

## FACTORS INDUCING WHOLE COLONY MOVEMENT AND REPRODUCTIVE SWARMING IN THE AFRICAN HONEYBEE

(Continued from *Apiacta* Nr. 3/1998)

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### *Migration*

In the plains and hills many colonies eventually emerged from their hives and flew away from the entire area irrespective of whether or not they had produced reproductive swarms. The peak of these migratory movements occurred when forage was dropping to a low level in September (Fig. 6).

Examination of the stores of vacated hives showed that the migrating colonies were on the brink of starvation and rarely had enough brood for self-maintenance. Their migratory movements were clearly caused by hunger. In circumstances where migration occurred but forage was still abundant it was concluded that the colony was probably 'absconding' but the cause was not identified.

Once a colony had vacated its hive it sometimes moved within the apiary, occupying empty hives or entering occupied hives and amalgamating with the colony within. Following this behaviour, a colony alone or in amalgamation might subsequently migrate a considerable distance.

In Athi plains the daily time of emergence and departure of whole colonies mostly occurred between 14.00 and 15.00 h whereas for all the other apiaries it was between 10.00 and 11.00 h.

A very few colonies that swarmed did not vacate their hives or exhibit migratory behaviour at all. They accumulated sufficient stores to see them through periods of dearth. They should make valuable breeding material.

### *Absconding*

The colony movement induced by disturbance is called 'absconding'. It is characterised by a colony abandoning extensive brood and stores. A major cause of absconding was nocturnal attack by the honey badger (*Mellivora capensis*) which ripped open hives exposing their contents (Fig. 7). Attacks reached their peak when forage was maximal. The survivors of the colony did not abscond at once after the attack, but only 10 minutes or so after the badger had left, when they clustered outside the hive or at a nearby site before moving right away from the area of the apiary. The other major enemy was the safari ant (*Anomia molestus*); attacks were continuous and severe and all colonies attacked were destroyed; because attacks were continuous, colonies were given no chance to organise themselves, to emerge and take off. But attacks were almost eliminated after hives had been placed on wires.

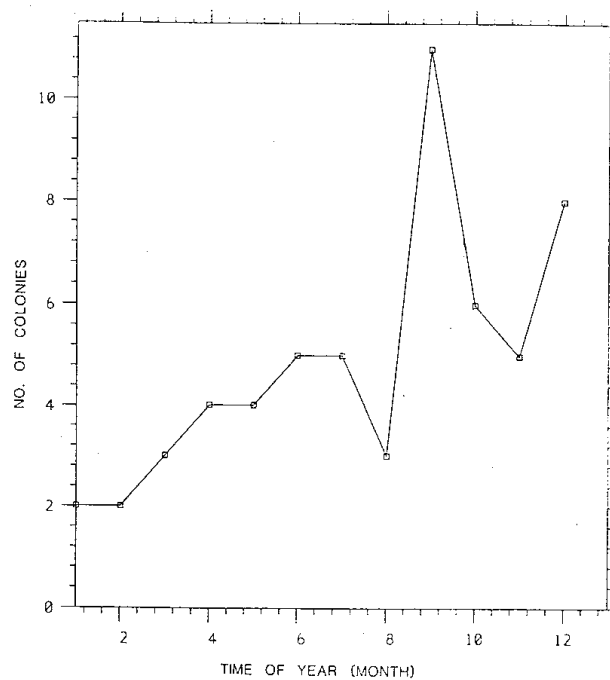


Fig. 6 – Distribution of colony movements induced by hunger throughout the year in all apiaries ( 1 = January)

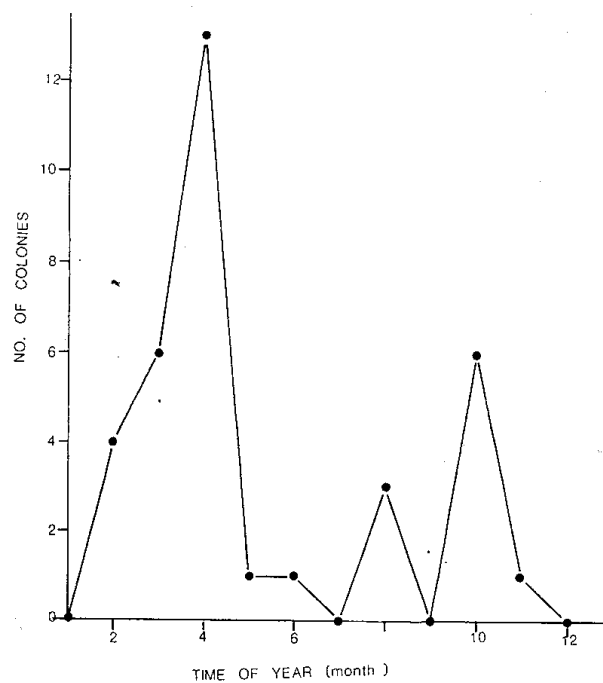


Fig. 7 – Distribution of absconding caused by honey badger or insect pests throughout the year in all apiaries ( 1 = January)

Hives were subjected to knocking, or shaking for various periods; and some bees were shaken from the hive, water was sprayed, and parafin oil vapour blown into the the hive. In no case did a colony emerge while a mechanical or chemical disturbance continued but did so about 10 minutes after the disturbance had ceased; apparently a colony requires a period to organise itself for departure, and is unable to do so while subjected to the disturbing influence.

Colonies were very sensitive to mechanical disturbance, and this was particularly evident when colonies were transported by truck over rough roads. They tried to abscond shortly after hives were off loaded or at a stop en route, and 82 colonies were lost in this way. If the mechanical disturbance stopped during daylight hours, the colony emerged and clustered prior to leaving. But usually they did not do this if the journey ended at dusk; however, in many of these colonies absconding behaviour appeared to have been determined by having experienced vibration, because the next day, they would emerge, cluster, and fly away. Some of these colonies even absconded after their entrances had been blocked with straw for two days.

Attempts were made to suppress absconding after the colony had clustered following artificial disturbance. These attempts included placing the cluster in a different hive, supplying brood and food and caging the queen but all without success. Such techniques are usually effective in inducing swarms of European bees to settle. In

one experiment when the queen was caged, the colony emerged, clustered a short distance away, and then returned six times in one day before it finally flew off and abandoned the queen.

### *Neighbour effect*

Neighbouring colonies sometimes exerted an influence on each other, when emerging from a hive or taking off from an interim cluster site. When one colony started to become airborne, other colonies were occasionally seen to start similar behaviour. The interaction between individual colonies seemed to vary greatly on different days, but any interaction was greatly reduced if they were more than 5 m apart (Table 3).

### *Settlement*

Whether colonies were captured in the wild, or brought from other apiaries, and introduced to empty hives, there appeared to be strong seasonal differences in the success rate of achieving settlement and establishment which has most important implications for beekeeping.

Many such colonies departed immediately or at any time during the following weeks; they were regarded as 'settled' if they remained for more than 50 days. Of colonies introduced to all apiaries in February, the start of the long dry period of flowering, 33% settled. In May and June pests were absent in the hills and 76% of colonies introduced to hill apiaries settled. In contrast, in the plains in May and June, when pests

were abundant and forage poor, little if any settlement was achieved and almost all of the colonies departed. The

time of year when successful introduction may be achieved in different locations is of great importance.

Table 3

The nearest neighbour effect at emergence or take-off from interim site

Time (min.)	The distance of the adjacent nest (hive) or cluster			
	Clusters less than 1 m from emerging colony	Colonies in hives 1 m from emerging colony	Colonies in hives 5 m from hive of emerging colony	From hives more than 5 m from hive of emerging colony
0	5	2		
1	1	2		
2		1		
3				
4		2	1	
5			1	
6				
7				
8				
9				
10				
11				
12				
13				
14				
15				
16				
Over 16		8	11	49

## Behaviour during movement

### *Flight direction*

The flight direction taken by a swarm or colony was not related to the type of movement or its cause, so that all departures (reproductive swarms, absconding and migrating colonies) are pooled for each apiary site (Fig. 8).

During the same time period, the direction of departure from an apiary of the majority of moving colonies fell within a sector of about 90 degrees or less. So it appears that there is a 'preferred' direction of movement, whether such a movement was by a swarm, absconding or migratory col-

ony. Whereas in Athi a majority of colonies tended to move south or south-east regardless of time of year, in Kimbo they moved north-east in April and May and south-west in July, August, September and October (Fig. 8). In Lewa and Ngong comparable but less pronounced changes, occurred at different times of the year. Colony departure records at different times of the year at different sites failed to establish whether there are regular back and forth movements between hillls and plains.

There was no evidence of any relationship between colony flight and wind direction. Sometimes they flew against the wind, across it, or with it.

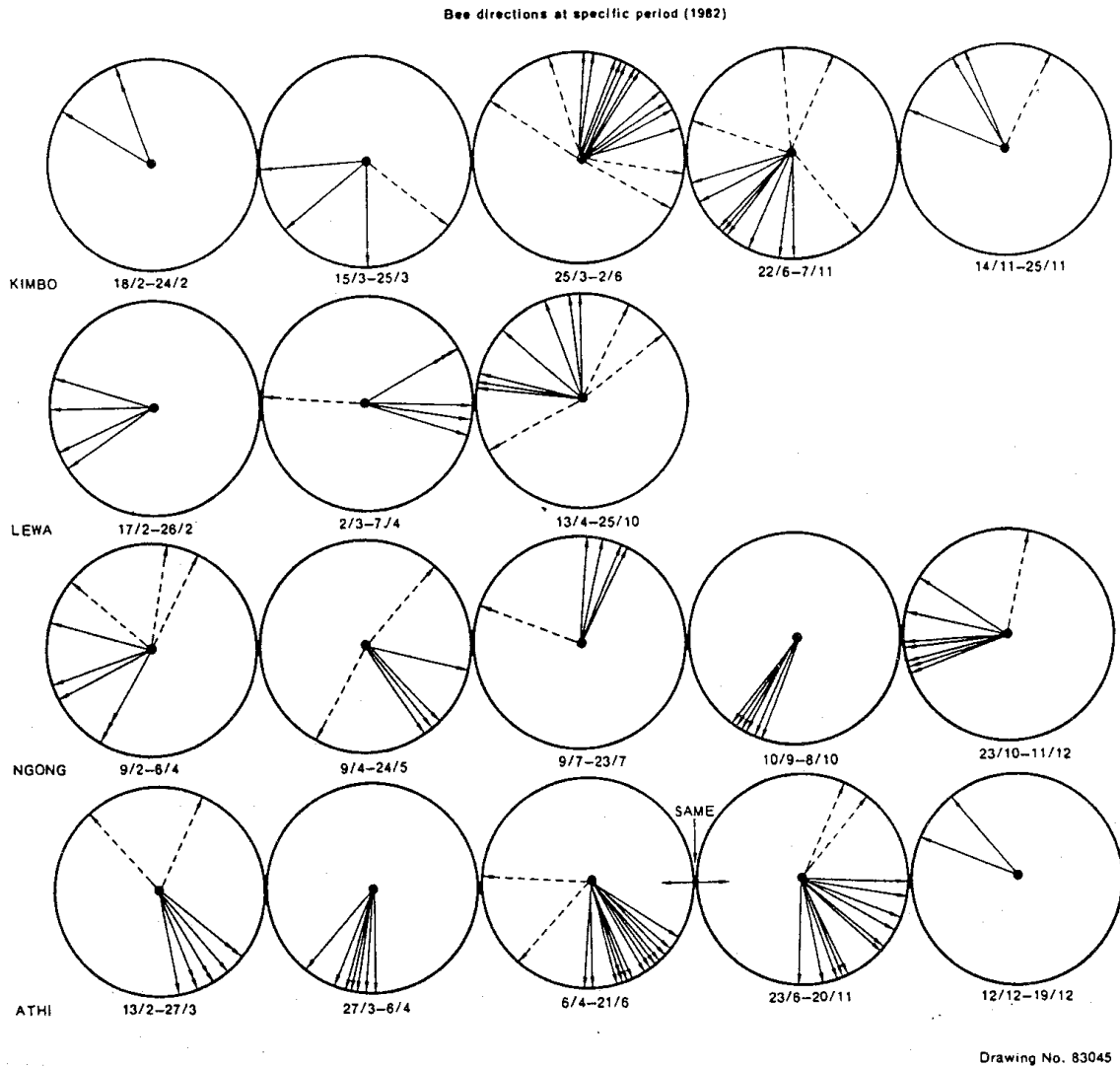


Fig. 8 – Colony flight direction (regardless of cause) at stated time of year in 1982 (broken lines: suggest flights which diverge from a 90° sector containing the majority)

At Naivasha many colonies in transit were observed from February to August. The peak of numbers was in March which coincided with flower initiation and the onset of rain in most of Kenya. Movement into Naivasha apiary occurred from different directions

independent of the time of year. More colonies arrived from the south west and south east than from elsewhere (Table 4). These two directions are from the vegetation rich portions of the Mau (s.w.) and Aberdare (s.e.) regions.

Table 4

Direction from which swarms in transit arrived at Naivasha at different times of the year

Month	No. of swarms observed			
	North easterly 0° - 90°	South easterly 90° - 180°	South westerly 180° - 270°	North westerly 270° - 360°
J				
F	1	5	6	3
M	4	11	16	3
A		1	10	
M	1	2	1	
J	2		4	3
J	3			2
A	4	1		
S				
O				
N				
D				
Total	15	20	37	11

#### *Control and maintenance of flight*

Reproductive swarms and colonies in flight appear to attempt to fly for long distances at constant height and in a more or less constant directions, which may be modified slightly and temporarily by obstacles in the flight route and changes in wind speed. When wind speed increases the colonies fly low. When a moving colony encounters an object in the flight path, the front section of the colony rises over it, thus maintaining direction, but the rear often flies round the sides, especially when it is high.

The behaviour of colonies in flight, which are about to cluster at an interim site, were often characterised by either

a single alteration of direction, or by a series of 'searching' flights taken one after the other while the bees still remained as a colony in the air. Colonies were rarely observed to change their course while in flight and when they did so they still continued their flight without stopping or clustering. Such changes were always less than 10 degrees. Occasionally colonies were seen to cluster at interim sites briefly and then take off again in a changed direction (mean change from original of 28 degrees). Most sites at which colonies and reproductive swarms clustered were one to four metres above the ground.

Over 250 colonies were followed in 1982 and 1983, by truck and motorcy-

cle, but because of the rugged bush covered terrain mostly on foot. The longest continuous flight distance from an apiary to the first resting site was approximately 15,100 meters and was covered in 96 minutes (i.e. at approximately 9.4 k.p.h.). Only 17 of the 250 colonies and reproductive swarms were seen to deviate significantly from their original direction.

### Discussion and conclusions

There are two main reason for extending our understanding of colony movement by the African honeybee. It is of direct importance to the African beekeeper who may loose the majority of his stock once or twice a year. It may help in the management of the africanised honeybee on the American continent where it is sometimes fierce and 'restless' (SPIVAK et al., 1991).

We have distinguished four kinds of colony movement: within an apiary, reproductive swarming, migration, and absconding through disturbance.

Migration is typically preceeded by apparent random movements of the emerged colony in the immediate area of the apiary which may last hours or a few days before setting off. Similar movements are exhibited by absconding colonies and by emerging swarms preliminary to flying away in a manner which has the characteristics of migration, but which does not take the swarms or absconding colonies out of the type of ecosystem in which the apiary is situated. The onset of migration and reproductive swarming are both

associated with a decline in available forage after a period of relative abundance. All the evidence points to conditions within the nest as the prime trigger promoting evacuation by a migratory colony. Since there was no evidence that swarming was ever a consequence of having outgrown the nest, it seems likely that a reduced brood area might lead to congestion and disruption in the distribution of queen pheromone. Both the African bee (CHANDLER, 1976) and the africanised bee (OTIS, 1987) are said to have an inherently higher rate of reproductive swarming in comparison with the unmanaged European bee (MORALES, 1986).

Reproductive swarming is one kind of dispersal, which in general only occurs when forage has been so plentiful as to support additional colonies; but once the period of abundant forage is past dispersal is necessary and the emerging reproductive swarms do not stay long in the immediate vicinity of their parent colonies and so do not increase competition.

In Kenya the African honeybee is found in two contrasted habitats, and its behaviour in the two regions is different. The hills are sufficiently moisture rich to provide a modest level of forage throughout the year, and an efficient colony can actually maintain itself permanently there. Its growth is slow and it is only during the long wet season that food is abundant enough to allow reproductive swarming at all. Even so, such a colony usually produces only one prime swarm every three or four years, and the remaining colony is very

small; afterswarms are rare. Apart from the fact that the climate and forage allows a colony to be active the year long, this is not significantly unlike the European honeybee.

It is in the plains that the African honeybee differs markedly from the European one. There is a great abundance of forage in two wet seasons, multiplication is greater, and there are two peaks of production of prime swarms, sometimes with several afterswarms, coming just after the peak availability of forage. The dry season is very limited and precludes maintenance: the colonies move out. This inherited tendency to fly during dearth periods would be self-eliminating in a European autumn.

The belief that colonies that have left a particular apiary will reappear later in the year is now difficult to support; neither does it appear that there is a regular migration between the plains and hills. Colonies do move between different ecological zones but do not necessarily return to where they previously came from. Thus time of year differences and even reversal of flight directions occurred at Kimbo, Lewa, and Ngong but flight directions did not seem to be a response to colonies moving in a given direction from which they later returned. Ngong had five general flight directions in one year and at Athi the majority of flights remained south or southeast throughout the year. Possibly before leaving to fly to a new site, scouts from the colony concerned fly in different directions as far as the fuel in their honey stomachs allows. If they find forage they can refuel, return

to their colony and direct the colony to move in the direction they scouted. If they do not find forage they fail to return to their colony and die.

More research is needed to prevent mass-migration from apiaries in areas where there are large seasonal fluctuations in forage. For the present beekeepers should not over-stock their apiaries in relation to the forage available. Most importantly, efforts must be made to select and breed from those few colonies that do not migrate.

Because many colonies move to hives in the same apiary and migratory colonies are attracted to empty hives near occupied ones, every apiary should have some empty hives, if possible with Nasonov lures. (KIGATIIRA et al., 1986).

The influence of an emerging colony on others may be minimised by spacing hives well apart in an apiary, and could reduce the number that eventually leave. The settlement of colonies taken to new sites is adversely affected by pest abundance and lack of forage; transporting colonies to new sites at such times is largely wasteful.

Whatever the initial stimulus culminating in the emergence of a colony from its nest, the processes which organise a large number of individuals into acting as a single body could be the same in all instances. The experiments inducing absconding clearly point to a period of time of at least ten minutes without external interference, for this organisation to take place, though if preliminary to unprovoked migration or reproductive swarming it may



well build up over a longer time. Such organisation ultimately leads to flight away from the immediate area and cannot be diverted easily once initiated. Also, particularly at times when forage for all colonies in an apiary was falling to a low level, so that conditions initiating movement may be approaching in several hives, a colony emerging and clustering very close to another hive appeared to promote the emergence and removal of the neighbouring colony too. The signals concerned may be auditory, visual, and/or chemical.

While remaining at one site colonies may amalgamate when colony size or stores falls below a viable level. Amalgamation may also provide a viable colony able to establish itself at the end of a long migration flight.

WINSTON (1980) suggested that the high rate of reproductive swarming of African bees is a strategy against a high level of predation. Predation is greatest when growth is great and stores are plentiful. But the behavioural sequence initiated by disturbance does not appear to be a particularly valuable response to predation because escape cannot be made during the actual attack. For this reason, it might be suggested that the apparent fierceness of the africanised bee in America (e.g. COLLINS 1987) may be related to the greater sensitivity of the guards to a predator at a much greater distance from the nest than the European bee displays. Attack might attempt to forestall an intruder because if it reaches the nest the colony is unlikely to survive. Per-

haps this greater sensitivity to predators is coupled in America with an inability in the new environment to distinguish what may constitute a predator.

In America the africanised bee has adapted to moving in search of new forage systems instead of accumulating stores to overcome adverse conditions i.e. it makes better use of its resources by turning more forage into bees and less into stores. It will continue to spread until it has no alternative but to try to overwinter on accumulated stores. The worst scenario would be if inter-breeding resulted in it inheriting the overwintering properties of the European bee while retaining the aggressiveness, absconding and migratory behaviour of the African bee.

### Acknowledgements

K.I. KIGATIIRA was supported by grants from the British Council, the International Development Research Centre, and the Government of Kenya. The Commonwealth Foundation supported a visit by J.B. FREE to Kenya at the start of the project.

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