ON THE CAUSES OF SWARMING IN THE HONEY BEE (APIS MELLIFERA L.): AN EXAMINATION OF THE BROOD FOOD THEORY

BY D.M.T. MORLAND, M.A.

(Rothamsted Experimental Station, Harpenden)

(With 3 Text figures).

From The Annals of Applied Biology Vol XVII No.1 - February 1930

CONTENTS

1. INTRODUCTION.

Up till comparatively recent times, bees were kept in hives of various types in which the combs were fixed, beekeepers had little knowledge of what took place in the hives and even less power of control. Loss of colonies was consequently frequent. In England the straw skep was the hive in common use, and the custom was to suffocate a proportion of the stocks of bees in autumn over burning sulphur for the sake of their honey. Natural swarms were necessary to replace those stocks destroyed by the beekeeper as well as losses occasioned by other causes, since the formation of artificial swarms and nucleus colonies are operations which were not general before the introduction of the movable frame hive. Beekeepers of the present day prefer to make artificial increase, to suit their own requirements. Natural swarming involves loss of time to the beekeeper at a busy season of the year, loss of working strength and interruption of breeding in the colony, resulting in a reduced crop of honey, and possible loss the swarm. In modern apiaries, therefore, every effort is made to control swarming or to prevent it altogether.

It is not intended in this review to consider the significance of swarming in the evolution of the social Hymenoptera, nor the possibility of producing strains of bees less prone to swarm, by selection and breeding; but to examine the brood food theory of Gerstung in the light of modern knowledge of the biology of the bee.

2. THE BROOD FOOD.

Honey, a carbohydrate food, is used by the adult bees as the source of heat and energy in the work of the hive, particularly in the production of heat for the maintenance of temperature in the winter cluster, and for the incubation of brood during the early part of the year.

The source of nitrogen (protein) in the hive is pollen, the consumption of which is typical of the growth phase of colony activity. Pollen is consumed by young worker bees; it is given together with honey to the older larvae of the worker and drone castes, and it is used indirectly in the preparation of the special brood food which we are now about to discuss.

In this paper the term 'brood food" is used in the special sense of the elaborated food which is given to the younger larvae of all castes, as opposed to the pollen-honey 'mixture, which worker and drone larvae receive from the third or fourth day onwards.

The fertilised (female) egg is potentially a queen, and will become one if fed throughout its larval existence on the richer food: workers are imperfect females produced under a system of nutritional castration by being weaned from the prepared food at an early age. The age at which the diet is changed was given by von Planta as the fourth day. Nelson and Sturtevant have shown more recently that the change takes place on the third day.

3. COMPOSITION OF THE BROOD FOOD.

The analyses of von Planta make it appear that the food of young larvae differs in composition from that given to those of drones of the same age, and also from the "royal jelly" received by the queen larvae of all ages. Koehler gives figures for fat and sugar, which, differing from those of v. Planta, appear to indicate that the food of the young worker and drone larvae are identical. Aeppler has also made analyses of the royal jelly.

Elser has also studied this problem, but his results appeared too late for inclusion in this paper.

TABLE 1.

Composition of brood food.

(Expressed as percentage of dry weight.)

	Queen (average)		Worker (under 4 days)		Drone (under 4 days)	
	v.Planta	Aeppler*	v.Planta	Koehler	v.Planta	Koehler
Protein	45.14	40.36	53.38	-	55.91	-
Fat	13.55	20.05+	8.38	23.3	11.90	24.23
Sugar	20.39	18.52	18.09	15.7	9.57	14.9

* See note 2 below. + Total ether extract.

1. The term "chyle food," which is often used in England, has been carefully avoided in this paper, for reasons given later.
2. Aeppler's figures were given as follows: "Larval food in air dried condition. . . . Moisture after drying at 1000 24.15 per cent. ; total protein 30.62 per cent. ; total sugars 14.05 per cent. ; total ether extract 15.22 per cent." The figures given in the table are calculated on the dry matter obtained at 100° C. as stated by him.

4. ORIGIN OF THE BROOD FOOD.

Two opposing views have been held as to the origin of the brood food.

(a) The glandular secretion theory.

According to Schiemenz it is a secretion of the lateral pharyngeal glands of the head, which are found in their greatest development in the social bees, and which are physiologically active in those bees that are engaged in nursing the young larvae. This view is shared by Cheshire and by most modern writers.

(a) The regurgitation theory.

This was put forward by Schonfeld and has been championed by Cowan, Cook and others. This theory maintains that the brood food consists of a pre-digested food regurgitated from the ventriculus or so-called "Chyle stomach" of the worker bee. In order to bring this about the honey stomach was said to be capable of being "short circuited" by pushing the stomach mouth forward of the oesophagus. Schonfeld claimed to have brought this about experimentally, but other observers say that such an action is impossible. The supporters of the regurgitation theory base their claim on the fact that insoluble matter such as lamp black, supplied experimentally to bees, has been recovered in the food given to the larvae, whereas no solid matter would pass through the gland. However, this might mechanical contamination of the food," current in this country, easily be brought about through mouth parts. The name "chyle is based on this view[1].

Arnhart[2] seems to adopt an intermediate position by stating that brood food is a combination of regurgitated contents of the stomach with the glandular secretion which reaction from alkaline to acid, the arguments are summarised by Snodgrass in his bulletin on the Anatomy of Honeybee. In his more recent book this is changes this is omitted, for he says: "It is now generally conceded that the pharyngeal glands are the organs which form the brood food or royal jelly."

Langar in 1912 proved by biochemical methods that the proteins of the. brood food are identical with those of the head gland. This is a further strong argument in favour of the secretion theory.

1. The word chyle, used in vertebrate physiology to denote the contents of the lacteal vessels, corresponds to the German Futtersaft. The word Futterbrei, used by von Planta, should be properly translated chyme, and is more appropriate in connection with the regurgitation theory.
2. Quoted by Snodgrass.

5. THE BROOD FOOD THEORY OF SWARMING.

About the year 1891 Gerstung, in Germany, propounded his brood food theory, which he subsequently elaborated in considerable detail, emphasising the view that the bee colony is to be considered as a unit, and not as a fortuitous collection of individual bees. He writes of "Der Bien" as an organism of which the constituent bees are members (organs) carrying out various functions. On this view the queen is the generative organ of the colony, and swarming is an act of reproduction.

Continuing this analogy the brood food may be compared to an endocrine secretion, a surplus of which creates a special condition within the hive leading to preparations for swarming. It is considered that when nurse bees, having the brood glands in a state of activity, exist in excess of the requirements of the brood in the hive, there is a tendency to build queen cells. Crudely stated, it may be said that the surplus is given to certain favoured larvae in order to get rid of it. These larvae develop into queens, and when the cells are sealed the colony is liable to give off a swarm.

6. DIVISION OF LABOUR IN THE BEE COLONY.

The work of Rosch on the biology of the bee has a direct bearing on the brood food theory. He makes the following statement: "Every worker bee is able to undertake all the tasks which present themselves; following - with advancing age - a definite sequence which is the same for each individual." according to him the life of a worker bee may be divided into three periods, which we may call (1) nursery work, (2) house work, and (3) field work. Specialisation such as we find in ants does not appear to exist in the honey bee.

The first duty of a newly hatched bee is to prepare the cells for the next batch of eggs and to do her share of keeping up the temperature of the nest by "brooding over" the developing larvae. From about the third to the sixth day she feeds the older larvae with pollen and honey taken from the store cells. The food glands are developing during this time in consequence of the rich food taken. From the sixth to the tenth or fifteenth day, the food glands being fully developed, she attends to the feeding of the very young larvae which are receiving the prepared brood food. “The end of the brood nursing period is not determined by age. When nurses are scarce it can be prolonged, but in normal stocks it does not continue beyond the 13-15th day. By this time the gland has atrophied again".

The second period begins with the first flight from the hive, the so-called orientation flight. During this period the bee receives nectar from the foragers, ripens and stores it; presses down pollen loads into the cells where they have been deposited and acts as house cleaner. It is bees of this age that secrete wax when there is building to be done. Towards the close of the second period the bee may become a guard at the entrance.

The bee then becomes a forager (third period) and gathers water, pollen, nectar and propolis; she continues at this work until overtaken by accident or old age. The following table compiled in part from data given by Rosch gives the normal succession of duties.

TABLE I Life of a worker bee.

Stage	Duration (days)	Age (days)
Development:		
Egg	3	1 - 3
Larva (unsealed) (weaned on 3rd day) ...	5	4 - 8
Sealed brood	12	9 - 21
Adult bee:		
1st period: Nurse bees		
Incubating brood preparing brood cells	2 - 3	1 - 3
Feeding older larvae with honey and pollen	3	6-10(up to 15)
2nd period: House bees		
First play flight ... ...)		
Storekeeper (receiving, ripening and) storing nectar)		
House cleaner ... ...)	10	10 - 20
Wax secretion ... ...)		
Guard (at the hive entrance ...)		
3rd period: Field bees		
Forager (water, pollen, nectar propolis))	20 - 30	20-40 up to 50

7. THE BROOD REARING CYCLE.

The seasonal activity of the queen has been studied by Nolan and is somewhat as follows: After the winter rest breeding starts on quite a small scale and increases until a maximum is reached early in the season, after which it falls off rapidly, though there may be a secondary peak in autumn.

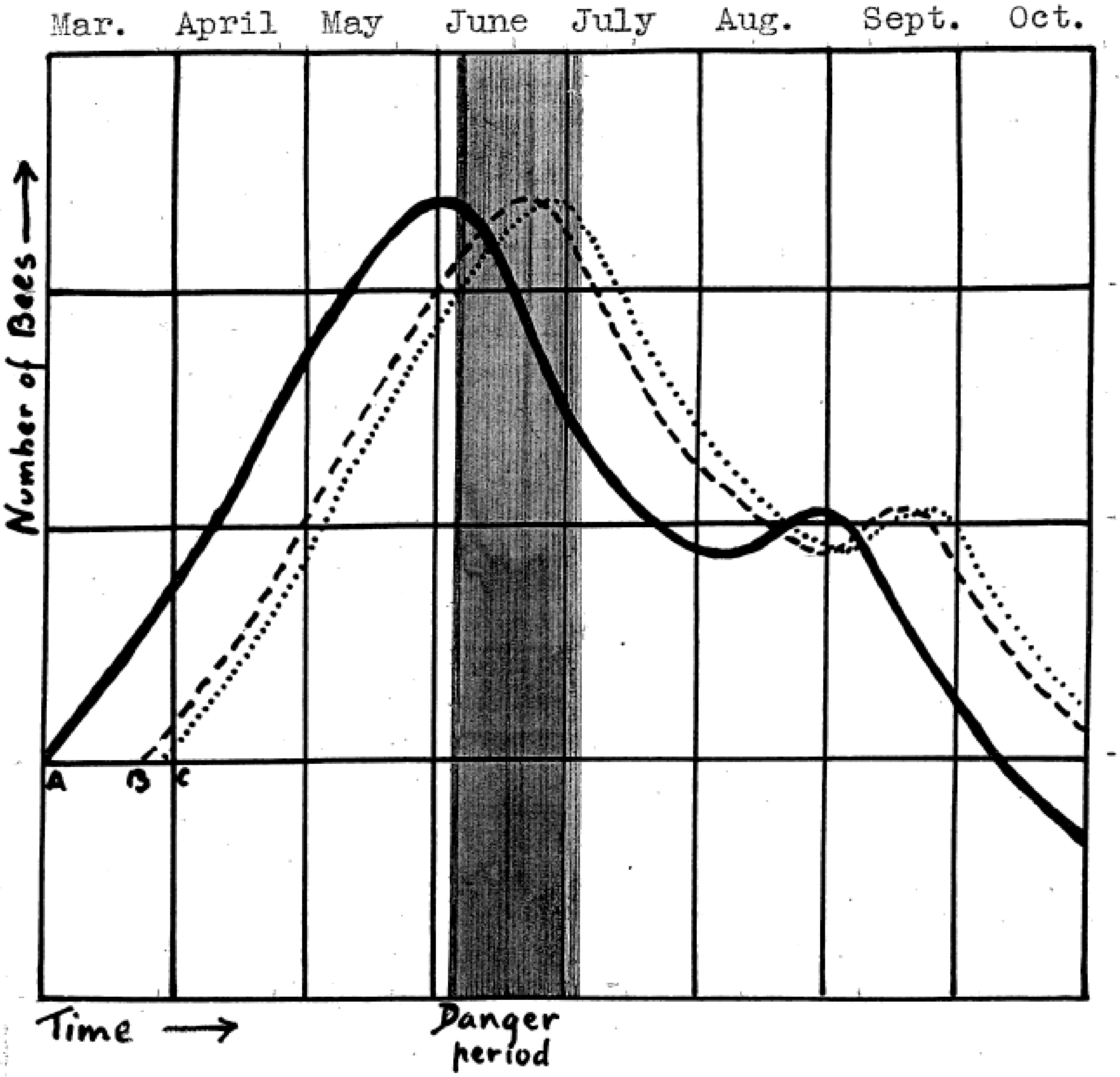

Figure 1 Hypothetical brood curve of a colony of bees (adapted from those of Nolan.

A Egg laying curve of queen rising to a maximum at **D**.

B. Curve of emergence of adult bees; on the assumption that there have been no casualties among the brood.

C. Shows the number of bees attaining the critical age, at which the brood food glands reach their full development. It is evident that the number of nurse bees (**C**) at any given period would be from four to nine times that represented on the curve, seeing that the duration of this period is from four to nine days (see Table II).

8. RELATION OF THE EGG LAYING CURVE TO THE ONSET OF SWARMING.

Assuming that there are no casualties among eggs or larvae, the curve of emerging bees will be parallel with that of oviposition, 21 days later. These bees, according to Rosch, will be at the height of their nursing activities - i.e. at the critical age - in a further 6 to 10 days, that is to say, 25 to 30 days after they themselves were receiving the brood food.

In the early part of the year, as the number of nurse bees and the abundance of brood food in the hive increases, the queen herself receives a share of the prepared nitrogenous food and is stimulated to increase her output of eggs. Thus egg laying increases at a progressively steeper rate until a maximum is reached, which may be determined by the fertility of the queen, by the capacity of the brood chamber of the hive, or by some factor which we do not yet understand.

The egg laying curve then begins to fall off, and, parallel with it and four days later, the curve of young larvae which are receiving the brood food. The curve of emerging bees, and that of bees attaining the nursing age, continues to rise, resulting in an increasing surplus of brood food for which there is no outlet. This leads to the construction of the queen cells, which will contain larvae capable of absorbing relatively large quantities of brood food.

9. VARIATIONS IN CYCLE OF DUTIES.

Rosch speaks of the division of labour as being flexible, without a hard and fast time schedule. Moreover, it is recognised that autumn-born bees are capable of raising brood and even Queens in the following spring. When there exists in the hive a need for bees to carry out certain specified-duties, it would seem that other younger beet are drafted on to the more mature tasks. Thus, while there is work to be done which properly belongs to the second period, nurse bees will continually be promoted to store-keeper or wax worker, while a need for foragers (third period) will produce vacancies in the ranks of the second period bees, which will, in their turn, have to be filled. Beekeepers know the kind of hive which is "too busy to swarm", and they are also only too familiar with the effect of enforced idleness, due to bad weather supervening when strong colonies have been built up for the harvest. It is commonly stated in books on beekeeping that a condition which leads to swarming is "congestion of bees in the brood nest." Now the bees which chiefly frequent the brood nest are those whose duties take them there, in other words, the brood nurses. This statement is therefore tantamount to saying that swarming is due to a superabundance of nurse bees, and therefore of brood food.

10. VALIDITY OF THE BROOD FOOD THEORY.

Even if the regurgitation hypothesis of Schonfeld were eventually proved to be correct, as Gerstung himself believed, this would not invalidate the brood food theory. Rosch and Soudek have both shown that the pharyngeal gland reaches its greatest development at the time when bees are engaged in brood feeding. It might be argued that this gland is merely concerned with the digestion of protein, at a time when bees are consuming large quantities of pollen for the elaboration of brood food.

11. "CONTROL BEES".

The idea has been put forward recently in America that the policy of the hive is determined by bees of between 14 and 21 days old. Whereas young bees are devoted to nursery duties, and old bees are fully occupied with foraging, these bees of middle age can turn to any task. These latter are the entrance guards, the scouts and the bees which compose the swarm. An abundance of such bees is the factor which decides the-issue of a swarm. They have been called 'control bees". It will be seen that these are the bees of Rosch's second period. It will also be obvious that the surplus of nurse bees of "critical age" which led to, the starting of queen cells, by the time the cells are sealed and the colony is ready to swarm, will have become a surplus of bees of the second period, i.e. "control bees". The fact that these bees are also of the age to secrete wax, and before coming out have gorged themselves with honey, accounts for the facility with which comb is built by a swarm.

12. SWARM CONTROL MEASURES.

The measures of swarm prevention, which are advocated on the recommendation of practical experience, mostly depend for their efficacy on manipulations which have the effect of removing some of the nurse bees from the brood nest. Conversely those conditions which lead to a surplus of these bees in the hive bring on the swarming fever.

(a) Capacity of the brood nest.

Restriction of the brood area, by causing a sudden drop in the oviposition curve when the limit is reached, aggravates the danger period following the peak of egg laying, and leads to swarming (Fig.2). This may be brought about by restricted hive accommodation, through the presence of unsuitable comb composed of cells unfit to contain brood, or by a rim of sealed honey which prevents expansion.

(b) "Building up" period.

"The tendency to swarm is greatest in those localities in which the bees increase brood rearing most rapidly in spring…during those years when the bees build up in the shortest interval in spring…in those colonies which reach their peak of brood rearing most rapidly". It will be seen on reference to Fig. 2 that the more rapid the rise just before reaching the peak, the more acute will be the surplus of nurse bees immediately following it. One of the advantages of spring protection is that brood rearing increases at a steady rate without fear of checks due to spring frosts. Contrast with this the hurried brood rearing of an unpacked hive, starting late and increasing rapidly to a peak. In this connection it has been claimed that one of the benefits of spring protection lies in the absence of checks in the upward trend of the brood curve, which are said to be reflected afterwards in a tendency to swarm. A check in the upward curve of egg laying before the maximum has .been reached will be followed in four or five days time by a surplus of brood food, owing to the absence of larvae to feed. This surplus being supplied to the .queen would lead to a spurt in the egg laying, followed in about thirty days by a corresponding excess of nurse bees (see Table II and Fig. 3).

(c) Effect of honey flow.

The advent of a honey flow, beginning just before colonies have reached swarming point (the critical stage) may cause colonies to divert their energies to foraging, to the neglect of swarming. This simply means that bees are promoted from house bees to foragers, and the house bees are in their turn recruited from the ranks of the nurse bees, while there is work for plenty of house bees to do in the supers, away from the brood- nest, starting and ripening the honey and providing wax for cells and cappings to contain it. On the other hand, a spell of bad weather, confining foragers to the hive, delays promotion and allows nurse bees to accumulate.

(d) Wax secretion.

Conditions which impel the bees to build comb provide work belonging to the second period to which nurse bees can be promoted; at the same time removing them from the brood nest. The mere provision of space or sheets of foundation is not always enough to bring this about. Simmins says that bees will not swarm until there is comb reaching to the entrance of the hive. He therefore advocates providing for comb building below the brood nest as a measure of swarm prevention.

(e) Effect of age of queen.

Colonies headed by young queens are apparently less liable to swarm than those that have old ones. The influence of the young queen began in the previous season, when she continued brood rearing later into the autumn so that the stock went into winter quarters with younger bees. In the new year the young queen starts earlier and increases the brood nest at a steady rate, being less liable to be put off by conditions which would cause a check in the oviposition of an older queen.

(f) Removing bees and brood.

It is not an uncommon practice to make nucleus colonies or artificial swarms from stocks which might be expected to swarm. By so doing sealed brood (which will require no more feeding, but will shortly give rise to nurse bees) and bees from the brood nest (nurse bees) are removed from the parent colony, the result being the same as the check in the emergence of young bees, which results after the departure of a natural swarm. Thus the colony is immediately put into the condition of a colony that has swarmed: there is no surplus of bees of critical age, and the impulse to raise queen cells no longer exists.

(g) Separation of queen and brood.

Most systems of swarm prevention are based on the separation of queen and brood. To this class belong the Demaree system and its modifications, wherein the queen is placed below a queen excluder and the brood above. This has the effect of removing the restriction of space on the activities of the queen. Part of the emerging bees is kept above the excluder to care for the brood, and there is less congestion of nurse bees in the part occupied by the queen. Queen cells are liable to be built above the excluder, but the apiarist expects these and takes care to destroy them.

(h) Influence of drones.

The rearing of excessive numbers of drones has been condemned as an expensive luxury, but it might be well to bear the following aspect of the matter in mind. The presence of drones in a hive undoubtedly has some effect on swarming, probably in ways not directly connected with the brood food theory. The production of drone brood and ministering to the food requirements of the drones themselves provide an outlet for brood food, which does not lead to the production of yet more nurse bees.

(i) Influence of temperature and ventilation.

Excessive heat and lack of ventilation are conditions leading to swarming. It may be that these causes operate directly, or it may be that they stimulate physiological activity of the food glands, just as warmth is necessary for wax secretion. In many cases they are symptoms of the congestion of bees in the hive, which is itself the cause of the desire to swarm.

13. SUMMARY.

1. The influence of nitrogenous food in the hive is discussed in its bearing on the question of swarming.
2. Theories of the origin of the brood food are examined.
3. The division of labour among the bees of various ages is considered in its relation to the brood rearing cycle.
4. A critical surplus of nurse bees is found to be associated with the formation of queen cells in preparation for swarming.
5. Recognised swarm control measures are reviewed in the light of brood food theory.

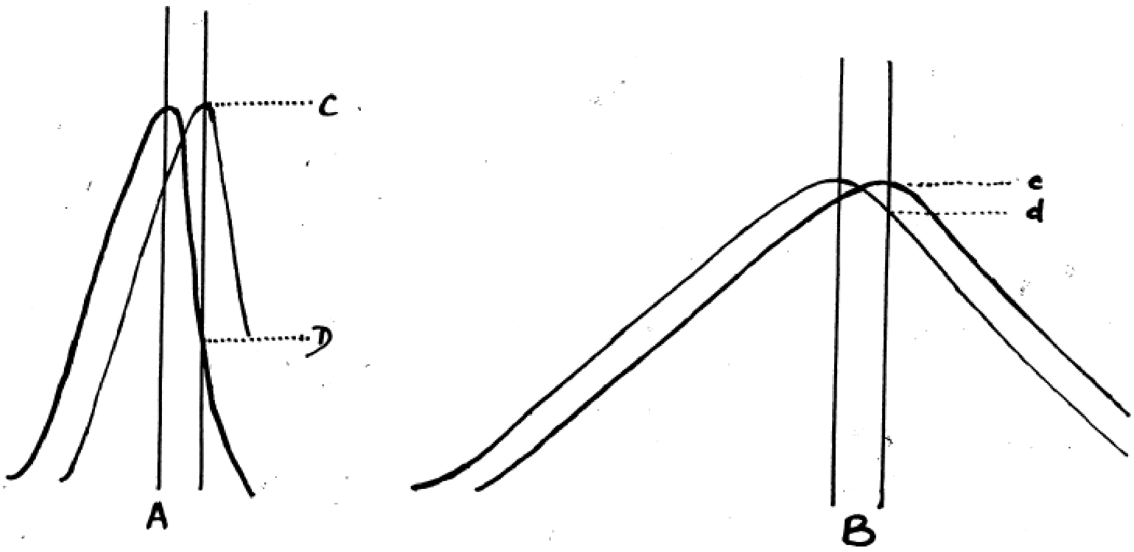

Figure 2 Effect of shape of brood curve at its maximum on the tendency to swarm.

A. A rapid fall from the maximum of egg production, giving rise to strong tendency to swarm as indicated by the surplus of nurses-over egg production **CD**.

B. Brood curve falling off gradually from maximum, producing a less acute surplus of nurse bees and consequently a less marked tendency-to swarm as indicated by the vertical distance **cd**.

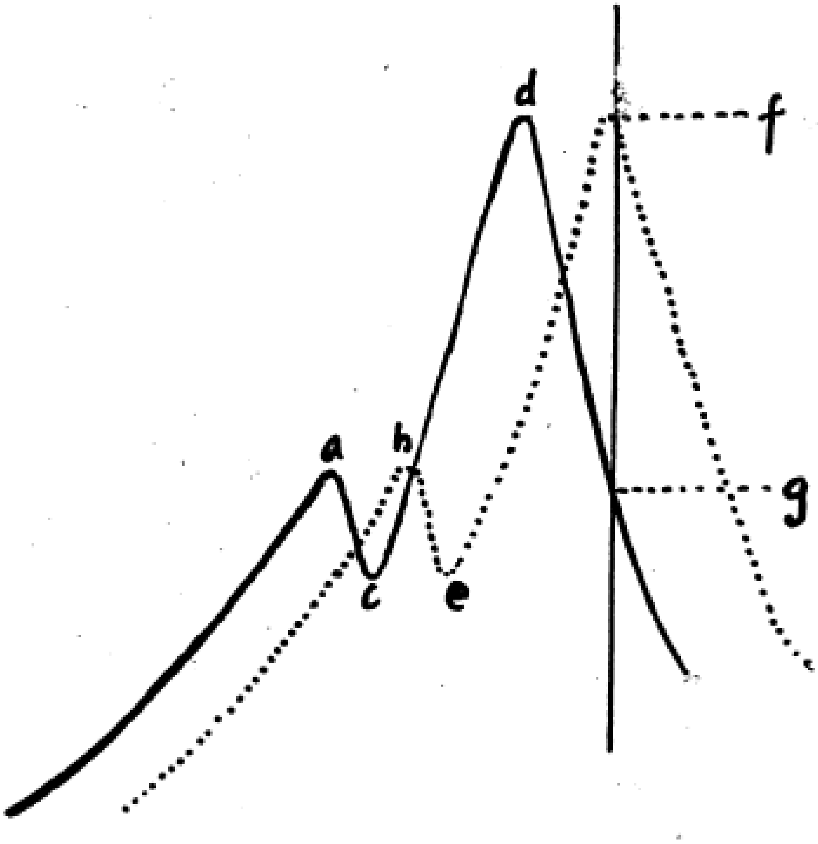

Figure 3 Effect of a brood check in spring

Effect of check in spring brood rearing (at **a**), producing a temporary surplus of nurse bees at **b** which stimulates the queen producing a sharper rise in the brood curve **cd**. The falling off of nurse bees **be**, if it coincides with the peak of egg laying **d**, would hasten the decline of the egg curve, and produce a critical condition represented by the vertical distance **fg**.. (Black = brood; Dotted line = nurse bees.)