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QUEEN SUPERSEDURE AND SWARMING

A LECTURE GIVEN TO THE
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QUEEN SUPERSEDURE AND SWARMING

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QUEEN SUPERSEDURE may be defined as a process by which a colony of honeybees replaces its queen with a new one without division of the colony itself into two or more parts—that is to say, without swarming. The old queen usually dies either before or very soon after the new queen has been successfully reared, but she may for a time live and lay eggs side by side with her successor.

When a colony swarms it also acquires a new queen, but the colony always becomes subdivided into two or more parts. One of these remains at the original site with a young queen and another migrates to a new site with the old queen.

If further subdivision occurs each of the divisions produced (casts or afterswarms) is headed by a young queen and similarly migrates to a new home. The bees forming that part of the original colony which left the parental home with the old queen often supersede her by a new queen within a few months—indeed, for reasons which will become clear later on, I suspect that they always do so before their new colony reaches a size comparable with that of their parent colony shortly before swarming occurred.

Swarming and supersedure are clearly somewhat similar processes as in each the old queen of the colony is replaced by a new one, and I wish to suggest to you that it is probable that fundamentally they are initiated by one and the same stimulus.

First let us consider the question of queen supersedure, a process which occurs very frequently; I suggest much more often than is generally realized. As a rule only a small number of queens are reared, and they are derived either from fertilized eggs in queen cell cups or from young female larvae in worker cells. In the latter case the worker cells are, of course, modified to form emergency queen cells. It is usual for only a single queen to be allowed to reach maturity, the other potential queens being destroyed before they emerge from their cells. Sometimes, perhaps often, the workers of a colony which, judging by the small number of queen cells they are producing, are attempting to supersede their queen will, even if left without interference, destroy these queen

cells. Indeed they may repeat this process several times before finally rearing a new queen to maturity, or apparently ceasing their attempts to supersede their old queen—at all events for the time being.

All being well, if a new queen is reared she mates and sooner or later takes the place of her mother, the old queen.

A number of theories have been put forward in attempts to explain the phenomenon of queen supersedure. For example, FARRAR (1947) has suggested that contraction by a queen of Nosema disease often leads to her supersedure. ROOT (1945) has suggested that inability of a queen to produce sufficient eggs on account of old age often leads to her replacement, and WEDMORE (1924) has suggested that this may happen because some injury adversely affects her production of eggs. However, so far as I can discover, neither of these authors has stated what he meant by the failure of the queen to produce 'sufficient' eggs.

SNELGROVE (1946) has suggested that the bees of a colony may become stimulated to replace their queen if she produces an abnormally high proportion of drones as the supply of sperm in her spermatheca nears exhaustion; and a few years ago I myself suggested (BUTLER, 1954, 1956) that the worker bees of a colony will attempt to supersede their queen if they fail to obtain from her a regular and adequate supply of a secretion which I called queen substance. I suggested that normally the supply of this substance is adequate both to inhibit development of the workers' ovaries and also queen production by them. Recently I have been able to demonstrate (BUTLER, 1957a) that an extract of this substance when fed to worker honey-bees is sufficient to inhibit development of their ovaries in the absence of a queen or queen-like object, and DOREEN GIBBONS and I (BUTLER and GIBBONS, 1958) have also been able to show that queenless worker honey-bees can be caused to behave in a queen-right manner and do not attempt to rear emergency queens if they are provided with an adequate supply of queen substance in their drinking water.

Let us consider some of these theories of the cause of queen supersedure. Before we do so, however, let me remind you that when a colony of bees is rearing queens there is no way of finding out definitely whether the bees are making preparations to supersede their queen, or whether, instead, they are preparing to swarm with her, unless they are allowed to complete the process they have begun. Therefore, when studying the nature of queen supersedure, it is far too dangerous to assume that because the workers of a colony are only rearing a few queens, perhaps only one or two, they are preparing to supersede their queen rather than to swarm with her.

Fortunately, in 1954, I obtained two colonies with mated laying queens,

each of which had been superseded by a younger queen, but was still living alongside her successor. In a preliminary experiment I took away the young queen from each colony, leaving the old superseded queen behind. Two days later emergency queen cells were found in each of these colonies, and it looked as though in each case the workers were once again preparing to supersede the old queen. Next, I destroyed these emergency queen cells and removed about three-quarters of the adult population from each of these colonies, leaving the rest of the bees with the queens that they had previously superseded. Unfortunately one of the queens died next day, but the other continued to live and to lay a few eggs, certainly not more than fifty each day. During the next eight days her bees made no attempt to rear another queen to supersede her. At the end of the eighth day about ten thousand workers were taken from a queen-right colony in which no queen cells could be found and were united to the bees of the colony with the superseded queen. Two days later emergency queen cells were found in this experimental colony. (For a full account of this and other experiments on queen supersedure see BUTLER, 1957 b).

Thus I was able to demonstrate that neither of these old queens which had actually been superseded was able to inhibit the workers of her colony from rearing further queens. But I was also able to show that the presence of one of these queens, which had survived long enough for further experiment, was sufficient to keep a small proportion of her workers from rearing queens, although insufficient to keep a larger group of bees, composed partly of members of her own colony and partly of bees from another colony, from so doing.

Similar results were obtained in experiments with other queens, and it is clear that these data support the hypothesis that the process of supersedure of a queen is initiated by her failure to produce sufficient queen substance to inhibit her workers from rearing further queens.

Now, each of the superseded queens used in these experiments was laying very few eggs in comparison with other queens in the same apiaries, and since it has been suggested, as I mentioned earlier, that if a queen's output of eggs becomes 'insufficient' her bees will supersede her, it might be argued that these queens had been superseded for this reason rather than because they were producing too little queen substance. However, let us examine this suggestion a little further.

First of all it is clear that the workers of a colony do not have to come into contact with newly laid eggs in order that they shall remain inhibited from rearing further queens. If this were not true, the workers of colonies in some of my early experiments on queen substance (BUTLER, 1954) which only had

access to the heads of their queens would have produced emergency queen cells, but they did not do so. Nevertheless, since the queens used in these earlier experiments of mine certainly continued to produce a few eggs, it seems possible that egg production by them was essential if access to their heads alone was to be capable of inhibiting small groups of workers from attempting to rear queens. It could, in fact, be argued that queen substance production is closely associated with egg production.

For some time I could think of no practical way to determine whether this is so or not; it seemed to be impossible to devise an experiment for this purpose. Then I had a great stroke of luck! A marked, mated queen was found which had earlier in the season been laying well but whose colony now possessed neither eggs nor brood. Apparently this queen had stopped laying a few weeks earlier, and yet there were no signs that the members of her colony had made any attempt to rear another queen to replace her. In order to test whether, given another chance, they would do so, I gave them a comb containing young worker larvae, but no eggs. Four days later I gave them another similar comb. However, although the bees reared the worker larvae to maturity, they made no attempt to rear a queen to replace the experimental one, which did not lay any eggs at all during the seven days of this experiment. Next, another comb containing young larvae only was given to this colony and at the same time the non-laying but apparently otherwise normal queen was removed. On examination of this colony three days later several emergency queen cells were found.

When this curious queen was removed from her colony she was substituted, by direct introduction, for the mated, actively laying queen of another colony and, at the same time, all combs containing eggs were removed, and others containing worker larvae used to replace them. After four days the queen had still laid no eggs, but the bees of the colony to which she had been introduced had made no attempt to rear another queen to replace her. This non-laying mated queen was then removed and substituted, for between three and six days at a time, for the mated, actively laying queens of other normal colonies of moderate size. In no case was a queen cell produced in a colony while this queen was present.

Similar results were obtained in experiments with a second mated, non-laying queen which I was lucky enough to obtain.

It is clear, therefore, from the results of these experiments that mated queens, even though they are not laying any eggs at all, can still be fully capable of inhibiting the workers of moderately strong colonies (30,000—40,000 bees) from rearing supersedure queens during the summer.

In passing I might perhaps mention that the interesting and probably important point that experiment has shown that virgin queens are in summer by no means always able to keep the workers of even small colonies from rearing further queens.

Many bee-keepers have stated that the workers of a colony tend to supersede their queen if she loses a leg or becomes lame, or is otherwise injured, (e.g. SNELGROVE, 1946; WEDMORE, 1942), and it has been suggested that this is because the damage she sustains in some way interferes with her egg-laying ability. However, as we have seen, it is sometimes possible for a mated queen that is laying no eggs at all to inhibit the workers of a colony from rearing supersedure queens.

Other theories can, quite obviously, be put forward to explain why (if in fact it does happen) the maiming of a queen tends to result in her early supersedure. One possibility which I have considered is that such a queen tends to be superseded because her mobility has been reduced, and during the summer of 1954 I tried to test this possibility. To do so I tethered each of forty-two mated laying queens to a comb in her own colony. The leashes with which the queens were tethered were made of thin wire fixed round the queens' waists. Each leash was about three inches long and, although it greatly hampered a queen's mobility, it did not prevent her workers from readily reaching all parts of her body.

No eggs were laid in cells by any of these tethered queens, although most of them continued to produce a few. Each queen remained tethered either until her bees had built one or more queen cells, or in those cases in which no queen cells appeared, for a minimum period of six days. It was noticed that the tethered queens were almost continuously being very actively licked by groups of their workers, as if the latter were desperately seeking something, perhaps queen substance, from them; indeed, this resulted in the bodies of many of the queens becoming highly polished.

The queens of control colonies in the same apiaries were, of course, left untethered, and care was taken to see that the experimental colonies were kept continuously supplied, like the control colonies, with young worker larvae so that their workers had the wherewithal to produce queens.

In seventeen of the forty-two colonies whose queens were tethered, queen cells were produced by the worker bees, but during the same period queen cells were found in only one of the control colonies. It is clear, therefore, that the bees of those colonies whose queens were tethered produced significantly more queen cells than the control colonies, and it seems reasonable to conclude that,

indeed, reduction of the mobility of a queen by tethering does tend to cause the workers of her colony to rear further queens. This could be explained on the basis of the queen substance theory by supposing that the tethering of these queens had resulted in a reduction in their output of queen substance below the minimum level necessary to inhibit their workers from rearing supersedure queens. If this is the correct explanation of the observed facts, one would suppose that when such a queen was released her output of queen substance would soon return to about the same level as it had been before she was tethered and that, in consequence, her bees would destroy the queen cells they had made. In order to obtain data on this point, I left the queen cells intact in thirteen colonies when their queens were released. In twelve of these colonies all the queen cells were destroyed within five days of their queens being released; in the remaining colony the bees swarmed with the queen a few hours after she was released.

From the data collected in these and similar experiments I think it can reasonably be concluded that shortage of queen substance is the only immediate cause of queen supersedure, and that any other factors, such as disease or injury, that tend to cause queen supersedure do so by reducing a queen's output of this substance.

So much, then, for queen supersedure. Let us now go on to consider the process of swarming and some of the theories that have been put forward to account for it.

Swarming is, of course, a method by which colony reproduction, as distinct from the reproduction of individual honeybees, takes place. Just as the reproduction of individual bees within a colony is essential to the continued existence of the colony, so reproduction of colonies is essential to the continued existence of the species; for without it any increase in the total number of colonies, or replacement of colonies destroyed by disease, etc., would be impossible.

So far as colony reproductive swarming is concerned, two principal theories have been put forward in attempts to explain why some colonies swarm in a given season and others do not. These are the 'Brood Food' theory of GERSTUNG (1926) and the 'Overcrowding or Congestion' theory, which is attributed to DEMUTH (1931).

Unfortunately very few experimental data or reliable observations are available with which we can test these, or any other, theories of swarming. The collection of such data is complicated by the fact that, as I have already mentioned, unless we allow any colony that begins to rear queens—that is to say, any colony that possesses queen cells containing eggs, larvae, or pupae—to

continue their behaviour without interfering with them, we cannot know for certain whether the bees were preparing to swarm or to supersede their queen. However, it seems to be general experience that queen rearing in summer is more likely to be connected with swarming than with supersedure. Again, unless we leave a colony undisturbed with its queen cells we can never be certain that the bees will rear them to maturity. Many colonies start to rear queens only to destroy them before they reach maturity; and they may repeat this behaviour several times in succession. However, let us assume that any colony that begins to rear queens during May, June, or July is likely to be preparing to swarm rather than to supersede its queen without swarming.

If we make this assumption certain experiments are possible: for instance, in mid-June 1956, Dr. J. SIMPSON of the Rothamsted Bee Department took seventeen colonies of bees, in which no occupied queen cells had appeared during that season. Each of these colonies was occupying at least two brood-chambers, and SIMPSON reduced the total hive space of each colony to a single brood-chamber. Twelve similar colonies were left uncrowded as controls. During the following three weeks eight of the crowded colonies produced queen cells, but none of the uncrowded ones did so. This result is significant and shows that the experimental overcrowding did tend to encourage the experimental colonies to rear queens, presumably in preparation for swarming —i.e. supports the 'Overcrowding' theory. But not all of the experimentally overcrowded colonies started to rear queens, and SIMPSON has shown, on another occasion, that some colonies do not readily swarm even when they are overcrowded to such an extent that many of their bees are forced to remain in clusters on the fronts of their hives for lack of room for them inside. So overcrowding is quite clearly not the only factor involved. Again, on the other hand, some colonies will swarm even when they have unlimited space in their hives, and it is these colonies that present a problem to the practical bee-keeper. It was in order to explain this type of swarming—the swarming of uncrowded colonies—that GERSTUNG (1926) propounded his Brood Food Theory. Briefly, GERSTUNG supposed that if in a colony the number of nurse bees with functional brood-food glands (pharyngeal glands) rises to such level that more brood food is being produced than is required to feed the larvae that are present, then the nurse bees are eventually compelled to find an outlet for this surplus brood food by rearing and feeding queen larvae, which require large quantities of it.

GERSTUNG believed, although he had no data to show it, that all adult worker bees pass through a stage in their lives in which their brood-food glands are producing large quantities of brood-food, and he further supposed that it is essential for such bees to find some way of disposing of this glandular material

and that the necessity to do so greatly influences their behaviour. He supposed that during the spring growth of the colony the presence of actively secreting pharyngeal glands results in the workers feeding both the worker larvae and the adult queen on brood-food. The feeding of the queen in this way led, he believed, to more rapid development and laying of eggs by her, with the result that a new outlet for the hitherto surplus brood-food became available in the shape of an increased number of worker larvae requiring food. However, in a short time, these larvae develop into adults which in their turn produce brood-food, so that, indeed, as a colony grows in size an impossible situation develops, as the queen eventually becomes unable to lay sufficient eggs to produce enough larvae to supply an outlet for the ever increasing output of brood-food. This leads, GERSTUNG supposed, to an accumulation of surplus food which results in increased wax production and the building of drone cells. He went on to suppose that the queen lays in these cells and, he thought, the resulting larvae would require even more brood-food than a similar number of worker larvae, so that once more an outlet for the surplus brood-food was provided. This, however, is, of course, only a temporary relief; for as soon as the drone cells are capped, a surplus of brood-food again becomes inevitable. Finally, GERSTUNG supposed, the only answer to the problem is for the bees to build queen cells and to rear queen larvae into whose cells the surplus brood-food is poured, with the result that a swarm ultimately emerges.

This, then, is a brief outline of GERSTUNG's famous Brood Food Theory—a theory that is still blindly accepted by many bee-keepers and still dominates their thoughts on this subject. It is still probably the most widely accepted theory of swarming; TARANOV's theory of swarming is, after all, only an extension of GERSTUNG's theory. There is no doubt that the latter theory has been frequently quoted in support of a number of bee-keeping practices of very doubtful merit.

There are a number of observations—a number of facts—which, as SIMPSON (1958a) has pointed out, render this theory quite unacceptable.

SIMPSON has carried out experiments in recent years in which he has attempted to induce swarming by adding very large amounts of sealed brood to colonies: he has also tried to induce colonies to swarm by removing their larvae so that their workers had no outlet for their brood-food in the shape of larvae to feed. Neither treatment proved to be an effective method of inducing colonies to produce queen cells. SIMPSON has demonstrated that a surplus of brood-food can definitely occur when larvae are removed in this way, as he found that the occasional worker larvae which are left behind by mistake have their cells flooded with brood-food by the workers. But this brood-food surplus did not cause these worker larvae to develop into queens.

Again, judging by the speed with which colonies will start to rear new queens after they have been dequeened, it has surely always been fairly obvious that the removal of a queen from a colony can cause its worker bees to start to rear queens long before brood-food, surplus to the requirements of the larvae of the colony, has been produced.

We must, I am afraid, discard GERSTUNG's Brood Food theory. Is there, then, any working hypothesis one can put forward on the basis of present knowledge to explain the swarming process?

Well, since it has now been demonstrated that the production of both emergency queens (BUTLER, 1954) and supersedure queens (BUTLER 1957b) is due to failure of the queens concerned to produce sufficient queen substance, it seems highly probable that queen rearing by a colony preparatory to swarming is also due to lack, or ineffectiveness, of queen substance. It seems probable in fact that swarming as well as supersedure is induced by failure of the queen to produce enough queen substance. However, the difficulty remains of explaining why sometimes one process occurs and sometimes the other—why bees sometimes supersede their queens without swarming and at other times do so only in connection with swarming.

Now, SIMPSON (1957) has demonstrated that bees of colonies whose queens are less than two months old are less likely to make swarm preparations than those of colonies headed by queens more than twelve months old. This, quite clearly, is evidence that the quality of its queen influences the tendency of any particular colony to swarm, which, of course, is evidence in favour of the hypothesis that swarming depends on her output of queen substance. Further evidence in favour of this hypothesis has been obtained by BECKER (1925), ZANDER (1925), WEAVER (1957) and others who have shown that a series of bees intermediate in physical structure between what we have come to regard as a normal queen and a normal worker can easily be obtained experimentally, and in nature queens have been found which, although they were reared under natural conditions, nevertheless lacked certain characteristics that most queens possess. It seems highly probable that such worker-like queens tend to have a low output of queen substance. Again, there is evidence that strongly suggests that colonies of some strains of honeybees are much more prone to swarm than those of others.

These facts suggest that the capacity of a queen to produce queen substance varies with her age, the conditions under which she was reared, and her genetical constitution, and may determine the tendency of her colony to swarm.

SIMPSON (1958b) has pointed out that, if this is the correct explanation of

the initiation of swarming behaviour in a colony, some other factor must come into operation to determine whether, when the workers of a colony suffer from a shortage of queen substance, they will supersede their queen or swarm. Perhaps, as he has suggested, supersedure occurs only when conditions are unsuitable for swarming.

According to ALFONSUS (1933) supersedure occurs most often just before and just after that period in each year when swarming is most frequent. SIMPSON (1958b) has suggested that any supersedure that occurs during the swarming season most frequently takes place in small colonies, and that the condition which determines that supersedure rather than swarming will occur, is always that the colony's queen substance requirement is small, either because it is itself a small colony or because the queen substance requirement of its individual workers is low. Perhaps the reason for the predominance of supersedure outside the swarming season is that the queen substance requirement of each individual bee becomes reduced so that even large colonies need only a small amount.

A number of preliminary observations seem to support this theory. For instance, a colony that has a virgin queen in the middle of the summer will often fail to destroy any other queen cells it may have, and may even rear further young queens if it has any young larvae with which to do so. On the other hand there is some evidence that a colony with a virgin queen in the late autumn will destroy any queen cells very quickly and will not rear any more queens so long as the virgin queen is present.

This theory of swarming also seems to be in accordance with the requirements for the survival of the species, since presumably a queen that fails to keep a small colony queenright is more likely to be a sickly or a failing one than another that fails to keep a large colony queenright.

Furthermore, if this theory is correct, it must be supposed that those colonies which fail to swarm must be those whose queens are producing sufficient queen substance to prevent them from swarming when they have reached full size. This will depend, firstly on the amount of queen substance the queen can produce and, secondly, on maximum size of the colony that she can produce and, thirdly, on the amount of queen substance that each bee in that colony neeeds. All three of these factors—the amount of queen substance produced, the maximum size of the colony, and the amount of queen substance each bee needs—may, very possibly, vary according to the time of the year, the weather, or the availability of forage, and thus determine not only the limits of the swarming season, but also the frequency of swarming in any particular season or apiary site.

Apart from environmental effects the only factors that would seem likely to

affect the output of queen substance by queens of the same age are their genetic characteristics and possibly the conditions under which they are reared; in the case of the queen substance requirement of the workers, on the other hand, probably only genetic characteristics will be important. Thus it is probable that amongst uncrowded colonies of the same size, in the same apiary, and with queens of the same age reared by sound methods, genetic characteristics are probably mainly responsible for determining which colonies will swarm. In support of this view we already have some evidence which suggests that the giving of additional queen substance to a colony that appears to be making preparations to swarm can be sufficient to cause a reversal of the process and reversion to a typical non-swarming condition. It is possible—and this possibility is being investigated—that it may be practicable in this way to prevent colonies from swarming during the swarming season and, after this is considered to be over, to allow supersedure to take place normally by withholding additional supplies of queen substance.

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