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WORK AT ROTHAMSTED ON HONEYBEE SWARMING

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Honeybee colonies reproduce by swarming. The queen of a colony, a proportion of the worker bees and sometimes some drones suddenly leave their nest and fly, forming a well-defined group in the air. Usually the swarm soon clusters on a suitable object, often a branch of a tree. Later it disperses again and flies to find a new home. Sometimes several swarms emerge from a colony over a week or two. Colonies usually begin to rear queens before they swarm. The original queen, if still alive, goes with the first swarm; otherwise swarms contain young unmated queens. Queen rearing in the presence of a laying queen also occurs during "queen supersedure", in which the old queen is replaced without swarming. No reliable method is known for predicting which of these two processes is going to occur.

The use of hives in which the combs are built into movable frames enables colonies to be divided artificially, so that beekeepers no longer need swarms and usually try to prevent swarming, because it weakens the colonies and lessens their honey yield.

The Annual Incidence of Swarming

When beekeepers needed swarming they found that nearly all colonies could be made to swarm by keeping them in small enough hives. Swarming is rarer from hives big enough to accommodate colonies easily when they reach full size, but it does happen. The proportion of colonies that will swarm under these conditions is difficult to discover exactly, because nearly all beekeepers interfere with the colonies they think likely to swarm. On one English honey farm a group of about 300 colonies headed by queens reared the previous summer had the following average percentages of troublesome colonies over 4 years (Simpson, 1957a):

A. Had unsatisfactory queens and were given new ones	5
B. Became queenless before beginning queen rearing and were given new queens	4
C. Began queen rearing, but stopped without swarming	24
D. Began queen rearing and subsequently may have swarmed or might have done so if not given new queens	18
Total	51

The incidence of queen rearing differed greatly from year to year and slightly, but significantly, between different apiary sites. The numbers in groups A and B show that swarming is not the only event that makes colonies require attention during the summer, though some of group B might have swarmed with the first young queens they reared had they been allowed to continue queen rearing instead of being given new laying queens.

Occupied queen cells were removed whenever they were seen, and as it is uncertain how far, if at all, this treatment inhibits swarming, it is impossible to say how many of group C should be included among the swarmers. Certainly not all of them should. Among 58 colonies in Rothamsted apiaries examined weekly without removing queen cells from early May to mid-July 1956, 16 began queen rearing, and although not divided to prevent swarming, did not swarm or change their queens. They destroyed occupied queen cells, often repeatedly, at various stages of maturity; 73 of the young queens reached the larval stage and 39 the pupal stage before they were destroyed. One colony, on which the observations were extended to mid-August, continued queen rearing for 13 weeks and destroyed 29 queen cells at the pupal stage or later. Gary and Morse (1962) showed that colonies sometimes allow young queens to reach maturity and then kill them after, or just before, they emerge from their cells.

Evidently many colonies that begin queen rearing will neither swarm nor replace their queens; the more often and thoroughly apiaries are examined, the more of this abortive queen rearing will be seen and the more the number of colonies likely to swarm will be overestimated.

The Time of Year when Colonies Swarm

Swarming is mainly an early or midsummer event. Jeffree (1951) found that swarming in Wiltshire was commoner before midsummer than after, and English commercial beekeepers do not consider it necessary to look for incipient swarming after mid-July.

Colonies suspend breeding during the winter and their population of adult bees declines. When breeding begins in spring the amount of brood increases for a time along with the number of adult bees available to feed it. Some records of the amounts of worker brood in colonies throughout the summer (Dufour, 1939; Brünnich, 1922; Nolan, 1925) show a maximum in early summer followed by a rapid decline. From this Morland (1930) concluded that swarming results from a seasonal decline in breeding, as would be expected on Gerstung's brood food theory (see below). It now appears that these early brood records were misleading, partly because they were collected in places where the foraging season begins and ends earlier than in England, and partly because their averages were based on the colonies that reared queens as well as on those that did not (Ribbands, 1953). The Rothamsted colonies that did not begin queen rearing in 1956 showed little decline in breeding before the end of July, i.e., well *after* the swarming season and not before it. Breeding declined earlier in the colonies that began queen rearing, but more often than not the queen rearing began while the brood was still increasing. The subsequent decline in breeding may therefore have been a consequence of queen rearing, but could not have caused it (Simpson, 1959).

Fully efficient supersedure (in which the old queen survives until the young one has mated and begun laying) most often occurs in late spring and early autumn. Queen replacement during the summer is usually less efficient, involving swarming, early death of the old queen or repeated destruction of queen cells. In the commercial apiary mentioned above transient queen rearing (group C) was most frequent just after midsummer, so much of it was probably abortive supersedure rather than abortive swarming.

The Causes of Swarming

Because swarming is usually preceded by queen rearing, a cause of swarming has generally been sought in the cause of queen rearing. Queen rearing nearly always begins after a colony is deprived of its queen, when a few of the larvae in worker cells are reared as queens. Huber (1792) showed that it is not sufficient for the worker bees to see, smell or hear their queen to be inhibited from rearing queens, and he supposed that the queen must communicate with the workers by touching their antennae with her own. Butler (1958), however, found that queen rearing, at least by small clusters of bees, could be inhibited by the residue from evaporated ethanol extracts of queens; his own and other work (reviewed by Butler, 1959; Butler, Callow & Johnston, 1961; Pain, 1961) leaves little doubt that a queen's power to inhibit queen rearing depends entirely on inhibitory substances ("pheromones"—Karlson and Lüscher, 1959) produced mainly, perhaps entirely, in her mandibular glands. One of these substances has been identified and synthesised. Butler (1957, 1960) has shown that supersedure is associated with queens that have little power to inhibit queen rearing and yield correspondingly ineffective ethanol extracts. Supersedure has been induced by amputating the reigning queens' front legs (Simpson, 1960a), which presumably interferes with the production or distribution of the inhibitory substances. Simpson (1956) suggested that failure of the reigning queen to prevent queen rearing can also cause swarming, but this has not yet been demonstrated. Several facts support the idea, but others are difficult to reconcile with it.

Small colonies, i.e., those that would require least of the inhibitory substances, rarely swarm when they have adequate hive space. Dividing a large colony into small ones is an effective method of preventing swarming. Queen rearing during the swarming season is more frequent in colonies with old queens than in those with young ones (Simpson, 1957, 1960b). When colonies become too big for their hives many worker bees may hang outside, but before this happens the density of bees inside the hive increases to about three to five times its normal level. The temperature among the bees does not exceed its normal maximum of 34–35° and is possible only because the densely packed bees remain almost motionless (Simpson: unpublished observations). This lack of movement perhaps causes queen rearing by hindering the distribution of the inhibitory substances. Butler (1960) found that queens of swarms from colonies whose owners said they had had ample hive space before swarming gave extracts relatively poor in their ability to inhibit queen rearing, whereas queens from swarms reputed to be caused by crowding gave fully effective extracts.

What is difficult to explain on the queen pheromone deficiency theory of swarming, is the swarming that occurs without queen rearing. The most common example of this is when a colony migrates, or "absconds". This behaviour rarely occurs naturally with European bees, but can be induced by depriving a colony of its hive and combs (Simpson, 1962). Colony migration might be thought a completely different phenomenon from reproductive swarming and one with quite different causes, but a gradation between the two appears when swarming is induced experimentally by putting big colonies into small hives. If the hive is much too small for the colony, so that a large proportion of the bees hang outside, the proportion that goes with the swarm is also large, and often queen rearing does not begin before the swarm emerges. During and after its emergence a swarm seems to behave exactly like an absconding colony.

Even if queen pheromone deficiency can cause both supersedure and swarming, something else must determine which occurs. Some other factor is involved, and this factor could cause both swarming and its associated queen rearing and not merely determine whether swarming or supersedure will result from lack of queen pheromone. Deficiency of hive space clearly is such a factor in the swarming of colonies from small hives, so perhaps the swarming of uncrowded colonies has an analogous explanation.

The factors that decide whether a colony that starts to rear queens will swarm, supersede or indulge in abortive queen rearing may be partly genetic, but the frequency of swarming in the summer and of efficient supersedure in the spring and autumn suggests that there is also a seasonal cycle involved. The growth of colonies to full size changes the proportions of bees of different ages. Gerstung (*c.* 1890) supposed that an increase in the proportion of adult bees to brood, and therefore of food available for larvae, led to the rearing of queens (queen larvae are given more food than worker larvae). Simpson (1957b), however, found that an experimentally induced brood-food surplus did not cause queen rearing or swarming. It is also unlikely that brood-food surplus predisposes to swarming rather than supersedure, as the proportion of adult bees to brood is largest in the autumn supersedure season. As swarming is most frequent at the time of year when most colonies are growing rapidly, it is more likely to be related to a high proportion of young bees to old ones than of adult bees to larvae.

There is some evidence for another kind of seasonal factor. Beekeepers mostly agree that colonies that are big early in the season are more likely to swarm than those that become big later (Holzberlein, 1952), and this cannot be explained on any age balance hypothesis. The decline in swarming after midsummer is often attributed to the prevalence of heavy nectar flows at that time, but nobody seems to have noticed any diminution with heavy nectar flows early in the season. It seems likely that the swarming is at least partially determined by an intrinsic physiological cycle, presumably initiated by emergence of colonies from their winter condition. The existence of some such cycle is also suggested by changes in the state of the fat bodies and salivary glands of worker bees in the course of the summer (Simpson, 1956, 1960c).

The Emergence of a Swarm from its Parent Colony

When a colony swarms some of the worker bees go with the swarm and some stay to continue the parent colony. At one time it was supposed that the bees that swarmed were either the oldest or the youngest, but Rösch

(1930) concluded that a swarm contains bees of all ages in about the same proportions as in the parent colony. At Rothamsted Morland began a more extensive investigation that was completed and published by Butler (1940). This also showed bees of all ages in swarms, but with a bias towards the younger ones. From this it seemed that the bees that stay behind when a colony swarms might be the ones that have flown enough to be familiar with their old position; this would explain why the bees of a swarm usually remain in any new position in which they are hived (Free, 1958), whereas when part of a colony is moved artificially to a new position many bees return to the part left on the old one. This hypothesis was disproved by an experiment (Simpson, 1960e) in which a swarm was found to contain many bees that had previously returned to their old position when moved artificially. Taranov (1947) suggested that the bees that go with a swarm are pre-determined at least several days beforehand. However, putting a colony in a small hive can make it swarm within as little as 24 hours, and colonies have absconded in as little as 4 hours when experimentally removed from their hives and combs. Colonies taken from their hives (one only ½ hour beforehand) have been induced to abscond by holding them close to colonies already absconding. Bees from the absconding colonies landed on the other colonies and started self-propagating disturbances in them that quickly led to absconding (Simpson 1962). Apparently, colonies can quickly become unstable and able to swarm when given the right conditions, so it is unlikely that the bees that go with a swarm are pre-determined. How a colony divides when it swarms is still unexplained.

Huber (1792) noted that an old queen leaving her hive with a swarm appeared to do so unwillingly, but it has been suggested that a swarm that emerges with a virgin queen does so by following her when she goes out to mate. However, Simpson (1960d) saw a virgin queen being driven out of her hive by swarming workers, whereas when the swarm was re-united to the parent colony no disturbance suggestive of swarming was associated with the same queen's later mating flights. When the swarming workers were driving the queen out they did not actually push her; those beside her stopped moving forward in the entrance tunnel whenever she did, with the result that those coming behind ran into them and formed a dense mass through which the queen could not penetrate. Some similar behaviour may explain how a swarm perceives its queen when flying across country (Simpson, 1962). If workers that have lost the smell of their queen because they have got in front of her fall back until they find it again the queen may always be kept in front of the swarm, leaving scent behind her to be perceived by the workers.

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