** – 1984) and swarm queen cells (**C** – 1983; **D** – 1984). Mean number (+ 0.5 sd) of queen cups (CP) and swarm queen cells (CL) per colony per season. The numbers above the bars indicate percentage of colonies that constructed queen cups and swarm queen cells. In 1983, the observations were based on 17 and 11 colonies with young and old queens, respectively. In 1984, they were based on 20 and 8 colonies with young and old queens, respectively.

headed by young and old queens was 3.4 and 2.8 times higher in 1984 than in 1983 (figs 3A and 3B), respectively. The differences between the 2 seasons are significant at $p < 0.01$ (table I).

Swarm queen cells

In 1983 colonies headed by old queens constructed 2.5 times more swarm queen cells than those headed by young queens (significant at $p < 0.01$), and the construction period lasted 5 and 3 weeks, respectively (fig 3C). In 1984, colonies headed by old queens constructed 3.9 more swarm queen cells than those with young queens (significant at $p < 0.05$) and the construction period was longer: 4 and 2 weeks, respectively (fig 3D, table I).

The effect of brood area and worker population on swarming

A relationship between brood area, and construction of queen cups, and swarm queen cells has been reported in temperate climates (Simpson, 1960; Allen, 1965; Caron, 1970), but we have no information whether this relationship exists in subtropical climates. We analyzed the correlation between the construction of queen cups and swarm queen cells and that of brood areas before and during the construction period. However, no significant effects of brood surface on the construction of queen cups and swarm queen cells were found in uncongested colonies. It is generally accepted that the density of worker population in a bee colony affects the construction of queen cups and swarm queen cells (Demuth, 1921; Simpson, 1973; Lensky and Slabezki, 1981). Our bee colonies were provided with extra hive volume during the entire swarming period. This was achieved by placing additional supers that were only partially occupied by workers. We thereby prevented congestion and high worker density. We studied the effect of population strength on the construction of queen cups and swarm queen cells in colonies with ample hive volume. No significant effect of worker population on the construction of queen cups and swarm queen cells was found.

Concluding remarks

Queen cups are constructed earlier and are more numerous than swarm queen cells. The cups are constructed by all colonies, but swarm queen cells only be some of them. The queen's age had a highly significant effect on the construction of swarm queen cells, but not on that of queen cups. There was a significant effect of the seasonal conditions on the number of queen cups, but not of queen cells. Neither brood area nor worker population affected construction of the 2 kinds of cells in uncongested colonies. There was only a marginally significant correlation ($r = 0.2$; $F = 0.10$) between the number of queen cups and swarm queen cells constructed by a colony during 1983 and 1984.

The effect of queen's age on honey yields

Significant differences in honey yields were found between colonies headed by old and young queens. The results in table I show that colonies headed by young queens yielded more honey (12.8 kg/colony, + 34% in 1983 and 10.9 kg/colony, + 39% in 1984; $p < 0.01$) than those with old queens. In 1983 honey yields of colonies with young and old queens were 30 and 35% higher, respectively, than in 1984 (significant at $p < 0.01$). The following is an analysis of several factors which may affect honey yields.

Two-way analysis of variance shows that the queen's age affected honey yields/colony during 2 consecutive years.

The effects of both queen's age and season are significant [*P(F)* = 0.81]. The queen's age had an impact on worker population during the 2 seasons. Analysis of variance shows that the effects of queen's age and season are significant [*P(F)* = 0.3].

Analysis of variance and covariance shows that queen's age and season affect honey yields through the population level of workers [*P(F)* = 0.97]. If worker population levels of both groups of colonies were equal during the 2 seasons then the difference in honey yields between the groups would be insignificant. The observed values of honey yields were corrected for a constant size of colony population of the 2 age groups for the 2 years. Thus the diferences were reduced from 34 to 5% for 1983 and from 39 to 18% in 1984, which are not significant at $p < 0.05$.

The effect of brood areas during nectar flow on honey yields

The size of brood area per colony may affect the quantity of collected honey either through the workers, which will emerge and become nectar foragers, or as larvae, which are consumers of nectar and are nursed by hive bees. In general, there was a positive correlation between brood areas in March and the quantity of honey collected by colonies [$r = 0.65$, *P(F)* = 0.000 1]. It seems that the negative effect, which might have existed due to the consumption of honey by larvae, was rather negligible, as compared with the positive effect of an increased number of foragers that collected nectar.

The effect of queen's age on survival

The survival of young queens was significantly higher than that of old queens: for 1983 it was 85 and 55% and for 1984 it was 90 and 47%, respectively. Our observations indicate that the colonies that superseded their queens had small brood areas, a high population of drones, a low population of workers, or a disease.

The effect on bee colonies of queens reared in June and in September–October

The following effects were observed during 1984 in colonies headed by queens that were reared in June and September–October, 1983 (fig 4). (i) Worker populations were slightly higher during the winter and early spring in colonies headed by September–October queens than in those headed by June queens. The difference between the 2 groups of colonies was significant only in December (37%, $p < 0.05$). (ii) In February worker populations were higher (14%, $p = 0.05$) in colonies headed by September–October queens than in those with June queens. (iii) Colonies headed by September–October queens collected 20% more honey (7.2 kg/colony) than those with June queens, but the difference is not significant at $p = 0.05$.

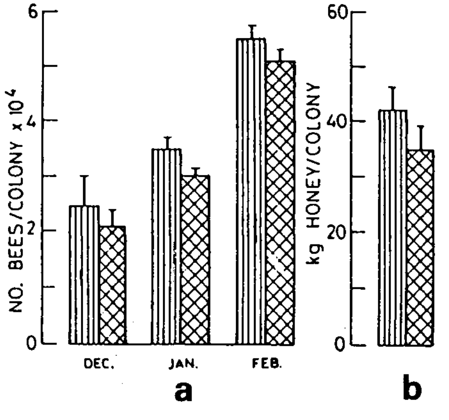

Fig 4. The effect of June (▩) or September–October (▥) queens on **(a)** worker populations (1983–1984) and **(b)** honey yields, kg (mean + 0.5 sd) per colony per group (April, 1984).

The general effect of the age of the queen on a bee colony

Table I summarizes the results of our observations carried out during the years 1983–1984. It indicates that colonies headed by young queens had more brood, worker population and honey, and less swarm queen cells than those headed by old queens.

DISCUSSION

In a subtropical climate, the growth of worker population in bee colonies during the expansion period from December through April, depends primarily on the increased egg-laying rate of the queen bee during this season, even though the longevity of workers may differ from one period to the next (Bodenheimer and Ben-Nerya, 1937). It is generally believed that photoperiod, ambient temperatures and food availability affect the egg-laying rate of female insects (Engelmann, 1970) and queen bees (Avitable, 1978; Kefuss, 1978; Shehata *et al,* 1981). The enhancement of the queen egg-laying rate, as expressed by brood area, between January and April in Rehovot, can be correlated with increasing day-length and temperature. The dimensions of brood areas of young and old queens were affected by ambient temperatures during 2 consecutive years. They were small in December–January and then gradually increased till the end of April. The decline of the surface of brood areas at the end of April/beginning of May is associated with the end of main nectar flow from citrus and wild flowers.

Using the same evaluation as Bodenheimer (1937b), our results show that Italian bee colonies in Israel reach a population peak of about 66 000 workers in April *versus* 46 000 workers in local *(A m syriaca)* colonies for the same period, as reported by Bodenheimer (1937b) and Bodenheimer and Ben-Nerya (1937). This discrepancy of about 30% between the peaks of worker populations belonging to 2 Mediterranean bee races may be explained by the fact that the local colonies were headed by queens of an unknown age, and that they might have issued swarms. It may also be due to the dearth of honey and pollen during certain periods. Our estimates of 66 000 workers, as the peak of colony population headed by a young queen, are similar (60 000) to those reported by Farrar (1937) and Matheson (1984), but higher than those recorded by McLeallan (1978), Moeller (1958), Nolan (1925) and Woyke (1984), 38 000, 54 519, 54 000 and 30 200, respectively.

The construction of queen cups and swarm queen cells by young and old queens was higher in 1983 when rain was more abundant, the flowering period longer and the ambient temperatures were lower than in 1984. Our results show that the intensity of the construction of queen cups and swarm queen cells drastically declined after the beginning of the main citrus nectar flow and do not support the view that the intensity of swarming is reduced during periods of low nectar flow (Winston *et al,* 1980). A high level of queen cup and swarm queen cell construction was observed during 1984 when ambient temperatures were higher than in 1983. Similar results have been reported from temperate zones (Allen, 1965). Moreover, enhancement of queen cup and swarm queen cell construction has been observed in Israel in experimentally overheated colonies that were housed inside black painted hives (Lensky and Seifert, 1980; Hyams, 1988).

The fact that there was no correlation between the brood area or adult worker population and the construction of queen cups, deserves a comment. By constantly increasing the volume of the experimental hives, we have prevented conditions of congestion and high density of workers in the brood-nest which induce swarming (Lensky and Slabezki, 1981). Even in these conditions, old queens less efficiently inhibited the construction of swarm queen cells than young queens. A similar trend has been observed in temperate zones where the performance of 1- and 2-year-old queens was compared (Simpson, 1960; Allen, 1965; Forster, 1969). Apparently, the reduced inhibition of the construction of swarm queen cells is due to the changes occurring in the rate of secretion and in the chemical composition of the mandibular and tarsal gland secretion (Hyams, 1988; De Hazan *et al*, 1989a; Lensky and Cassier, 1992), and to the ability of a queen bee to evenly distribute tarsal secretions along comb edges (Lensky and Slabezki, 1981; Cassier and Lensky, 1992). There was no effect of the queen's age on the construction of queen cups in uncongested bee colonies. However, an effect of congestion on the construction of queen cups has been reported (Lensky and Slabezki, 1981).

Regardless of the length of the citrus nectar flow, higher honey yields were obtained during 2 successive years from colonies headed by young queens than from those headed by old queens. The correlation between honey yields and population strength of the 2 groups of colonies did not reveal any differences in the efficacy of workers belonging to the 2 groups. It seems that the higher fecundity of young queens accounts for higher honey yields. In temperate zones like Poland (Woyke, 1981) and New Zealand (Forster, 1969) honey production by colonies headed by 1-year-old queens was 20 and 30% higher, respectively, than by colonies headed by 2-year-old queens. However, our results show that colonies headed by 6- to 7-month-old queens had stronger worker populations and collected more honey than those headed by 10- to 12-month-old queens. Interestingly, in the Far East tropics (Thailand, Taiwan) many commercial beekeepers who use *A mellifera* bees for the production of honey or royal jelly, requeen the colonies every 6 months.

The survival of young queens was 4 to 5 times higher than that of old queens. In all cases but one, we observed that adult queens were eliminated before the emergence of new queens from supersedure queen cells. Similar results of the survival of 1- and 2-year-old queens have been reported from temperate zones (Noland, 1925; Allen, 1965). The results of this study have been implemented in Israel as a routine practice of annual requeening of bee colonies in commercial beeyards.

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Résumé — Influence de l'âge de la reine (*Apis mellifera* L) sur la population, l'essaimage et le rendement en miel en climat subtropical. Nous avons comparé la performance de jeunes reines et de vieilles reines dans des colonies d'abeilles italiennes (*Apis mellifera ligustica* Spin) pendant 2 années consécutives au cours de la période d'expansion de la colonie, de décembre à avril, dans la plaine côtière d'Israël. En décembre, au début des observations, les jeunes reines étaient âgées de 3 et 6 mois et les vieilles de 15 mois. Dans les colonies comportant une jeune reine (CJR) la surface de couvain et la population d'ouvrières ont été supérieures d'environ 20% à celles des colonies comportant une vieille reine

(CVR) (fig 2). En 1983 et 1984 les colonies CVR ont respectivement construit 2,5 et 3,9 fois plus de cellules royales d'essaimage que les colonies CJR (fig 3). Ni la surface de couvain ni la taille de la population d'ouvrières n'ont affecté la construction des 2 types de cellules (cellules royales de supersédure / cellules royales d'essaimage) dans des colonies non surpeuplées. Les colonies CJR ont produit 34 à 39% de plus de miel d'agrumes que les CVR (tableau I). L'âge de la reine et la saison influence le rendement de miel par le biais du niveau de la population d'ouvrières. La survie des jeunes reines a été significativement plus élevée que celles des vieilles reines (respectivement 85% et 55% en 1983, 90% et 47% en 1984). Les résultats de cette étude sont appliqués en Israël par la pratique de routine qui consiste à renouveler chaque année les reines des colonies dans les ruchers de professionnels.

reine / effet âge / essaimage / rendement miel / dynamique population / Israël

Zusammenfassung — Auswirkung des Alters der Königin auf die Population der Arbeiterinnen, auf das Schwärmen und auf die Honigernte bei der Honigbiene (*Apis mellifera* L) in subtropischem Klima. Wir verglichen die Leistung von Bienenvölkern der Rasse *A m ligustica*, die entweder eine junge oder eine alte Königin hatten. Die Untersuchung wurde über 2 Jahre jeweils während des Volkswachstums von Dezember bis April in der Küstenebene in Israel durchgeführt. Zu Beginn der Beobachtungen im Dezember waren die jungen Königinnen 3 und 6 Monate alt, die alten 15 Monate. Brutflächen und Anzahl der Arbeiterinnen waren in den Völkern mit jungen Königinnen etwa um 20% größer als in den Völkern mit alten Königinnen (Abb 2). Die Völker mit alten Königinnen bauten 1983 und 1984 2,5 bzw 3,9 mal mehr Schwarmzellen als solche mit jungen (Abb 3). Weder die Größe der Brutflächen noch die der Population der Arbeiterinnen beeinflußte den Bau von 2 Zellarten (Nachschaffungs- bzw Schwarmzellen) bei den Völkern, solange diese genügend Raum hatten. Völker mit jungen Königinnen ernteten 34% bis 39% mehr Zitrushonig als die mit älteren (Tabelle I). Das Alter der Königin und die Saison haben einen Einfluß auf die Honigernte durch ihre Einwirkung auf die Populationsstärke der Arbeiterinnen. Die Überlebensrate der jungen Königinnen war signifikant höher als die der alten (85% und 55% im Jahr 1983; bzw 90% und 47% im Jahr 1984). Auf Grund der Ergebnisse dieses Versuchs werden in Israel die Bienenvölker in der Routinepraxis der kommerziellen Imkereien jährlich umgeweiselt.

Königin / Altern / Schwärmen / Honigernte / Populationsdynamik / Israel

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