THE FORAGING BEE. HOW SHE FINDS AND EXPLOITS SOURCES OF FOOD

Prof. K. von FRISCH, Nobel Prize

Honorary Member of APIMONDIA, FRG

Three noted scientists were awarded in October 1973, the Nobel Prize for Medicine for 1973. Their research and findings refer to animal behaviour. One of them is Prof. Karl von FRISCH.

Already in 1920, Karl von FRISCH, now 88 years old, published studies about the behaviour of the honey bee. Since then, his research has provided significant evidences about the sense of orientation of this social insect, about communication inside the hive, about bees' language.

The bee became thus the first animal, after human beings, to have a code language which it can decode. The scientific world first, and then ever broader circles of people have considered, appreciated and wondered about the unexpected capability of an insect; the newly discovered behaviour pattern was yet another proof of the through unity of the living world.

In his scientific papers, Prof. von FRISCH substantiated and advanced the fundamental principles of his discoveries. In his books he described – in the fullest and most noble sense of the world – his findings, the reality.

In his tireless research he was constantly concerned with fundamental aspects of bees behaviour, and the results obtained as many lessons for common people. Nothing is more illustrative than his books, of what he wrote once: "A through research always rises more problems than it elucidates".

He was a teacher in the true sense of the word; he founded a school, has students, has disciples. For Prof. von FRISCH, the bee was both the object and instrument of his activity. His studies provided knowledge to beekeepers, and brought acknowledgement to apiculture. The bee dance has been considered an amusing oddity by the outsiders, for a long time; its importance for ethology and the acknowledgement of its value by the recently awarded Nobel Prize made it one of the most significant knowledge of mankind. The bee has also been promoted officially to a higher stage in the range of values. Our apicultural world owes respect and gratitude to the author of such changes.

We avail ourselves of this opportunity to congratulate him for the natural way in which he won, for himself and for the bee, by over 50 years of work, the highest distinction of the contemporary world.

In 1969 Prof. von FRISCH honoured by his presence the XXIInd Congress of APIMONDIA held at Munich. All participants and APIMONDIA rendered homage to the distinguished pathfinder. We are most pleased to publish again the lecture given by him, a Honorary Member of the International Federation of Beekeepers' Associations, in August 1969.

Of all the creatures on earth the bee is perhaps the most beloved. Sung by poets, cared for by beekeepers, studied by scientists and admired for its achievements, the bee is also popular with many people simply because they like honey. The beekeeper sees his bees mostly at home, and he watches keenly to see whether they gather a good harvest. It is less obvious how the harvest is won, and this is what I want to talk about today, as far as time permits. So we shall accompany the bee on her foraging flight.

What is the origin of the world *Tracht* used by German beekeepers, and what does it mean? The noun *Tracht* is derived from *tragen* and, like this verb, can mean two things. Apple trees *tragen,* i.e. they "bear" apples; gardeners gather these apples and *tragen,* i.e. "carry" them home. In the language of beekeepers *Tracht* is also used in a twofold sense: for the product of the flowers and for its transport home by the bees. [In English the word "flow" has a similar dual meaning.] Probably you do not know that a thousand years ago the world *Tracht* was also used for the food set on the table: a three-course dinner was a meal with three Trachten. This meaning did not become obsolete until the nineteenth century.

Let us now turn to the bees. After emerging from the brood cells they sped their first two weeks in the hive, engaged in nursing and other domestic activities. Only then are they ready to forage. In a normal colony in the spring there is such rapid increase in the number of young bees that about a thousand a day mature to begin their foraging flights. It would, however, be a great mistake to think that these thousand young bees, eager for work, set out daily to find suitable flowers. Only a very few do this; the majority remain lazily in the hive until they are summoned to a certain type of work by the dances of their fellows. Scout bees which find new sources of food – the pioneers – are few in number. This is one of the many parallels between the bee colony and human society. Scout bees are attracted by the colour and the scent of flowers, as we can see if we place an observation hive in a large flying space which contains only what the experimenter has provided. Scout bees will settle on flowers, but also on coloured or scented pieces of paper. Any colour that bees can perceive, and scent reminiscent of flowers, will exert an attraction. Although many bees are flying around, only a few may approach the bait, and this will continue as long as they find nothing there. The situation is the same, for a free-flying colony. Lindauer numbered some hundreds of bees on the day they emerged and carefully noted their activities. The transition from house duties to foraging was observed in 159 bees, of which only 9 started to forage independently, and 150 were summoned to foraging by means of dances. And this is good, because it means that the large reserves of bees are available and can be mobilized when and where it is profitable for the colony to do this.

Distance to the Flow

When a scout bee has found a rewarding food source, she flies home with her honey sac filled, and then something unique happens: she alerts her fellow bees, which have been idling in the hive, by means of dances, describing through these the site of the source she has found. Round dances (Fig. 1) indicate that goal is in the vicinity of the hive. The *appearance* of the food source cannot be conveyed, but its *scent* can be. The scent of flowers adheres strongly to the bodies of bees, and those which “follow” the dancer can perceive her scent and use it as a reliable guide for recognizing (outside the hive) the type of flower on which the scout has been foraging, because each type of blossom has a specific scent. If the source is farther from the hive than 50-1000 meters, the indication of the scent alone is not sufficient indication, and the distance and direction of the food are then shown by means of wagtail dances (Fig 2).

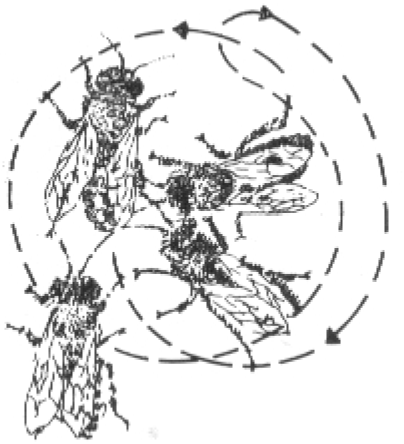

Fig. 1 – Round dance

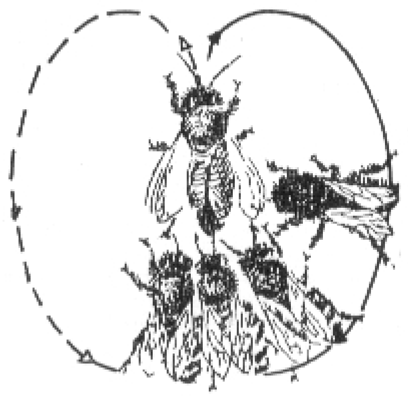

Fig. 2 – Wagtail dance

The distance is indicated by the tempo of the dance: in 15 seconds 9-10 dance-cycles are completed for a distance of 100 m; 8-9 for 200 m, 6 for 500 m, and 4-5 for 1000 m. The longer the way to the source, the longer and at the same time the more impressive the individual waggle run becomes: for 200 m it takes roughly ½ second, for 500 m 1 second, for 2 km 2 seconds. Various experiments have convinced us that the time taken by the wagtail run is the decisive signal which conveys information about the length of the flight to be made. It is characterized not only by the wagtail movements, but also by a specific sound, whose vibrations are perceived by the followers. But how does the forager get to know the distance, and what means of measurement does she employ during her flight? The method of measuring seems strange to the human mind: distance is measured by the energy used in covering it. A number of experiment have led to this conclusion; I will mention only one here. Bees can be made to *walk* from the hive entrance to the feeding place by placing the food in a gallery which is so low as to prevent flying. In free flight the transition from the round dance to the wagtail dance occurs at a distance of 50-100 m; with walking bees it occurs at 3-4 m. The effort involved is indicated by the bees’ sugar consumption, and this can be measured. The sugar in their blood is the fuel for the work they perform, and HERAN and his collaborators found that the amount of sugar consumed is the same for a 55-m flight as for a 3-m walk. It is apparent that walking is much more arduous for bees than covering the same distance in flight; it is equally apparent that the transition from round dance to wagtail dance, that is from the signal meaning “nearer than 50 m” to that meaning “farther than 50 m” is not determined by the distance as such, but by the consumption of sugar – for the bee the source of her energy.

Direction of the Flow

The direction towards the goal is given in the wagtail dance in relation to the direction of the sun. What happens can be most easily understood when the dance takes place on a horizontal plane, e.g. on the alighting board in front of the hive entrance. On her flight to the food source the bee has become aware of the position of the sun; later, when dancing, she makes the wagtail run at the same angle to the sun, and pointing directly towards the goal. The bees which "follow" the dance learn in this way how to angle their flights in relation to the sun.

When bees are working a particularly good flow, the beekeeper may want to know its source; he might be able to move his hives to the spot, shortening the bees' flights for his own advantage. He can make the bees tell him where the flow is. All he need do is to lift out a comb on which bees are dancing, and read the distance by his watch. If he hold the comb horizontally, and so that the bees can see the sun, they will show him by the direction of their wagtail runs the direction to the source of the flow, just as we should do it by raising an arm. It is not necessary, however, to let the sun shine on the comb – and this actually disturbs the bees – all they need to see is a patch of blue sky. Astonishingly, they can recognize the position of the sun from the polarized light of the blue sky. If, however, the horizontal comb is held in such a way that the bees can see neither the sun nor blue sky, they will be completely disoriented, and unable to show the direction.

Under normal conditions, on a vertical comb in a dark hive, this method of indicating direction cannot be used; the bee then adopts a different mode of expression; a wagtail run *upwards* represents an objective in the same direction as the sun, and any angle to the right or left of the sun is represented by the corresponding angle *to the vertical.* Ligth-orientation is so to speak translated into gravity-orientation.

Reactions of Other Bees to the Dances

That other bees understand this information, and act upon it, can be shown experimentally. For example 20 numbered bees are fed, and then the food is moved 600 meters away from the hive in a certain direction (the sugar solution fed is so dilute that the bees do not dance, and no new foragers are alerted). At the final site, concentrated sugar solution slightly scented with lavender is offered. Now the bees will dance, so new foragers set out looking for the scent they have perceived on the dancers. Small dishes scented with lavender, but without food, have been placed in the same direction as the food source, but 50 m short of it and fanning out 15^{o} on each side (fig. 3). These dishes attract the new foragers which approach them: in the present example, during the period of observation, the number of visits to the 7 dishes was 1, 1,2, 42, 5, 3, 0, respectively counting from S to N. By far the largest number of bees were searching in the middle, i.e., in the direction of the food source indicated by the dancers. If instead of being placed fanwise, the various dishes are put at various points in the line of the objective but far beyond it, the results will show that the recruited foragers stick surprisingly closely to the distance reported by the dancers.

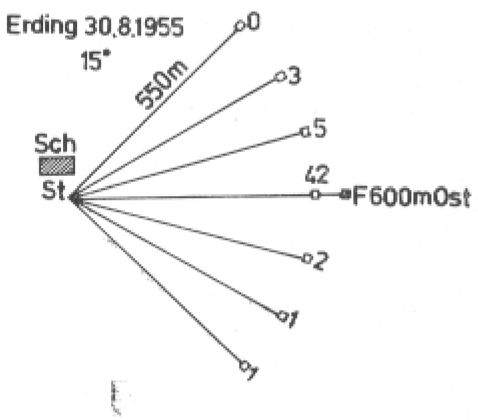

Fig. 3 – Number of visits by new recruits to scented dishes without food 550 m from the hive
H = observation hive; F = food dish with lavender scent, 600 m east of the hive; B = building

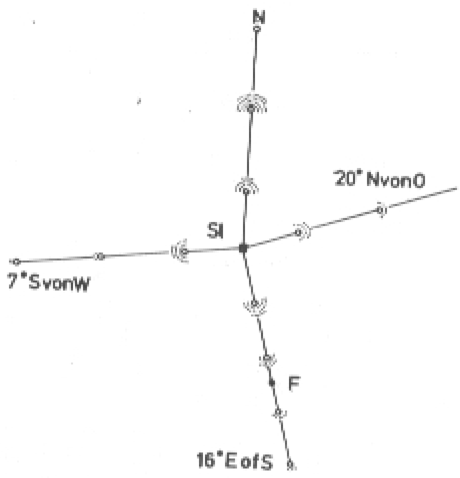

Fig. 4 – Number of visits by new recruits in an experiment giving disoriented dances. Each dot represents one visit
H = observation hive, laid horizontally;
F = food dish 200 m from hive; O = scent baits

A group of American scientists, led by Dr. A.M. WENNER, has recently denied this. While admitting that the dances indicate the distance and direction of the objective, they believe that new recruits are guided by the scent characteristics of the food source, not by the dance information. This opinion is not compatible with our experimental results: the new recruits cannot have been guided in the correct direction from the hive to the objective by a scent dish 600 meters away. But apart from this and other arguments, I will only mention here two experiments to show that the dances are understood. First, we use an observation hive, placed so that its comb is horizontal. The sky is screened off so that the bees can see neither the sun nor any blue sky. Under these conditions the dances are, as I said, disoriented pointing at random to any direction. Scent baits which have been placed not only to the S, where the food source is, but also E, W and N, are all visited (fig. 4). Without altering anything else, we then raise the hive from a horizontal to a vertical position. The dances can now take their orientation from gravity and indicate direction: within 10 minutes the stream of new recruits now leaving the hive is turning towards the south, and during the second half hour of the observation period not a single new recruit visits the scent bait E, W or N of the hive (fig. 5). Exactly the same thing happens in a different experiment after the bees have been given a free view of the sky while the hive is still in its horizontal position: the disoriented dances immediately become directional, and haphazard search becomes directed. The scent characteristics of the food source have remained unchanged, and nothing else has been altered, except that the dancers have been enabled to tell their fellows the direction – in the first experiment by the hive being righted, and in the second by the sky being made visible to the bees.

We do not need to believe that in the long course of their evolution honeybees have acquired an elaborate mechanism for conveying to others in the hive the distance and direction of an objective, but that these other bees do not understand the information and cannot make use of it. Nor need we return to the situation in 1823, when Unhoch described the dances of the bees and, without realizing their significance, thought of them as some sort of entertainment within the colony.

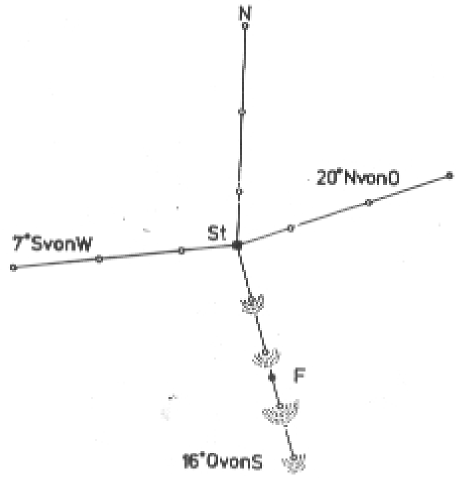

Fig. 5 – Fig. 4, except that the hive is now vertical and the dances have become oriented

A current investigation in Professor RUTTNER's Institute at Oberursel is intended to establish *how many* of the bees which have been in contact with a dancer in the hive actually, appear at the food source, and how soon. Mr. MAUTZ, who is carrying out the experiments, numbered each of the 1000 bees constituting his small observation colony. Each bee which followed a dancer was individually identifiable by her number. Circumstances were much less favourable for effective alerting than they usually are in natural conditions. Firstly, only one bee at a time was allowed to forage at the food source (100 m away) during the 15 days that the experiment lasted, so that it was quite certain that no contact between a hive bee and a dancer was overlooked. So only one bee could give the summons to the food source, and none at all while she was out foraging. Secondly, no scent was added to the food; this makes it more difficult for new recruits searching in the area to find the food. Nevertheless, of 339 bees which had followed the dancer on the comb, 108 (23%) found the food, on an average 3-4 minutes after leaving the hive, and a third of them on their flight. The average time of return after an unsuccessful flight was 7-8 minutes. The bare statement "32 % successful flights", however, gives a false picture: of the 339 bees which were in contact with a dancer, 152 (about half) were under continuous observation and, of these, 56 were known to have remained in the hive, the summons being too weak to incite them to fly. So these could not have found the food. Of the 152 bees continuously observed, the remaining 96 flew out and, of these, 58 (61%) found the food source. Under the given conditions this is a considerable achievement. Of the 38 bees which failed to find the food, 15 flew once only, suggesting that the stimulus to do so was slight. It is noteworthy that bees which followed a fair number of dances made a higher percentage of successful search flights than others, as though more through information produced better results. The experiments are being continued, including some with the food source at greater distances.

The Source of the Flow

There are many types of flowers whose "flow" varies during the day, their nectar or pollen being offered only for a certain period. This situation poses a problem for the foragers which, by virtute of their constancy, are "tied" to these flowers. Usually they stop foraging when it is no longer worth while to do so, and retire into some quiet corner of the hive to idle away the useless hours. If the foragers of such a group are marked with red spots of paint, an intriguing spectacle can be seen in the observation hive when, on the following day, the nectar starts to flow in the flowers again: from every part of the hive the bees with red marks emerge from their hide-outs and move gradually towards the area of the comb where the dancers take place; their inner clock has roused them to renewed activity. Once the bees are crowded on their "dance floor", they are easily alerted by the first successful scout.

Not all the marked bees behave in this manner, however. Bees have their own personalities, and there are marked individual differences between them which are revealed in various ways. In our case, some of the foragers do not remain idle, but are summoned by the dances of a different group, to a second type of flower that has something to offer at that particular moment. Hence we find bees visiting one flow early in the morning and another flow later in the day: they show a time-linked constancy. They remember the hours at which food is to be found in one place and in the other, and they remember the scent and colour of these different sources of flow. Again and again bees exhibit a high learning ability.

If a bee has found a rich flow – whether in a flower or a honeycomb carelessy left about by the beekeeper – she will, having filled her honey sac, circle around as she starts on her return flight. Any beekeeper is likely to be familiar with these "orientation" flights. It is tempting to assume that the bee does this so that she learns the characteristics of the feeding place and can find it again. The question whether it really is the moment *when the return flight begins* which is decisive in this learning was investigated by Miss OPFINGER in our Institute 38 years ago. In her experiments the bee was made to find a dish with sugar solution, on a glass plate covered with, say, a piece of blue card-board (Fig. 6). As soon as the bee has settled the card is removed and, while she is sucking, the bee sees a yellow card which had been underneath the blue. As she is flying off, her honey sac filled, the yellow card is taken away, and what she sees on her orientation flights is the dish on white card. When she returns, she is offered 3 dishes (without food) side by side, placed on blue, yellow and white card respectively. The result is significant and surprising at the same time. The bee settles on *blue*: it is the colour noted on arrival that is decisive. Whatever the sequence in which the three colours are offered, on her return the bee will choose that which she first saw on flying to the source. Further experiments have shown that a function of the orientation flights is to give the bee knowledge of landmarks beyond the immediate vicinity of the site, which will help her to locate it.

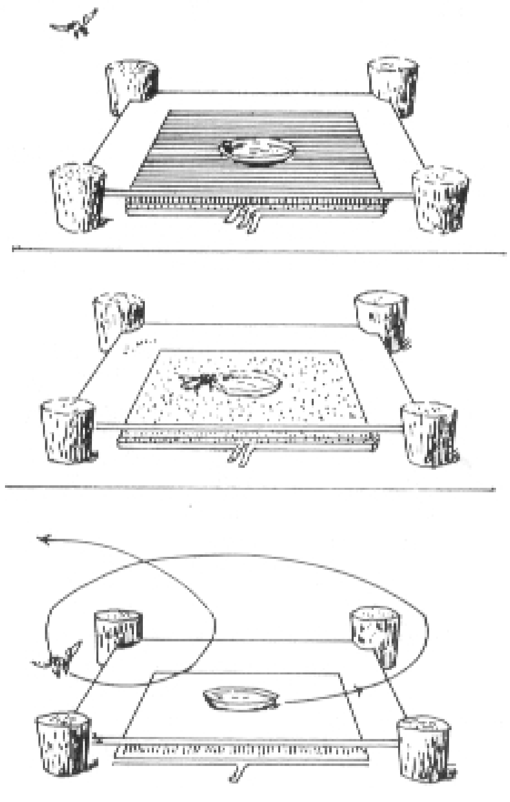

Fig. 6 – Opfinger's experiment
A = A bee approaches a dish of food which is standing on a blue surface; B = The bee drinks syrup from the dish while this is on a yellow surface; C = The bee sees the dish standing on a white surface as she flies off

Learning process of this kind have recently been examined by LINDAUER and his pupils in greater detail and with more refined methods. The results are interesting, in themselves, and also in comparison with studies done on higher animals and human beings. Universal characteristics indicate the essentials. R. MENZEL applied to bees a method similar to that developed by DAUMER in his experiments on colour vision. The bee flies through a window into a room in semi-darkness, and there she is offered food in a dish placed on an opaque sheet illuminated from below by light of a pure spectral colour, e.g. blue. Having taken her fill, the bee flies home. When she returns she finds sheets of spectral blue and spectral yellow, side by side, and both without food. Most bees returning for the first time will choose and search for food on blue. If a bee is caught at that point and kept caged in her own hive, she will remember the training colour she has seen once only, for up to six days. If the bee has been allowed to take food on blue 3-5 times, instead of only once, she will choose the colour without fail, and remember it for at least two weeks; tests were not made for a longer period. Since the coloured illumination can be turned on and off to the second, it was possible to determine the exact moment of learning. The colour is learned in a strictly limited, astonishingly short, time: from two seconds before to two seconds after the moment when the proboscis is dipped into the liquid. If a bee can see the colour as she approaches, but not for the last two seconds before she begins to suck, she learns nothing. If she is not shown the colour until two seconds after she has begun to suck – and then for some minutes while drinking and during orientation flights – she will learn nothing. The importance of the moment of arrival, already established by OPFINGER, is emphasized with unespected sharpness. It is true that in 10 minutes' time the bee will have forgotten what she learned in these few seconds; in order to imprint the color firmly in her memory she must be shown it for at least 5 seconds while she is sucking the syrup. In working flowers – think of the clover heads for example – bees usually visit several individual florets in quick succession. Each visit involves an act of learning, and a bee will have learned the colour of her flower, as well as she can ever learn it, long before she returns from her first foraging flight.

Bees can learn *scents* even better. Here a single act of sucking is sufficient to teach them to distinguish, for instance, the scent of thyme from that of geraniol and other flower-like scents, with almost 100 % certainty. It is in fact not even necessary for a bee to have experienced the food at its source: once she has perceived the scent of a flower on the body of a dancer, a bee will – given a choice on her flight – choose that particular scent with the same certainty. This is a fact reported by Mr. KOLTERMANN in a recent paper. If we recall that many types of flower produce a flow only at a certain time of day, and that industrious bees may visit one source of flow in the morning and another later in the day, one of KOLTERMANN's experiments becomes of particular interest. A bee is fed syrup with a certain scent three times running, and after that only from unscented dishes. Memory tests are carried out after different time intervals – with different individual bees, of course – and it appears that during the following 12 hours memory of the scent becomes somewhat faint, the training scent no longer being chosen with the same certainty as at first. Subsequently, however, the number of positive choices increases again, and 24 hours after the three initial acts of learning, the bees' choice has once more become certain; moreover, the bees are particularly persistent in their search near the training scent. The process of learning is to some extent tied to the time of day at which the flow was discovered. You see how closely and significantly these things are connected.

The needs of the Colony

If the flow is rich, bees are extremely busy. HERAN once calculated that one of the bees he tested covered 100 km a day in flights between the hive and the food source, and this is by no means exceptional. Every effort is made to make full use of a rewarding food source. Not only is the needed reserve foraging force mobilized from among idle bees; the working period is extended too, flights beginning earlier in the morning and ceasing later in the evening. The bees even increase the speed of their flight, thus shortening their travelling time; they carry heavier loads of very sweet nectar than they do of more dilute nectar, by filling their honey sacs more completely; between the foraging flights there is none of the dawdling in the hive which is common when the flow is less good. We are justified in regarding the bee as a symbol of industry. We must, however, remember that it is usually the industrious bees that we notice, not the lazy ones sitting in the hive.

Looking at the matter more closely, we must appreciate these idlers as well. There is a proper time for idleness as well as for industry, and either may be justified. Before young bees leave the hive they spend a good many hours of the day in idleness, as well as carrying out their domestic activities. LINDAUER watched numbered individuals, and saw them working about the combs in a leisurely manner, but always – following their innate instincts – joining in where some work that was needed was not being done: the idle are ready to act when required. The transition from house bee to forager is similar: there are only a few scout bees; most of the bees in the hive remain idle, forming a large reserve which is deployed on the labour market with a firm objective as soon as this becomes worth while to the colony. When a certain flow begins to dwindle, some of the foragers turn into idlers – no matter, laziness prolongs life, at any rate for bees. Those which work hard every day die relatively young; those which have saved their strength, because of bad weather or a lull in the labour market, may be of use to the colony at a later stage. Life in a honeybee colony follows strict rules, but it is not a rigid routine. Again and again we observe individual differences in actions and achievements which, hereditary adherance to firm traditions not-withstanding, have retained some degree of freedom. It is this which gives meaning to the complicated system and enables it to meet changing demands. The effect of the dances is a case in point: when, say, a good flow has been discovered 500 metres south of the hive, dozens of dancers indicate the site, and hundreds of foragers recruited by them set out to search the area. But there will be a few bees that fly in a different direction, and a few that do not search at the distance shown, but fly far beyond it or remain close by the hive. These are outsiders, the individualists, but they are nevertheless useful to the community. For, supposing a group of lime trees has come into flower to the south, it will be well worth finding out whether perhaps the lime are blossoming also the east or west, or at a different distance from the hive.

What I have been telling you today about the foraging flight of bees is only a fraction of what is worth knowing, and moreover it is given in a fragmentary form. It would need much more time than is available to provide convincing proof of the results mentioned. Many minutiae have to be noted and examined; the experiments require complete dedication, long experience, and an amount of time which the layman can hardly conceive. But it is the very difficulties of this sort of work with bees that make it so fascinating. The work continues, for however many secrets these mysterious insects have so far revealed to us, the problems whose answers the bees have so far kept to themselves would seem to be inexhaustible.

Acknowledgement

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