Appendix

ON THE FLIGHT PATHS OF MALE HUMBLE BEES

BY

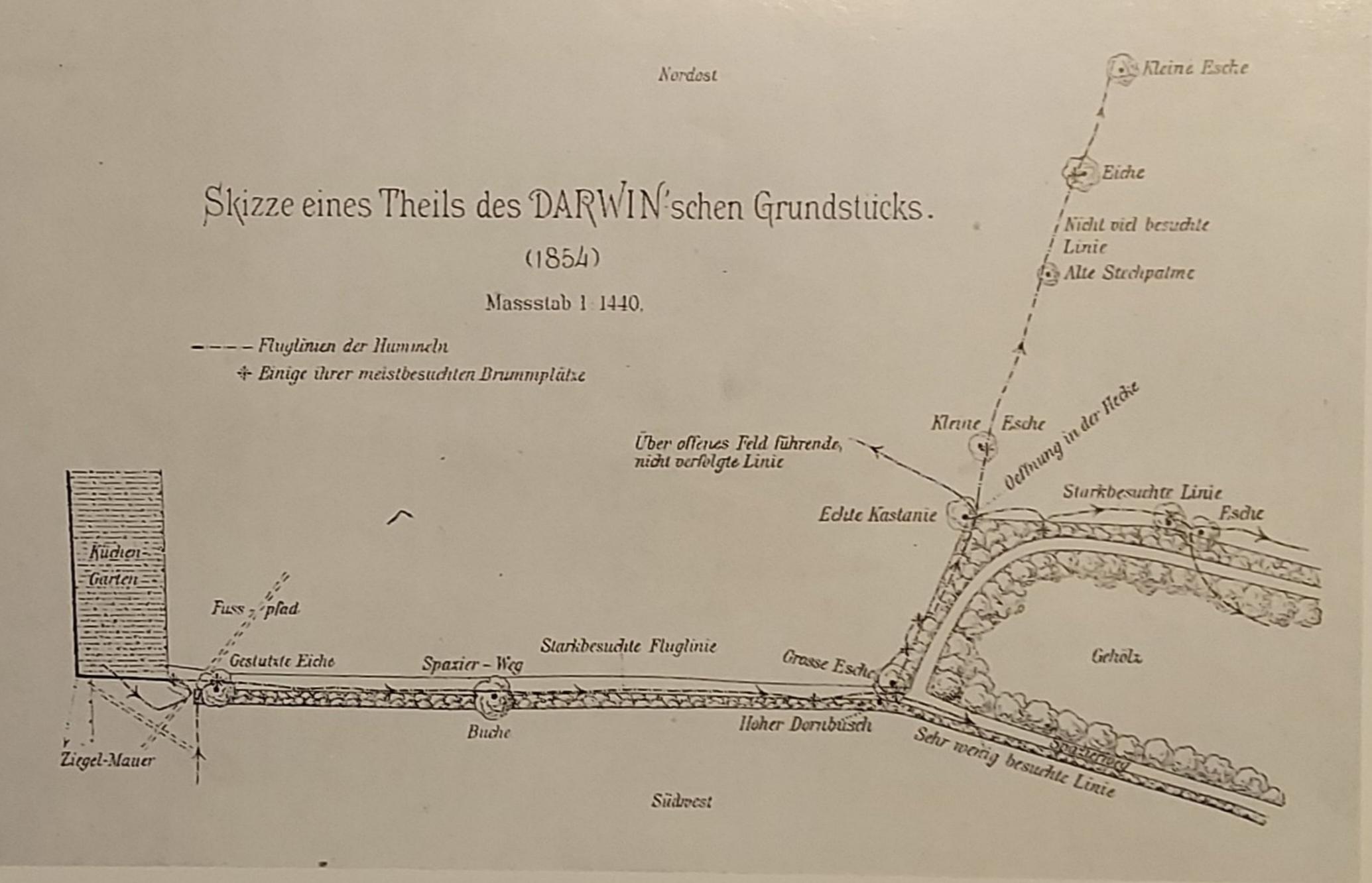
CHARLES DARWIN

(Translated from the German in No. 533.)

On September 8th 1854, one of my sons saw some humble bees enter a hole at the base of a tall ash tree. I looked into this hole hoping to find the entrance to a nest, but was unable to see one. Whilst I was examining the hole, another humble bee entered it, and, after flying off, returned almost immediately and, flying upwards for about a yard, flew

away through a fork between two large branches of the ash.

I now removed all the grass and other plants which were growing around the hole, but still could not find any entrance. After a minute or two, another humble bee appeared. It buzzed over the area that I had cleared and then flew up and passed, like the previous one, through the same fork. I watched many others behaving in the same way, all coming from the same direction and arriving at intervals of a few minutes. The only exception was that some flew round the stem of the large ash instead of through the fork. I was later able to confirm that all these bees were males of Bombus hortorum. I made similar observations on many other occasions, and was able to follow the bees from the ash to a bare spot at the side of a ditch where they buzzed again, and then for several yards further to an ivy leaf where the procedure was repeated. I am going to call these spots where they stopped for a few seconds "buzzing places." From the ivy leaf they went into a dry ditch which was covered over by a thick hedge and flew slowly along the ground between the dense branches of hawthorn. I could only follow them along this ditch by making several of my children crawl in, and lie on their tummies, but in this way I was able to track the bees for about twenty-five yards. They always came out of the ditch by the same opening, but from here there were three routes leading in different directions which I have indicated on the plan by dotted lines. I have marked them as far as I was able to follow the bees. There were several buzzing places on each of these routes, always a few yards apart. One of these was very odd because the bees had to fly down several feet to a fallen



Plan of the grounds of Down House. 19.5 cm. In No. 533

leaf at the bottom of a very thick hedge, and then fly back again by the

way that they had come.

I then followed their flight path for about a hundred and fifty yards until they came to a tall ash, and all along this line they buzzed at various fixed spots. At the far end, near a propped-up oak, the track divided into two as shown in the sketch. On some days all the bees flew in the direction I have described, but on others some arrived from the opposite direction. From observations made on favourable days, I think that the majority of individuals must fly in a wide circle. They stop every now and then to suck at flowers. I confirmed that whilst in flight they move at about ten miles an hour, but they lose a considerable amount of time at the buzzing places. The flight paths remain the same for a considerable time, and the buzzing places are fixed within an inch. I was able to prove this by stationing five or six of my children on a number of separate occasions each close to a buzzing place, and telling the one farthest away to shout out "here is a bee" as soon as one was buzzing around. The others followed this up, so that the same cry of "here is a bee" was passed on from child to child without interruption until the bees reached the buzzing place where I myself was standing.

After a few days the flight paths were slightly changed. The bees first buzzed at the base of a tall slender hawthorn in a hedge opposite the tall oak; they then flew slowly upwards close to the trunk of the thorn, and, ascending to a considerable height, crossed over a big branch of the oak where they buzzed, and were lost to view as they flew high over it. I saw scores of bees flying upwards by this particular hawthorn, but never saw one come down again. I kept up these observations for several years from the middle of July until the end of September. The

best time for observation is the middle of a warm day.

Now I must describe the strangest part of the whole business. For several successive years male bees followed almost the same paths, and several of the buzzing places were exactly the same, for instance in the hole at the foot of the tall oak; furthermore the bees always flew away through the same fork. They also travelled along the same dry ditches and flew in or out through the same small opening at the end of the hedge, although there were many similar openings at this spot which could have served their purpose just as well.

In the first year I saw dozens of bees coming through this particular opening and flying along the bottom of the ditch to the tall oak. But in the second year the bees visited the hawthorn mentioned above and flew upwards from there, and in a third they visited a different hawthorn nearby. At first I was astonished by these facts, and could not understand how bees born in different years could apparently learn

exactly the same habits. But they seem to prefer to fly along hedges and paths, and they love to buzz around the feet of trees, so that I assume that the same tracks and the same buzzing places have some kind of attraction for this species; but I am unable to understand in what this attraction consists. At many of their buzzing places there is nothing particular of note. When one of them has been frequently visited, it is possible to change its appearance completely without interrupting the visits. For instance, I pulled up all the grass and plants from the one at the foot of the oak and sprinkled white flour on the spot, without this making any change in the visits. It is just as difficult to understand how individual males from the same nests in the same area follow the same tracks and buzz in the same places in one particular year as it is to understand how the bees follow the same tracks and choose the same buzzing places year after year; for I believe that they emerge one after another, and I have never seen two travelling together. I have also been unable to understand the purpose of this habit of always flying along the same routes and buzzing at the same places, thereby losing a great deal of time. I have kept a look out for queens on these flight paths, but have never seen one.

The males of Bombus pratorum also have buzzing places and behave in many respects like those of Bombus hortorum, but their habits and flight paths are somewhat different. On a visit to Devonshire, I was able to confirm that males of Bombus lucorum visit buzzing places in the same way.

Mr. J. Smith* of the British Museum knew nothing of this habit, but he referred me to a short note by Colonel Newman in the Transactions of the Entomological Society of London (New Series, Volume 1, part 6, 1851, p. 67). I have always regretted that I did not mark the bees by attaching bits of cottonwool or eiderdown to them with rubber, because this would have made it much easier to follow their paths.

Translator's note. I have been unable to find any information on the present whereabouts of Darwin's original manuscript, if indeed it survives. It must certainly have been written in English because Darwin had very little German. The above is therefore a retranslation back into English, and I have in consequence rendered it rather more freely so as to restore English idiom where possible. The plan of the grounds of Down House was redrawn from a sketch by Darwin, and I have preferred to leave it as it is, rather than draw it again with English captions.

Neither of the two British books devoted to the humble bees, those * Presumably Frederick Smith, the hymenopterist on the staff of the British Museum at the time.—Translator.

of Sladen (1912) and of Free and Butler (1959), mention this work, although the latter devotes several pages to the flight paths of the males. A considerable amount of research on this subject has been undertaken in recent years which has confirmed and extended Darwin's observations, but his own work is not usually referred to, nor is his name mentioned. The best paper is that of Arthur Frank (1941) in which he describes closely similar flight paths for males of Bombus hypnorum and Bombus terrestris, but he is apparently unaware that accurate observations on the subject had been made nearly a hundred years earlier. Haas (1952) has explained one of Darwin's difficulties by showing that the male humble bees mark their buzzing places with secretions from the mandibular glands which attract others to the spot. These secretions are only put on and renewed once a day, in the early morning. The only paper that I have seen which refers to Darwin's work is one by Krüger (1951) which gives an excellent summary of his findings.

REFERENCES

Frank, Arthur 1941 Eigenartige Flugbahnen bei Hummelmännchen.

Z. vergl. Physiol., 28: 467-84.

Free, John B. & Butler, Colin G. 1959 Bumblebees.

8vo, xiv + 208 pp, Collins, London. (New Naturalist Series.)

Haas, A. 1953 Die Mandibeldrüse als Duftorgan bei einigen Hymenopteren. Naturwissenschaften, 39: 484.

Krüger, Edgar 1951 Über die Bahnflüge der Männchen der Gattungen Bombus und Psithyrus (Bombidae Hymenopt.).

Z. Tierpsychol., 8: 61-75.

Sladen, F. W. L. 1912 The humble-bee. Its life history and how to domesticate it. 8vo, xiii + 283 pp, Macmillan, London.