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THE HOMING OF ANTS

AN EXPERIMENTAL STUDY OF ANT BEHAVIOR

A DISSERTATION
SUBMITTED TO THE FACULTY OF THE
OGDEN GRADUATE SCHOOL OF SCIENCE
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

(DEPARTMENT OF ZOÖLOGY)

BY
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C. H TURNER.

WITH PLATES II–IV, AND ONE FIGURE IN THE TEXT.

CONTENTS.

INTRODUCTION.

Technique.—In the following experiments on ants the attempt has been made to have the conditions so simple that disturbance of the normal activities is reduced to a minimum, and yet to present in each experiment a definite problem which the ants must solve. Excepting where it is otherwise stated, each experiment recorded represents one of several similar experiments.

The apparatus used consisted chiefly of stages, inclined planes and dark chambers. All of these were constructed of cardboard. Occasionally a LUBBOCK or a FIELDE nest was used, but for most experiments I used a modification of the JANET nest. These nests were 39 x 15 x 2.5 to 3 cm. Each contained a well 10 x 5 x 1.5 cm., two living chambers, each 10 x 7 cm. and from a few mm. to a cm. or more in depth and a food-chamber of the same dimensions as the living chambers. The edges of the top of the nest, as far back as the beginning of the well, and the partitions between the cham-

bers and between the last chamber and the well were covered with Turkish toweling one layer thick.

With a fine camel's hair pencil, the upper surface of the abdomen of any ant used for individual experiments was marked with water-color paint. If more than one ant was used simultaneously for such experiments, each was given a distinctive hue. In all experiments with marked ants, any unmarked ant that visited the stage was immediately imprisoned.

The stage used consisted of a piece of white bristol board 15 cm. square; in the edges of two opposite sides perpendicular slits were made 2 cm. from each corner, for the purpose of attaching inclines to the stage. The center of this platform was attached, by means of a pin, to the cork of a bottle about 12 cm. high. Unless otherwise stated, a new stage was used for each series of experiments.

All the inclines were made of the same bristol board as the stage and were about 3 cm. wide and usually 30 cm. long. For special purposes inclines were made by pasting two of these end to end. They were also modified in other ways. When an incline led from a stage downward, it was always attached so as to project 2 cm. above the stage except when a dark chamber was used. When the incline led from the stage upward it was always attached so as to project 2 cm. below the stage. The dark chamber consisted of an inverted pasteboard box 8 x 4 x 1 cm. A flap about one centimeter wide and attached above was cut out of one end, and was pressed inwards to furnish a door through which the ants could enter the dark chamber. In order to observe what was happening on the under side of the stage and incline, a small mirror, inclined at the proper angle, was placed on the island, at one side of the stage.

Unless otherwise stated, preparatory to each series of experiments, the nest with its entrance open was placed on a LUBBOCK island for one or two days in order to familiarize the ants with the island.

Historical Résumé.—Students of ant behavior may be conveniently grouped into four schools: first, those who claim that ants lead a purely reflex life; second, those who hold that ants lead a purely instinctive life; third, those who grant that ants possess a limited amount of intelligence; fourth, those who insist that ants are endowed with anthropomorphic intelligence.

The first school, of which BETHE ('98, '00, '02) is the most noted modern member, claims that these animals are mere machines which respond to certain stimuli, always with the same fixed action or set of actions. Some of these machines are, indeed, quite complex; but so is the linotype. And as the linotype, in mechanical response to a variety of definite stimuli, turns out line after line, no two of which are exactly alike, just so the most complex activities of the invertebrates are but unconscious mechanical responses to diverse stimuli. In other words, the life of these creatures is a life of mechanical responses or tropisms. For them there is no content of consciousness. Heliotropism, galvanotropism, stereotropism, polarized trails, etc., explain all their behavior. They do not learn. All reflexes may not be possible at birth, because the physical mechanism is not yet perfected; but once the mechanism has responded, thereafter under the same conditions, it always responds to the same stimulus in the same way.

The second school, to which I, hesitatingly, assign PIERON ('04, '05), admits that reflex actions, some of which are connate and some of which are deferred, do not fully explain the habits of ants. According to them, the so-called instincts of these creatures are decidedly plastic. They profit by experience; but not by associating present sensations with revived sensations, nor by inference, nor by any of the higher forms of rational thought, but by what MORGAN ('00), THORNDIKE ('98), and others have called the method of trial and error.

The third school, to which belong EMERY, FOREL, LUBBOCK ('81), WASMANN ('98, '00, '02) and others, holds that ants have elementary feelings, ideas, and even what the English have called a simple association of ideas, but that they do not have rational thoughts and emotions.

The fourth school, including L. BÜCHNER ('80), HUBER ('10), MACCOOK, ROMANES ('92) and others, insists that there is difference only in degree between human consciousness and the consciousness of lower animals.

To separate the third from the fourth school is to make a distinction which savors more of convenience than of scientific accuracy; for it is probably true that an idea differs from a product of rational thought, not in kind, but in degree.

Acknowledgments.—The studies on the behavior of ants, of which this contribution is the first fruit, were begun about five

years ago, while I was connected with Clark University of Atlanta, Georgia. They were continued at the University of Chicago during the summer and autumn of 1906 and the winter of 1907. I take this opportunity to express my gratitude to the University of Chicago for the scholarship privileges granted me, without which the publication of this contribution would have been much delayed. I also wish to acknowledge my indebtedness to the members of the Zoölogical and Psychological Departments for their encouragement, and especially to Dr. C. M. CHILD for his sustained interest in my work and for suggestive criticisms, and to Dr. F. R. LILLIE for his assistance in revising the manuscript.

I. EXPERIMENTS ON TROPISMS.

BETHE's insistence ('98, '02), in spite of the opposition of WASMANN ('98, '99, '01), BUTTEL-REEPEN ('00) and FOREL ('01), that ants are merely reflex machines, led me to plan the series of experiments discussed in this section. The purpose of the experiments was to see what rôle, if any, tropisms play in the homing of ants. These homing activities were selected for study because they could easily be investigated under controlled conditions sufficiently simple to yield reliable results. Only such forms of stimuli were investigated as might possibly influence the normal activities of the ants.

Heliotropism.—"The essential feature of heliotropic reaction" says LOEB ('06, p. 124), "consists in the fact that the light automatically puts the plant or animal (Eudendrium, Spirographis) into such a position that the axis of symmetry of the body or organ, falls in the direction of the rays of light." Light may play an important rôle in the life of an organism without that creature being heliotropic. "Heliotropism (LOEB '06, p. 135) covers only those cases where the turning to the light is compulsory and irresistible, and is brought about automatically or mechanically by the light itself."

A large number of experiments were made to see what part heliotropism as defined by LOEB plays in the home-going of ants. In each experiment one or more cardboard stages and inclines were used. Illumination was furnished, in some cases by diffuse daylight through a window, and in others by a 16 c. p. incandescent light. For each experiment a new cardboard stage and inclines

were used. Pupæ and ants were placed on the stage and the ants allowed to find their way home.

These experiments fall into the following groups:

1. Those in which the ants in passing home must pass obliquely towards the source of light, then parallel to the rays but away from the source.
2. Those in which the ants must pass obliquely away from the source, then parallel to the rays and towards the source.
3. Those in which the ants must pass obliquely away from the source and then at right angles to the rays.
4. Those in which the ants must pass obliquely towards the source of light and then at right angles to the rays.
5. Those in which the path was practically equally illuminated on all sides.
6. Those in which the ants must pass obliquely towards the source of light, then parallel with the rays and towards the source, then at right angles to the rays, then parallel with the rays and away from the source.
7. Those in which the ants must pass obliquely away from the source, then parallel with the rays and away from the source, then at right angles to the rays, then parallel with the rays and towards the source.

In the sixth and seventh cases two inclines and two stages were used. The stages were connected by an incline and one incline led from stage number two to the ground. The pupæ and ants were placed on stage number one.

All of the above experiments were performed with each of the following species: Cremastogaster lineolata Say, Forelius maccooki McC., Lasius niger L., Myrmica punctiventris Rog., Pheidole sp. ?, Prenolepis imparis Say, Tapinoma sessilis Say, Formica pallide-fulva Latrl., Formica fusca var. subsericea Say, Dorymyrmex pyramicus Rog., Aphænogaster lamellatus Mayr, Monomorium minutum, Mayr. In most of these cases experiments were performed with several different colonies of the same species.

If ants are heliotropic in the sense of LOEB, they should move from or to the light, in the direction of the rays, until the edge of the stage is reached; then they should pass to the under (shaded) side of the stage, or else remain on its margin until the direction of the rays of light is changed.

But under each of the seven conditions mentioned above, and

with each of the species observed, the neuter (worker) ants when first put on the stage made random movements in every possible direction. After a time in almost every case (over 95 per cent), some one or more ants would find the way from the stage to the nest and back. Such ants then began to convey pupæ to the nest regularly. Gradually they were joined by others. The time required for ants to find the way home varied greatly; not only for different species, and for different colonies of the same species, but for the same colony at different times. That, however, is an irrelevant matter. The essential thing is, not how long did it take them, but which way did they go? In the few exceptional cases mentioned above, after a number of random movements, the ants ceased to search for an outlet and settled down quietly upon the stage. In such cases they usually collected the pupæ in the center of the stage and huddled over them. This getting lost was not confined to any particular species and it was only an occasional thing; no species got lost each time it was used.

It is thought that the above experiments prove conclusively that heliotropism does not influence the home-going of neuter ants. This is in harmony with LOEB's conclusions, for he says ('02, p. 196), "I have never found true heliotropism in the workers."

When winged females were placed on the stage with the pupæ, they would pass sometimes to the under side of the stage, sometimes they would roam about until they found the way home, and in some cases they actually assisted in carrying the pupæ home.

In a very few cases (less than 1 per cent) males placed on the stage with the pupæ flew away; but in almost every case they rushed to the under (shaded) side of the stage. Sometimes these males again returned to the top of the stage; but in no case observed by me, did any of these males reach the nest again until carried there by the workers.

Geotropism.—Any animal moving under the influence of geotropism is automatically forced to orient its body so that its axis of symmetry is at right angles to the horizon; or, if that be impossible, with that axis parallel with the component of gravitation which lies in the plane along which the animal is moving.

In the majority of experiments on heliotropism, the apparatus was so arranged that the ants were forced to go down hill to reach the nest. To determine whether geotropism led them downward, the apparatus was so adjusted that the ants had to go up-hill to reach the nest. The neuter ants readily learned the way home.