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South African "Fertile-Worker Bees."

By G. W. ONIONS.

In the *Agricultural Journal* of November, 1909, an announcement was made of my discovery that laying workers of the native honey-bee are more common than is generally supposed, and that their eggs usually give rise to workers and will produce queens.

Since this statement appeared sufficient time has elapsed for observant beemen to have put it to the test, and some no doubt who have been induced to investigate the subject have obtained conclusive evidence for themselves. A detailed account, therefore, of the observations and experiments which led to these conclusions is now more likely to meet with due appreciation. The first part of this article dealing with the subject was prepared for insertion in the *Journal* in October, 1909, the publication of which it was thought advisable to defer for a time.

"Bee parthenogenesis in the production of drones, and drones only, is regarded as universally true. It may be, however, that the ability to produce males only is but a modified form of parthenogenesis peculiar to the few varieties of bees that have come under scientific observation in this connection, for the rule as understood in its application to German and Ligurian bees does not appear to be altogether without exceptions. Instances have been reported from time to time in the various bee journals of the unaccountable presence of queen cells in queenless colonies, and the reason usually assigned for this, namely, that bees probably purloin eggs from other hives, is far from being a satisfactory one. With African bees, on the other hand, the production of females without male impregnation (i.e. impregnation by a drone) appears to be the rule to which male development is the exception.

"As a practical beekeeper and queen breeder who has always endeavoured to verify in his own experience the facts and theories of bee culture, I submit the following observations and conclusions regarding the faults and faculties of African laying workers:—

"One day in 1901 I found the queen of one of my colonies on the outside of the hive surrounded by an interested group of three or four drones. This was a young queen, and the reason for her being found in this unusual situation was the fact that I had clipped her wings a day or two previously under the impression that she had mated, whereas she had not, though the presence in the hive of hundreds of eggs fully justified my mistake. This was the beginning of my acquaintance with laying workers, but I need hardly say that before I was able to realize how matters stood I had begun to find out that our bees differ from those described in bee literature. One of the doctrines of bee culture is that bees will not tolerate a fertile worker while a laying queen is in the hive, except in rare instances. With

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African bees, however, in contrast to European races, laying workers are always present, if we may judge from the facts (1) that in queen-right colonies the old queen cell bases almost invariably contain many workers' eggs (a condition supposed to be a sign of queenlessness), and (2) that workers' eggs have frequently been found in combs above a queen-excluder with a laying queen below.

"But to give an instance of the assiduity of these little pests of the apiary, I will describe a particular experience:—I removed a frame of bees and the queen from one of my Golden Italian colonies to an observation hive for exhibition at Rosebank Show. The following day I returned the frame to its hive, taking the precaution to protect the queen with a pipe-cover cage. Next day I liberated the queen, and she was well received; but on looking over the combs for queen cells I found an African laying worker. That she was a pseudo queen was evidenced by her demeanour and by the peculiar attentions of the surrounding bees towards her. It should be noted that this Italian colony occupied a separate part of the apiary, and was well out of the range of flight of young African bees in orientation, that it was at a time when the honey flow had ceased and there was a strong tendency for bees to rob, and that Italian bees guard their entrances too well to let ordinary strange bees in. This laying worker was positively the only African bee present in the hive. Perhaps I should remark that the contrast is so striking between the little dark African bee and the larger Golden Italian that an African is conspicuous amongst 'goldens.' I mention this case because there were no other queenless bees in the apiary at the time, but where a laying worker colony (or queen-right African colony for that matter) exists they are apt to throw laying workers into other hives and thus become a menace to the welfare of the apiary and a fatal obstacle to queen-rearing operations.

It is no doubt a fact that bees on the 'let alone' policy seldom allow the laying worker tendency to predominate, but owing to the natural irritability of the African bees the least amount of handling necessary to artificial methods is apt to get them demoralized. For instance, if a hive swarms and it is left absolutely untouched it will generally succeed in having a laying queen in due time, but even when left entirely alone I frequently find the dead queen outside the hive about ten days after hatching. Supposing that we divide the colony into nuclei, we may be almost sure of finding the dead queens about mating time. Two seasons ago I tried hard to get some queens reared from imported stock. I succeeded in raising several dozens of fine queens, and with very few exceptions got them safely introduced to nuclei, but the majority of them were found dead in front of the hives at about the time when they should have commenced to lay. I have given up trying to get queens mated in African bees, and am careful not to have any laying-worker hive about when queen rearing is proceeding.

"I will here describe an experiment. On 27th September I prepared two baby nuclei, which I will call A and B. They were each composed of about 400 African bees on three 5 in. by 4 in. frames containing honey and pollen. The same evening a one-day-old English virgin was given to each. By 18th October both these nuclei had eggs and brood, but neither queen had mated. I then prepared another 'baby' (C), composed of English bees, took the queen from B and gave it to C. By the 21st she began to lay. On the 24th

A's queen was still unfertilized, and I gave her also to a nucleus of English bees; by the 27th she was laying. Now, I must explain that my strain of English bees are usually slow in mating, but why was there the extra long delay in this case when everything was apparently favourable? May it not have been on account of lack of inducement from the bees? If so, was it not because these Africans were too well satisfied with their laying workers? The answer to this question may perhaps be found in the sequel to this case, which will appear when I refer to these nuclei again, as I will do later on. If the queen is removed from a hive, laying workers' eggs will appear in two or three days, but if deprived of brood as well they will be found in twenty-four hours. These laying workers appear in great numbers. I once counted over a dozen of them in the act of laying at the same moment. This point is further evinced by the large numbers of eggs produced by them. I should say that four is about the average number per occupied cell in a colony of average strength, and I have frequently found as many in the same hive as would, if singled out, fill three or four sides of a Hoffman frame. In order to prove that worker bees actually do lay eggs I deprived bees of queen and brood and confined them to the hive with wire gauze; though they did not begin to lay so soon in confinement as they otherwise would, eggs were found within a week.

"Another dogma of bee science is that eggs laid by laying workers invariably produce drones—this rule does not apply to African bees. Obviously, African bee-laid eggs either do or do not hatch! This was how the matter presented itself to me at the commencement of my bee-keeping experience, until now, for the first time, I had occasion to form my own conjectures. I had endeavoured to verify the statement that they invariably hatch drones, but all I can say with certainty is that occasionally a drone is produced in laying-worker hives. African workers' eggs, then, not only do not invariably hatch drones, but, broadly speaking, it may be said of them that they do not produce drones.

"Bee-laid eggs do hatch, however, and in order to prove this I hived queenless bees on clean combs, where they produced eggs and hatched them in segregation. It is a characteristic of 'fertile workers' that they lay several eggs in a single cell, and therefore a common sight to see four or five little larvae lying huddled together until, as they grow larger, all but one are removed by the bees. The majority of bee-laid eggs never hatch, and such as do are usually selected haphazard; for, as a rule, the nursing instinct is deficient in laying-worker hives, though I have seen laying workers' broods that none but an expert would have known from the work of a queen. I have had scores of laying worker colonies in my experience, and every one of them produced eggs which hatched, the bees developing from them being almost invariably workers. The conclusion may easily be drawn that if worker-laid eggs develop worker bees they must also be capable of producing queens. Practical observation has borne out in scores of instances in my experience the correctness of this deduction.

"On the 14th November, 1908, I took a weak laying-worker stock that had reared two or three worker-produced queens in succession and destroyed them, putting them into another hive fitted with shallow frames containing starters only and a feeder. On the 16th they had worker comb built which contained eggs. On the 27th they had

capped worker brood and four queen cells. On 9th December three of the queens were picked up near the hive, while the other was found in safety within. I may mention the fact that no drone comb had been built. African queenless bees, if they build comb at all, invariably build worker comb.*

"On 10th September I formed a strong nucleus (No. 49) of queenless and broodless bees on empty combs, and one—a nice, complete new comb—I marked. Next day I inserted a strip of comb containing Golden Italian eggs and larvae, queen cells were built, caged as soon as capped, and all hatched. They were removed from the hive on the 23rd. By this time they had a quantity of workers' eggs, some capped brood, and an open queen cell on the fourth frame from the one where the queens had been reared. This cell afterwards hatched an African queen. On the same date (23rd September) I removed another hive (No. 45), a strong, double-storeyed hive, to a new stand. I then removed the upper part of the hive (which was separated from the lower by a queen-excluder) containing honey, capped brood, and one frame of advanced open brood, back to its former stand. On the 25th I examined them and found six queen cells on the open brood comb. The cells contained larvae too large for making good queens, there being no very young larvae anywhere that I could see. I then extracted the larvae from all the queen cells and grafted them with newly-hatched larvae from the marked frame in No. 49, which by this time was filled throughout with workers' eggs and larvae, taking care to select the smallest I could find, where they had hatched together. I took four of them from a single cell. I watched the larvae develop, examining them frequently during the first two days to see that the bees did not exchange them for others, and satisfied myself that they did not. Four out of the six cells were completed and hatched queens. Now to return to the baby nucleus (A) before mentioned. It is to-day, the 29th October, hatching worker bees and has just started a queen cell."

At this point the account ends, but I find on referring to my notes on this case that the two English queens both proved to be drone layers, confirming my statement that they had not mated. The nuclei A and B were united and left to their fate. They did not succeed in maturing their queen cell, which was not to be expected of so few bees, and soon disappeared. A laying-worker colony seldom succeeds in getting back to a normal condition, notwithstanding that it can raise workers and queens; for the rule is that, according to its strength at the beginning of fertile-worker control, and probably through the influence of other factors as well—such as season, pasturage, etc.—it will last for several weeks or months and gradually dwindle down to the last bee, or, as often happens, the last remaining handful of bees will desert the hive and form a little cluster on some hedge or bush near by and there perish. But the exception to the rule, i.e. for them to succeed in getting a laying-worker-produced queen, is impossible while active laying workers are in full possession, and can only occur when a colony, strong at the commencement of laying worker control, after raising several queens in succession and destroying them has managed to outlive the laying-worker faculty while still strong enough

* According to Dr. C. C. Miller, "Queenless bees, if they build comb at all, invariably build drone-comb."

to breed a queen, or before their latest attempt was hatched. Without any record of the number of queens which I have known to have been bred in long-queenless bees—a fact which cannot be accounted for by any known theory of bee culture—I venture to say that there would be at least a hundred, and yet I only know positively of three cases in which these bees ultimately mated a queen of their own making. Queens from workers' eggs are comparatively small and inferior looking. This may only be due to poor feeding. In the three cases just mentioned they were superseded in the same season.

The "fertile-worker" energy of a colony weakens in time, and, in some cases, almost disappears. There are many probable causes for this, I might mention, but I will merely state the fact as I have found it. *The falling off of laying-worker activity is accompanied by the appearance of a few diminutive males.* I will here mention that, incidentally, the restriction of drone comb with foundation imported or made on imported machines does not repress the laying of drone eggs by the queen, as the foundation suited to European bees results in cells measuring one-fifth larger in diameter between parallel sides than cells built naturally by African bees, and are frequently used for raising drones in the absence of drone comb. The size of the cells may sufficiently account for the smallness of the drones reared in them, but does not check the inclination of a queen to lay drone eggs, nor does it influence the sex of laying-worker progeny produced in them. It is remarkable that laying-worker colonies, in all their efforts to raise queens, do not build their queen cells upon old cups. If any such are in the hive they are sure to be packed with eggs which never seem to hatch, nor are their queen cells ever specially prepared, as in the case of swarming. Invariably their queen cells are built over young larvae in worker cells on the surface of the comb. Any condition which impels a colony to construct queen cells, as the removal or caging of the queen, failure of the queen through age or debility to lay eggs in sufficient number, or congestion of the hive with stores or brood, is certain to be accompanied by the appearance of active laying workers. The following instances, taken from my record book, will serve to illustrate some of the foregoing conclusions.

History of nucleus No. 47: A box hive of bees purchased in the near vicinity of my out apiary was transferred to a frame hive and left on the spot. Later, it was removed to the apiary enclosure, and a frame, containing mostly advanced brood, in a nucleus hive was left in its place for returning bees. This nucleus (No. 47) was brought to my home apiary a week later. At this time it was examined, and a couple of queen cells were found and destroyed. Workers' eggs were in evidence, and another nucleus containing a laying queen protected with a pipe-cover cage was united to it. After the queen was with due caution released, she was killed by the bees. I found her outside the hive. A week later a queen cell was started which, in due time, hatched a queen. Ten days later this queen was killed and thrown out; she had not mated as I found on dissection. Eight days later (this was 18th September) there were queen cells again. On the 22nd I destroyed the queen cells and united the nucleus (No. 47) with No. 50. No. 50 had been brought in from my out apiary on 15th September. The following day I had removed the queen and given the bees a frame containing partly drawn ~~new~~

comb with hatching eggs from an imported English queen and twelve cell cups grafted with larvae from the same comb. Eleven of the grafted cells had been accepted and eight built on the comb. On the 22nd I caged all these queen cells and united nucleus No. 47, as before stated. By 27th September all the queens were hatched, and on that day I found another queen cell started on the comb of English brood. I then divided the bees, leaving the caged queens with No. 50 and taking the other half, which I again called No. 47, with the new queen cell to another stand. All the young queens were placed in nuclei between the 28th and 30th. On the 30th, also, No. 47's queen cell was capped. On 1st October No. 50 was found to have three queen cells started over their own worker larvae. All of these queen cells hatched queens. The queen cell in No. 47, on the frame of English brood, hatched an African queen. There were no drones raised in either of these hives.

Another case: An Italian queen in a small nucleus of her own bees was given hatching brood of African bees and fed regularly. Although not twelve months' old, and apparently a fine queen and laying, she was picked up dead outside the hive three weeks after giving the first African brood. The cause of this is apparent in the light of my experience with imported queens, but is not relevant to the *subject in hand*. Looking into the hive at this time, I found three queen cells just ready for capping. These cells were extended worker cells, and there was unmistakable evidence of laying workers on one of the other combs. The two cells were caged as soon as capped, and immediately more cells were started on the comb occupied by laying workers. These latter cells hatched African queens, the first three resulting in Italians. African worker bees, but no drones, were reared from the laying-worker eggs.

Having several Italian queens in my apiary has afforded me much interesting experience, reference to which will only be made for the sake of elucidating my subject. I might here mention one experiment suggested by an incident given in the early part of this account. An African laying worker, introduced as a queen to a few Italian bees, was accepted as such, and produced African worker bees.

Here is another account from my record book: On 30th November a colony having an old queen was found to be superseding. I removed the queen and part of the bees into a nucleus hive; 15th December I found a capped queen cell, and on 27th December a virgin queen, the old one still being present. There were also unmistakable signs of laying workers. I was satisfied of this, though at the time fully aware of the statement often met with in bee writings that the ovipositing of a worn-out queen may closely resemble that of a laying worker, a statement very rarely verified in African beekeeping, however, because usually the queen is superannuated by the bees before this stage is reached. But to proceed with this case. Four days later I found the old queen thrown out dead and the young one still in the hive. On 1st January she was missing. At this time I captured a laying worker and dissected it, finding the ovaries well developed and showing a number of eggs ready for laying. 3rd February I searched again for the queen without success. The capped brood in the hive then consisted of workers and a few drones, and they were running very short of stores. On 18th February the remaining bees were only sufficient to have

(2) Possibly an African queen was introduced into the colony...

properly covered one side of a Hoffman frame. The brood was reduced to a small patch on either side of one comb, still hatching workers, and a few very small drones. There was also a queen cell just started and I found it necessary to feed. 26th February the bees had dwindled down to about two hundred, carefully estimated. The queen cell had been abandoned before capped and the base of it contained about twenty eggs; besides these I could only find two other eggs. There was nothing in the larvae stage, and of capped brood there were thirty-seven, all in worker cells. I lifted the cappings off all of them, six being dead, and the sex undistinguishable. Of the remainder all but three were in the nymph stage, the heads well developed, and the drones easily distinguishable from the workers. Some of each were ready to hatch. I counted fifteen workers, the rest being drones.

Here is another interesting case: A colony being unquestionably queenless, raised and destroyed three successive batches of queens, producing worker bees all the time, but no drones. I divided this hive (a ten-framed "dovetailed" hive) into three bee-tight compartments with separate entrances. Each section of bees continued egg laying, and each of them had one or more capped queen cells within a fortnight. The queens hatched and I saw them all daily until they were destroyed by the bees, between the eighth and tenth days after hatching. Worker bees were hatching continually in all compartments, but no drones appeared. I then reunited the three lots, after which they raised two other queens in succession, destroying them as before. By this time the stock had dwindled down to about one frame of bees, very few eggs could be found, and several days passed without any further attempt at queen rearing. After this I took no further notice of them, expecting them to abscond or die off quickly. But something happened which altered the fate of this lot. I had occasion to move four colonies standing in this part of the apiary, which was in danger of being swamped, to higher ground, and quite a swarm of stray bees from the moved hives found their way into my derelict. When I examined them a day later they had started a queen cell; I saw the queen after she had hatched, and the next time I looked into the hive to my great surprise found her laying.

On 12th January, a hive containing an African-mated Italian queen was taken to my out apiary. I first examined it on the 28th, after having picked up three dead queens outside the hive on that day and five on the day previous, but did not find a queen. Four times after this I examined carefully, and, again, on 26th February, without success.

There was at this time, however, a large amount of laying-worker brood and eggs scattered throughout the hive. No sign of any attempt at raising another queen could be found, although some old queen-cell cups contained clusters of eggs. Under 12th March my record reads: "Examined thoroughly for queen or queen cells; none found; nearly all brood is in the capped stage, and consists of worker brood with the exception of a couple of dozen drones. There has been very little honey coming into the apiary since this colony was brought here. No queen-right bees would raise drones under present conditions. The drones appear in a small patch of old drone comb, and a peculiarity is that the majority of these drone cells contain

(5) Perhaps a queen

(6) None seen in the hive

workers." 14th May: "Several examinations have been made since last date, and the proportion of drone brood has gradually increased, but is confined to one frame scantily filled. There are now two capped queen cells, one built over an old cell cup, the other an entirely new cell." 21st May: "One queen cell which was put under a pipe-cover cage hatched an African queen, which was found dead. The other appears to have hatched normally. Queen could not be found. Very few bees." Here is another exception to the rule that the eggs of African workers develop females. Exception also in respect to several particulars, viz.: (1) The unusually long interval between the first attempt to re-queen and the subsequent ones; (2) the comparatively early production of males; (3) the manner of their appearance (i.e. in a small patch of old drone cells contained in the centre of a frame of worker comb, and the disorderly mixture of drones and workers, mostly workers); (4) the building of a queen cell over a previously used one; and (5) the erection of an entirely new queen cell. It should be remembered that this was a hybrid stock, and any diversity of result may have been on that account. The ability to raise workers from workers' eggs was evidently imparted to it by the cross. In respect to point (3), however, the disorderly mixture of occasional drones amongst worker larvae in drone cells added to the facts previously ascertained, that laying-worker colonies from the commencement to the end of their career never build drone comb although they build worker comb readily and that drone comb given to them fails to encourage drone production, points to a lack of incentive to raise males if not due to inability to do so in the early stage of their history. I must mention one or two very significant facts in connection with this subject. In European bees it has been thoroughly demonstrated that laying workers produce drones only, and that they do very often build queen cells, but these always contain drones which fail to develop fully. I leave the question for others to decide whether the occasional production of queens under similar conditions as sometimes occurs are genuine exceptions to the rule, or correctly attributed to the resourcefulness of the bees in stealing eggs from other hives. In African bees, when a normal queen has been removed from a hive amongst the first batch of queen cells resulting, I have often seen queen cells built over drone larvae in transition cells, and once I took a fully developed but dead drone out of a capped queen cell. But I have not met with a single instance of a drone from a laying-worker egg being reared in a queen cell found in a laying-worker hive.

It has been found possible with some strains of bees, under favourable conditions, to keep two or more queens of a certain age working together. Always keen on following up anything new relating to bees, I pursued this matter with interest and made many experiments. Well, I have found that several old queens will live peaceably together, and in the same hive two or three may manage to provide eggs enough to satisfy the bees and so avert supersedure and the laying-worker tendency, but a young blood or a queen in her prime will not endure the presence of another under any circumstances, and bees dominated by laying workers, or the laying workers themselves, will not admit a strange queen at any time. I have tried repeatedly to introduce laying queens to them by every known method, and by methods of my own, without success. As to mother

and daughter working together, I have seen several instances of this in my bee experience, but it was only a matter of days before the old queen disappeared. As to the possibility of swarms entering queenless hives, I merely state the fact that at my apiary at Retreat during the three years when most of these observations were made, I had only one natural swarm issue from my own hives, and not a single swarm came my way although I had decoy hives out for a great part of the time. The probable reason for this is that there were very few bees in the neighbourhood, that the honey flow there is confined to two months of the year, and that the time referred to was a succession of poor seasons.

In conclusion, I wish to say with regard to the detailed instances here exemplified that they are taken from records of observations and tests purposely made and preserved as being illustrative of many other similar occurrences during the twelve years of my study of bees. It must not be supposed, therefore, that these are solitary instances. Since these particular cases occurred I have dissected numbers of fertile workers. By constant practice I have acquired ease in detecting them by other signs besides the act of ovipositing, and whenever I have pronounced laying workers present I have generally managed to secure one or more of them and confirmed my convictions by dissection.

In presenting these views for the first time I have carefully refrained from introducing any theories or opinions of my own, confining my account to a plain statement of facts which observation and experience have enabled me to detect.

Salisbury, Rhodesia, March, 1912.