THE BEHAVIOUR OF ROBBER HONEYBEES

by

J. B. FREE 1)

(Bee Research Department, Rothamsted Experimental Station.)

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INTRODUCTION

Bees which are attempting to rob colonies of their stores of honey, fly to-and-fro in front of the hive entrance with a characteristic swaying motion as though watching for an opportunity to enter the hive unchallenged by its guards. Butler & Free (1952) suggested that although these robber bees were primarily recognised by their behaviour, all other intruders were identified by their strange body odours.

The present work was carried out in an attempt to discover the causal factors of this characteristic flight of robber bees, and to investigate further the relationship between robber and guard bees.

Some of the experiments were performed in spring, at a time of year when no robbing was seen to occur, and a high percentage of the inhabitants of the colonies would probably never have previously acquired robbing behaviour. Other experiments were carried out in autumn in large nylon screen cages with colonies which had been individually isolated in these cages for over 10 weeks so that they consisted entirely of bees which were unconditioned to robbing.

BEHAVIOUR OF BEES WHEN FORAGING AT A HIVE

On 21st and 22nd March 1953 members of a colony, of approximately 15,000 bees, were trained to forage at a dish of sugar syrup which was placed in an empty hive situated a few yards away from their own and similar in appearance to it. Nearly 400 of these foragers were marked so that they could be recognised again, and their behaviour was observed in the later

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stages of the experiment. On 23rd March when several hundred bees were foraging, the dish was replaced by two combs containing honey. Later the same day the hive was exchanged with one which contained a colony of bees enclosed in the back of the brood chamber by screens of wire-gauze; the two honey combs minus bees, were placed in the front portion.

In all the above circumstances the marked foragers entered the hive without hesitation. It was only after the enclosed colony was released by the removal of the screens and the hive thumped to alert the inmates and cause some of them to guard their hive entrance, that approaching foragers exhibited the characteristic flight behaviour of robber bees. When the hive containing the alerted colony was replaced by one which only contained a dish of sugar syrup or combs of honey, the marked foragers again entered without hesitation within a few minutes.

This experiment was repeated on the 10th April, 18th September and 1st October 1953 with colonies of similar strength to those above.

It was concluded that the foragers did not assume the robber flight on entering a hive other than their own, even when they collected honey from combs in the presence of the odour from bees belonging to another colony. The robber flight was only released by the presence at the hive entrance of the bees of a foreign colony. Since in the two later experiments it was exhibited by bees which had no previous opportunity to observe or perform such behaviour, it was regarded as an innate rather than a conditioned response.

REACTIONS BETWEEN GUARD BEES AND ROBBER BEES OF DIFFERENT COLONIES

In the first of the above experiments it appeared that the majority of the trained foragers adopted the flight behaviour of robber bees, as soon as the foreign guard bees appeared at the hive entrance. In order to confirm this, in the experiments on the 10th April, and 1st October, a total of 49 trained foragers were given individually distinctive marks, and immediately afterwards the colony of bees enclosed inside the hive, was released and alerted. Only 8 of these marked foragers subsequently landed at the hive entrance. Another was seized by a guard in the air at about 15 cms above the alighting board. Although the remainder made no contact with the guard bees they assumed the characteristic swaying flight of robber bees and subsequently returned to their own colonies. It was thus apparent that in the majority of cases the typical robber flight was released by the presence of

the foreign guards at the entrance, without any actual contact with them being necessary.

During the later part of these experiments a congestion of bees often occurred at each hive entrance. On several occasions when they were swept aside by the observers, the foragers again entered the hive without hesitation and continued to do so until the congestion formed again.

In the experiments described above, there were usually sufficient guards present to discourage attempted robbing, and soon after the enclosed colonies were released most of the foragers soon returned to their own hives. However, when only a small proportion of the enclosed bees were released, the foragers displayed the robber flight, but continued to enter the hive. On one occasion on 24th September, only about 20 of the enclosed bees were released; they were completely overwhelmed by the greater numbers of the foragers and were examined and mauled by them (c.f. Butler and Free 1952). There was no question of the foragers being repelled by the guards and yet the presence at the hive entrance, of groups of examining and mauling bees, in which members of their own colony were performing the dominant role, resulted in the ensuing 'jittery' behaviour of the foragers.

In a further experiment foragers from a colony 'A' were trained to collect sugar syrup from a dish in an otherwise empty hive and were distinctively marked. The entrance to the hive of this colony was closed on the evening of 25th September. The next day over 1,000 bees from another colony (B) were trained to forage at the same empty hive and 550 of them were marked with a different coloured paint to that used for colony A. Colony A was then released. The first few members of colony A to arrive at the entrance to the empty hive landed there without hesitation, but many of them were soon examined and mauled by the members of Colony B which were much more numerous. None of the later arrivals from Colony A landed immediately but all adopted a swaying flight in front of the hive entrance. It appeared that the formation of groups of examining and mauling bees at the entrance had released this behaviour, although none of the bees were guarding their own colony.

On 18th September bees from a colony which had been isolated in a large cage were likewise trained to forage for syrup in an empty hive. When there was a large entrance and no congestion occurred at it, they entered without hesitation, but when it was reduced sufficiently to cause congestion many of them assumed a swaying flight. On some occasions when a bee, which was about to enter, met one of its companions leaving the hive entrance, it jerked back in a manner which was very reminiscent of the behaviour of a robber bee when about to be challenged by a guard.

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From these observations it was concluded that one of the prime factors which releases the robber flight is congestion at the hive entrance; in an alert colony this condition can result from the presence of guard bees.

REACTIONS BETWEEN GUARD BEES AND ROBBER BEES FROM THE SAME COLONY

The following experiments were carried out in order to investigate the reactions of guard bees to members of their own colony which were behaving in a robber-like manner at the entrance to the guard bees' hive. In order to prevent the intrusion of 'foreign' bees the first two experiments were carried out on a site, the vicinity of which was believed to be free of other colonies. No evidence of the presence of foreign bees was apparent during the experiments, on the contrary the fact that no animosity occurred until guard bees were posted at the entrance of the hive that was being robbed strongly supports the view that they were not present (c.f. experiment on September 25th in which quarrelling occurred between bees of two different colonies when foraging at the same empty hive). The third experiment (4th October) was carried out in a nylon screen cage.

On March 24 the members of a strong colony of approximately 40,000 bees, whose brood nest occupied two brood chambers, were trained to forage at a hive which contained only honeycombs. The next morning the upper brood chamber was removed and its contained combs, worker bees and queen were enclosed by wire gauze screens as previously described; (a floor and roof were added so as to make a complete hive). Two hours later, when large numbers of the bees from the queenless part of the colony were foraging and had been marked, the queenright part was put in the position of the empty hive and the honeycombs were transferred to the front part of it.

The foragers continued to enter and collect the honey, but when, within 30 minutes, the enclosed bees of their own colony were released and guarded the entrance they exhibited the swaying flight and fighting with the guards occurred. Two and a half hours later 97 recently dead foraging and guard bees were counted at and around the hive entrance. On many occasions a guard seized a would-be robber but quickly released it again, suggesting that the latter had been recognised by its scent as a member of the guard's own colony.

This experiment was repeated on 13th April. Fewer guards were present however, and although they were observed to seize would-be robbers belonging to their own colony, no killings occurred. In a final and similar

experiment on 4th October in which a small colony of approximately 15,000 bees was used very few guards appeared and although they were seen to seize some of the intruders, most of the latter entered the hive without being intercepted. Even when bees from another colony were allowed to rob it, the inmates offered little defence and appeared 'demoralised'.

Since in these experiments the foragers and guard bees could be assumed to have the same colony odour, the attacking response by the guard bees must have been released entirely by the robber-like behaviour of the foragers. The foragers were not deterred from 'robbing' a hive which contained a colony whose members possessed the same odour as themselves. This was further emphasised when near to the end of each of the last two experiments bees from a comb of the robbed half of the colony were shaken onto the alighting board of their hive. They moved slowly into the entrance, fanning as they did so, with their Nassanoff glands exposed. Marked foragers continued to enter and rob the hive despite the presence of large quantities of actively produced bee scent of their own colony at the entrance.

DISCUSSION AND CONCLUSIONS

In the above experiments it has been found that bees which foraged for sugar syrup or honey at a hive other than their own did not assume the typical swaying flight of robber bees at the entrance to it, even when it contained an enclosed colony of bees having the same or different odour as themselves. The foragers adopted this behaviour when there was a congestion of bees at the hive entrance. It was thought to be more the indirect result of the guard bees presence, in that they caused these congestions to be formed, rather than their actual presence, which released the typical flight of the robber bees. Thus a crowd of robber bees, in and around the entrance to the hive that was being robbed, was sufficient to elicit this response when no guard bees were present.

The majority of the trained foragers which attempted to enter a hive, at the entrance to which guards were posted, adopted this characteristic flight before they alighted and made contact with the guards. This behaviour of robber bees may facilitate their escape and it is conceivable that it acted as a social releaser, alerting other members of the robbers' colony which were approaching the hive. As a result of their behaviour robber bees were quickly recognised by the guards without previous olfactory examination. From experiments with colonies which had been individually isolated throughout the entire life of their inhabitants, it was shown that this flight behaviour of robber bees was an innate response.

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Their flight did not become jerky as a consequence of their recognition as suggested by RIBBANDS (1953 and 1954) whose observations were based on bees which returned by mistake to the wrong hive and did not attempt to rob one.

The present observations have provided further evidence in support of the conclusions of Butler and Free (1952) who showed that the fate of intruding bees depended not only on their behaviour, but also on the degree of alertness of the colony whose hive they attempted to enter. They noted that, under natural conditions, colonies became alert and guards were posted during a nectar shortage in the neighbourhood; this was to some extent explained when it was found that many bees alternated between foraging and guarding the entrances to their hives; it was also under these conditions that robbing occurred. The degree of alertness of a colony also appeared to be partly governed by its size. From observations, not yet published, Free found that the presence of guards in bumblebee colonies also depended on their strength.

RIBBANDS (1953 and 1954) arranged two hives so that their entrances, each 2.5 cms wide, were only 5.0 cms apart. He concluded that "when robbing was likely no intruders were willingly admitted irrespective of their behaviour".

In observations and experiments carried out with colonies whose hives were some distance apart, Butler and Free (1952) found that the guard bees of a colony simultaneously treated inadvertent intruders and would-be robbers in a different manner. (Although they omitted to clarify this point in their paper.) It is probable therefore, that whereas under normal robbing conditions the guard bees of a colony discriminate between the various classes of intruders under certain conditions the guard bees may become so excited that they attempt to attack all intruders.

Further evidence that guard bees could recognise robber bees by their characteristic flight behaviour, irrespective of their scent, was obtained, in the present work, when it was shown that the guard bees of one half of a very recently divided colony attacked and in some instances even killed members of the other half of the colony which attempted to rob them. Since Kalmus and Ribbands (1952) showed that when a colony was divided into two parts a significant odour difference between them "might develop within three days" it is safe to assume that there was no odour difference between the parts of the colonies used in the above experiments.

The only alternative to the explanation that the robber bees were identified as such by their behaviour appeared to be the hypothesis that they produced a 'fear odour' and were identified by it. This hypothesis would not explain why bees attacked moving artificial bee-like lures (LECOMTE, 1951 & 1954), nor why on many occasions after a guard has seized a member of its own colony, which was behaving in a robber-like manner, it quickly released it again. These latter observations strongly suggest that the identity of robbers is normally established by their behaviour, and then confirmed by their 'foreign' odour. This same mechanism acts as a safeguard to members of the guards own colony which approach the hive in a hesitant manner, although under what are probably exceptional conditions some of them may be killed by the guards.

The practice among beekeepers of reducing the size of the entrance to a hive during the robbing season therefore not only leaves a smaller area for the guards of the colony to defend, but also causes congestion at the entrance and accentuates the innate hesitant flight of robber bees, which are not as well orientated to the entrance as the bees of the colony and so facilitates their recognition.

SUMMARY

- I. The factors which cause the characteristic swaying flight of robber honeybees have been investigated.
- 2. This flight occurs as an innate response to the presence of a congestion of bees, of their own or another colony, at the entrance to the hive they are robbing.
- 3. Foragers enter without hesitation, hives other than their own to collect syrup or honey in the absence of a congestion of bees at the entrance, even when these hives contain a colony of bees.
- 4. Guard bees quickly recognise would-be robber bees by their flight behaviour and confirm their identity by olfactory examination.

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ZUSAMMENFASSUNG

1. Es wurde untersucht, welche Faktoren den pendelnden Anflug räuberischer Honigbienen auslösen.