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49 West 44 Street
New York.

Three Odd Incidents in Ant Life.

BY ADELE M. FIELDE.

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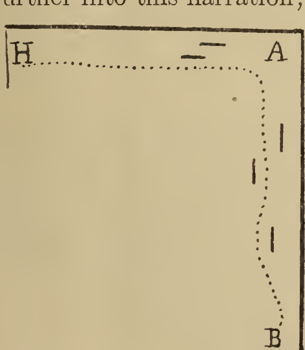
THREE ODD INCIDENTS IN ANT-LIFE.

BY ADELE M. FIELDE.

1. A case of hypnotism among ants?

I had a small artificial nest containing twelve workers of *Cremastogaster lineolata* that had spent the first month of their lives in a mixed colony of *Lasius latipes*, *Stenamma fulvum* and their own kind. They had then been transferred to their present abode, where they had lived for eleven months, never meeting ants of other species, except upon a few rare occasions when I introduced a visitor into their nest. On August 20, 1904, they were happily occupied in care of some promising pupæ from their old wild nest, when I dropped into their nursery a single *Lasius latipes*, somewhat larger and probably older than any of their number. She was a stranger from the wild nest of their quondam associates. As I dropped the strong-smelling, vigorous yellow worker into their nest, I glanced at my watch to note the minutes they would spend in slaying the intruder. When I looked back at the ants, I was at once impressed by the curious and sudden change in the positions of all the little black *Cremastogasters* and by the remarkable rigidity of five of them. Five were in the food-room, and they do not enter further into this narration; two were on the roof-pane of the nursery; and five were motionless under the touches of the *Lasius*, who, instead of fleeing or hiding, as do ants who are among enemies outnumbering them, was traversing two sides of the nursery at a leisurely-rapid pace from the hallway, marked H, to the corner marked A where there was a little pile of pupæ, and then on to the B corner where was a similar pile. She made more than eleven journeys to and fro, taking nearly the same track, sometimes walking over an ant or two, sometimes brushing the side of one as she passed, sometimes slightly varying her route so as to pass between two on the A B side of the nest. Whatever her course, every ant of the five swayed the abdomen slowly toward her as she passed, and swayed it back as soon as she had passed it. This swaying of the



The straight lines indicate the sides of the nest; the dotted line the path of the yellow ant; the dashes the positions of the five black ants.

abdomen, with slight movements of the antennæ, were the only signs of life given by any of the five ants during forty-five minutes. Meantime one of the other residents came down from the roof-pane, and while the yellow ant was at H with the heads of all the spellbound ones turned away from her, this solicitous sister went and touched three of the entranced ones, but failing to rouse them, she withdrew again beyond the line of the yellow visitor's march. I was observing the ants through a pane of orange-tinted glass which protected them from such light as they were aware of, and I several times lifted the pane, letting the daylight fall full upon them, but even this stimulant did not impel any of them to move.

During all this time none of the five ants that were in the food-room returned through the only ingress therefrom, the hallway H, and the young, ordinarily attended upon without intermission, were wholly neglected. The yellow ant finally stayed awhile in the hallway, and within the ensuing five minutes all the three ants between A and B began to walk slowly forward. I then shoved the other two with the end of a needle, and they also moved slowly about.

I did not again look into this nest until the following morning, when I found the yellow ant dead, and carried to the rubbish pile. I then introduced another ant of the same colony and of the same appearance, but this second ant was no Svengali, and only the expected thereupon happened.

Yet another, introduced later, came in like manner to an immediate and violent death.

2. A wolf in sheep's clothing?

I had in August, 1904, a nest of *Cremastogaster lineolata*, containing one queen, a hundred workers, and much young in the egg, larval and pupal stages. These ants had been in my care during all their lifetimes, and I know that they had never met *Lasius latipes* in active life. In the previous June I had introduced into their nest a half-teaspoonful of the larvæ of *Lasius latipes*, for them to use as food, and this alien larvæ had been taken care of, had become pupæ, and had gradually disappeared. On August 21 there hatched from what was perhaps the last of these alien pupæ a tiny *Lasius*, that the *Cremastogasters* permitted to live. Its bright amber-yellow body was very conspicuous among its jet-black associates. During several days the infant *Lasius*, of a different subfamily from its foster-sisters, shared their labors and passed unnoticed among them, and then it was nipped to death.

It is probable that this *Lasius*, having been long among the *Cremastogasters*, had acquired an overlaying of their inherent odor, concealing its own, and that it thereby escaped hostile attack until such time as it inherent odor became subject to the critical examination of an associate or of the queen. Then instinctive race-prejudice impelled the *Cremastogasters* to eliminate from their community one whose education had already been such as to secure them from injury through her misbehavior.

3. Can an ant remember acquaintances after lapse of three years or more?

In August, 1904, I had a nest of *Camponotus pennsylvanicus*, containing some larvæ and fourteen large workers, all of whom had hatched in my nests between May 1 and May 10, and who were therefore about three months old. They had spent the first two months of their lives with *Stenamma fulvum* ants who were from seven to nine months old, and they had not met ants of other species. They had been segregated about one month, when I dropped into their nest two *Formica lasiodes* of unknown age, several newly hatched *Stenamma fulvum* of the C colony, two adult *Stenamma fulvum* of the X colony and two *Stenamma fulvum* that were more than three years old, having been captured as adults and kept three years in one of my artificial nests, a section of the C colony. From the first introduction of these ants to the nest of *Camponotus*, one of the three-year-old Stenammas, who was of the same colony as were the early acquaintances of *Camponotus*, went freely and happily among them, apparently without fear and without reproach. She was permitted to stand among or upon the cherished larvæ, or on the backs of the resident ants. The affiliation between her and them was as complete as if she had always lived among them. Her odor may have become familiar to them in the nest of Stenammas where they had spent their early lives. But if this *Stenamma* had ever been acquainted with *Camponotus* it was at a time previous to her residence in my artificial nests, and more than three years since she had met any ant of other species than her own. The remarkable ease and friendliness of her intercourse with these ants, among whom she was as a brown pigmy among black bristly giants, is a fact requiring explanation; and the only explanation offered by known characteristics of ants lies in her recognition of an odor that she had previously encountered, and that she recognized the odor after the lapse of more than three years.

All the other ants introduced at the same time as was this *Stenamma* were killed by the resident *Camponotus* within a few hours. The *Stenamma* continued to live among the *Camponotus* until I removed her at the end of eight days.

The incidents were observed at the Marine Biological Laboratory at Wood's Hole, Massachusetts.

79

The Reactions of Ants to Material Vibrations.

BY

ADELE M. FIELDE AND GEORGE H. PARKER.

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THE REACTIONS OF ANTS TO MATERIAL VIBRATIONS.

BY ADELE M. FIELDE and GEORGE H. PARKER.

While it is well established that some insects react to sound vibrations that reach them through the air, and in this sense may be said to hear, many competent authorities, such as Huber (1810), Perris (1850), Forel (1874, 1900), and Lubbock (1894), have admitted their inability to bring to light any evidence that ants are thus stimulated. Even the discovery of the so-called chordotonal organs in ants by Lubbock (1894) and Janet (1894) has not led to positive results, so far as the reactions of these animals to material vibrations are concerned, though two American investigators, Weld (1899) and Metcalf (1900), have claimed that ants are very sensitive to certain tones.

Because of these somewhat conflicting opinions, it seemed to us desirable to reinvestigate this question,[1] and for this purpose we carried out experiments on the following species of ants:

Camponotine ants:

Camponotus pennsylvanicus (Deg.), workers;
Formica sanguinea Latr., queens and workers;
F. fusca L., var. *subsericea* Say, queens and workers;
Lasius umbratus (Nyl.), queens and workers;
L. latipes (Walsh), workers.

Myrmicine ants:

Stenamma fulvum Roger, var. *piceum* Emery, queens and workers;
Cremastogaster lineolata (Say), queens and workers.

Ponerine ants:

Stigmatomma pallipes (Haldm.), workers.

All these ants had lived more than a month in the artificial nests in which they were tested. They had established their nest-odor, had their young in charge and were well domesticated in their respective abodes.

These ants were tested for two general classes of material vibrations: first, those that reached them through the air surrounding them, and, secondly, those from the solid base upon which the ants rested.

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[1] These investigations were made in the summer of 1903, at the Marine Biological Laboratory, Woods Hole, Mass.

As sources for air vibrations we used a piano, a violin, and a Galton whistle. The keys of the piano gave us a range from 27 to 4176 vibrations per second. The Galton whistle had a range from about 10,000 to about 60,000 vibrations per second, and was provided with a movable threaded core whereby any intermediate vibration could be obtained. The range from the highest note of the piano, 4,176, to the lowest one of the whistle, about 10,000, was bridged over by vibrations obtained from the violin. Thus a series of vibrations from 27 to 60,000 per second were available for experimental purposes.

In testing the ants with these vibrations the artificial nests were so arranged that their air was in free communication with the outer air in which the vibrations were produced, but this was carried out in such a way that draughts, to which ants are very sensitive, could not enter the nests. The nests were placed upon thick paper, so as to isolate them from vibrations that might reach them through the table upon which they rested. The observer then closely watched a quiescent ant under a hand magnifier, while a second person at several metres distance produced the vibrations as desired. As a rule, each key of the piano was struck ten times in slow succession. If the ant under observation seemed to respond, it was given a resting period, and then retested at the pitch to which it apparently reacted. The range of the whistle, 10,000 to 60,000 vibrations, was divided into sixty intervals, and these were treated as the keys of the piano, each note being blown ten times while an ant was under observation. Ants were also watched while the pitch of the whistle was gradually changed by slowly screwing the core either in or out. A gradual change of pitch was also produced on the violin.

All the species mentioned as tested by us were subjected to this range, 27 to 60,000 vibrations per second, and in no single instance was any unquestionable reaction observed. Now and then an ant would seem to respond to a given note, but in every case repetitions of the experiment gave a negative result. We, therefore, conclude that aerial vibrations between 27 and 60,000 per second give rise to no observable responses in the ants we worked upon, and as these included representatives of three subfamilies of the Formicidæ, it is highly probable that a like condition will be found among other ants.

Our results, then, agree with those of Huber, Perris, Forel and Lubbock, but are opposed to what is stated by Weld and by Metcalf. In one instance we worked upon the same species as Weld, namely, *Cremastogaster lineolata*, and tested it with a note approximately that used by Weld (4,096 vibrations), but obtained from the piano and from the violin instead of from a metal bar. Nevertheless we got no reaction. Weld does not make clear that his ants were always isolated from all except aerial vibrations, nor that their reactions were constant under repeated stimulation. It seems to us possible that his ants may have reacted at times to vibrations of the solid base upon which they rested and to which, as we shall show presently, they are very sensitive, or their supposed reactions may have been accidental. Certainly our own experimental evidence gives us not the least reason to suspect that ants are stimulated by sound waves in air.

Having reached this conclusion we next endeavored to ascertain whether ants would respond to vibrations of the solid base upon which they stood. When a nest containing *Stenamma fulvum* was held in the air within a centimetre or so of the woodwork of a piano, and the C, giving 261 vibrations per second, was struck, no response followed. When, however, the nest was allowed to rest on the woodwork and the note was again sounded, almost all the ants started forward simultaneously. Thus a vibration that comes to an ant through the air is not necessarily followed by a reaction, though the same vibration when it reaches the ant through a solid may be very stimulating. All the eight species of ants with which we experimented were thus stimulated, though they failed to react to the same vibrations in the air. The range of the different species was by no means uniform. All reacted to the 27 vibrations per second and to higher notes up to a certain pitch characteristic for each species. *Cremastogaster* reacted at 522, but to no higher note. The superior limit for *Formica fusca*, var. *subsericea* was 1,044, and for *Lasius latipes* and *Stigmatomma* 2,088. *Stenamma* always reacted at 2,088, usually at 3,915, but failed at 4,176. *Camponotus* regularly reacted at 3,480, but failed at 4,176. *Formica sanguinea*, which invariably responded at 2,088, occasionally did so at 4,176, a pitch regularly reacted to by *Lasius umbratus*. Thus each species seemed to have a characteristic superior limit for stimulating vibrations received through solids.

Ants are not only sensitive to the tones of a piano transmitted through a solid, but they are also sensitive to vibrations from other sources similarly transmitted. This is well seen in the following experiment on *Stenamma*. When the edges of two Petri dishes were rubbed against each other in the air, the ants did not respond; but when the edge of the dish in which the ants were held was rubbed even lightly by the edge of another dish, they reacted with great precision. These reactions occurred even when the Petri dish containing the ants was floating on water and the edge of the vessel containing the water was rubbed. Some idea of the delicacy of these reactions may be gained from the fact that ants in a Petri dish resting on a pine table-top reacted to the scratch of a pin on the table at a distance of ten feet from the dish. A measure of the stimulus necessary to call forth the most delicate reaction, usually a jerking movement of the antennæ, was obtained in the following way: A small artificial nest was built on the end of a long board clear of knots and, after the ants had become accustomed to their nest, stimuli were introduced by dropping a shot weighing half a gram on the board at different distances from the nest and from different heights. It was found that the ants reacted to a blow given to the board 4.3 metres (14 feet) from the nest when the shot fell from a height of 15 centimetres (6 inches), but that they did not react when it fell through only half that distance.

Ants not only react to material vibrations received through wood, glass, water, etc., but they will also react to such vibrations when resting on a bit of sponge in an artificial nest or on the soil in which they construct their nests. Thus ants within their natural earth nests may be stimulated by the vibrations of the material on which they stand, though they will not respond to similar vibrations in the air about them.

To ascertain what parts of the body of the ant are concerned in its reaction to the vibrations of non-gaseous materials, we performed experiments on a number of individuals of *Stenamma fulvum piceum* that had been deprived of portions of the body.

All the mutilated ants, except those lacking heads or abdomens, had undergone the necessary surgical operations so long as three or four weeks previous to the experiments, and had therefore had time for full recovery from shock-effects.

The irritability of workers deprived of their funicles, or of the whole of the antennæ, was such as to make it necessary to isolate each in order to prevent mutual slaughter, though all were of the same colony. This irritability continued even after they had recovered from shock-effect, had become alert and active, and had been more than a month without funicles, or without both funicles and scapes. Queens similarly mutilated were scarcely more irritable than when in normal condition, and nearly all of the thirty operated upon survived the operation more than two months and laid eggs.

Queens and workers deprived of only one antenna were no more irritable than normal ants, and hardly any deaths resulted from this mutilation, while not more than twenty per cent. of the workers survived the loss of either both funicles or both antennæ.

Queens and workers deprived of a pair of legs, the amputation being made at the coxal joint (see figure), lived in groups as amicably as do whole ants, and there was little loss of life through this operation. The delicate structure of the leg manifestly renders it a probable communicator of vibration from any solid with which it might be in contact.

Prothoracic leg of a young *Stenamma fulvum piceum.* × 48.

There was throughout a direct ratio between the degree of irritability produced and the percentage of deaths consequent upon the surgical operations. The operations were as far as possible carried out aseptically and careful nursing was attempted for all cases.

The mutilated ants were tested in Petri dishes, first by scratching together in the air the edges of two Petri dishes to ascertain whether the ants were stimulated by air vibrations, and next by gently scratching the edge of the dish in which the ants were. As might be expected, no reaction was ever obtained from mutilated ants submitted to air vibrations. The reaction of the ants to the vibrations of the dish containing them and the states of the ants, so far as the operations that they had undergone were concerned, are given in the following summary:

1. Queens from which both funicles had been removed reacted by slight locomotion, usually moving backward or sidewise, rarely forward.

2. Queens from which one antenna had been removed reacted like normal queens by forward, backward or sidewise locomotion.

3. Queens deprived of the whole of both antennæ reacted by moving backward or sidewise.

4. Workers deprived of both funicles moved forward, backward or turned sidewise.

5. Workers deprived of one antenna moved forward or turned sidewise, as did the normal workers.

6. Workers without antennæ moved forward or backward or turned sidewise.

It is thus evident that the antennæ are not essential to the reactions of these ants to vibrations from a solid, for the ants invariably reacted irrespective of the conditions of the antennæ, and the slight differences in the nature of their reactions seem to us insignificant of the function of hearing in parts removed. This opinion, that the antennæ are not essential to these reactions, is in accord with certain observations on normal ants. When a normal ant in a Petri dish was resting with its antennæ high in air, it was observed to react vigorously to a slight scraping on the edge of the dish, without, however, bringing the antennæ in contact with the dish.

7. Decapitated queens and workers reacted by movements of the legs, without, however, showing any determinate form of locomotion.

8. Queens and workers deprived of their abdomens reacted by moving forward or sidewise.

9. Queens deprived of any one pair of legs reacted by moving forward, backward or sidewise.

10. Workers deprived of any one pair of legs reacted by moving forward or turning sidewise.

11. Queens and workers deprived of any two pairs of legs reacted by making ineffectual efforts to walk, their direction of locomotion being very irregular.

It is thus evident that the reactions of the ants to the vibrations of the underlying solid are not dependent upon the antennæ, head, abdomen, any pair or two pairs of legs. It seems to us probable that stimulation is effected by the transfer of the vibration from the underlying solid to the body of the ant, without reference to any special sense-organ. That the various movements of the ants are true reactions, and not merely motions transferred mechanically from the vibrating base to the body of the ant, as to any small particle capable of vibrating, is seen from the fact that the body of a dead ant does not show these movements, and further that in a live ant these movements cease after the stimulus has been repeated a few times, but begin again after the ant has been allowed a resting period of at least ten minutes.

In none of our experiments was there any evidence of a directive influence exerted by the stimulus on the movements of the ant.

The observations and experiments recorded on the preceding pages lead us to conclude that ants are insensitive to air vibrations, such as are audible to us, and that they are very sensitive to the vibration of the solid material upon which they stand, be this wood, glass, sponge or the earth of their nests. These vibrations apparently affect their whole bodies, reaching them through their legs or any other part in contact with the solid base. It is of course conceivable that if an air vibration were strong enough—*i.e.*, if the sound were loud enough—it might stimulate the body of the ant directly, but apparently this is not usually the case; for, as we have already shown, sounds of ordinary intensity, which call forth no response from the ants when they reach these animals through the air, are very effective as stimuli when they reach the animal from a solid base. It therefore seems probable to us that ants in their nests are stimulated, not by the sound waves in the air of the nest, but by the vibrations of the solid parts of the nest itself. Hence the effectiveness of a heavy footstep in the neighborhood of an anthill as contrasted with the ineffectiveness of the human voice in causing an active emergence of the ants. These animals are, as it were, in the condition of a perfectly deaf person who feels through his feet the vibrations caused by a passing wagon, but cannot hear the sound it produces in the air. This sensitiveness of the ants to the vibrations of the base upon which they rest and their insensitiveness to air vibrations is exactly what would be expected from the requirements of their subterranean life as contrasted with that of aerial insects.

Because of the analogy between the ants and a deaf person we do not wish, however, to be understood to deny hearing to ants; neither do we affirm it.

It has long been recognized by physiologists, if not by the scientific public, that touch and hearing in the vertebrates are very closely related. The apparent separateness of these senses in us is due to the fact that the air waves by which our ears are usually stimulated are too slight to affect our organs of touch. If, however, we transfer our experiments to water, we at once meet with a medium in which, as has long been known, vibrations can be both heard and felt. In dealing with a like question among the lower animals it therefore seems to us misleading to attempt to distinguish touch from hearing, and we shall be more within the bounds of accuracy if we discuss the question from the standpoint of mechanical stimulation rather than attempt to set up questionable distinctions based upon human sensations. We therefore prefer to ignore the question of hearing in ants and to restate our conclusion in the form already given, that these animals are insensitive to the ordinary vibrations of air, but are very sensitive to the vibrations of the solid upon which they stand.

It seems to us probable from our experiments that the material vibrations that stimulate ants reach them in this way rather than through the air. Janet (1893; 1896, p. 19) has described an ingenious method whereby the stridulating of ants can be heard by the human ear, and Wheeler (1903, p. 66) has been able to note a faint sound when a large number of stridulating ants are collected in a bottle. Undoubtedly these stridulations are of ecologic importance to an ant community, but it is our belief, based upon our experiments, that what can be heard by the human ear through the air is probably not the vibration that affects the ants, but rather that the stridulation produces a vibration of the solid constituents of the nest, and that this vibration is the effective one in stimulating the inmates.

Summary.

1. The ants experimented upon did not react to aerial sound waves from a piano, violin, and Galton whistle, which collectively gave a range from 27 to 60,000 vibrations per second.

2. They reacted to most vibrations that reached them through the wood, glass, sponge or nest-earth upon which they stood, though different species seem to have different superior limits in respect to the rate of the vibrations.

3. These reactions are not dependent upon the funicles, the antennæ, the head, the abdomen, any pair or two pairs of legs of the ant, but are usually received through the legs, and probably affect the body of the ant as a whole.

4. The stimulation of ants by the vibration of the solid upon which they stand, and not by the vibration of the surrounding air, accords well with their subterranean life as contrasted with the aerial life of most insects.

5. It is misleading to ascribe or deny hearing to ants; they are very sensitive to the vibration of solids, not to those of air; their reactions could be as appropriately described as resulting from touch as from hearing.

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TENACITY OF LIFE IN ANTS.

ADELE M. FIELDE.

Maimed Ants.

Remarkable tenacity of life is sometimes exhibited by ants lacking a portion of the body.

A queen, *Stenamma fulvum piceum*, deprived of the funicles of her antennæ, lived fourteen months in one of my artificial nests, where she laid eggs, sought her own food, and received kindly treatment from the resident workers and several unmutilated queens.

The head of a *Formica fusca subsericea* worker under my observation, continued to move its antennæ seven hours after decapitation.

Ants lacking a leg or two may live several weeks. A *Stenamma fulvum* worker, deprived of its mesothoracic pair of legs, was returned by me to an artificial nest where were hundreds of its former comrades and it safely lived there a month or more, disproving any general assertion that ants destroy maimed members of their colony.

Worker ants deprived of the abdomen sometimes run with great speed, continue to care for the young in the nest, fight with aliens of their own or other species, and they may for some days behave as if unconscious of loss. A *Stenamma fulvum* queen deprived of her abdomen lived thereafter for fourteen days in one of my artificial nests, and was seen to eat. A *Formica subsericea* worker lived without her abdomen for five days.

M. Charles Janet mentions [1] an ant that lived nineteen days after decapitation. In experiments made by me, headless ants have continued to walk about for many days. In all these experiments aseptic surgery was attempted, the instruments used being carefully sterilized. The Petri cells in which the maimed ants were

[1] "*Extrait des Compte rêndus hebdomadaires des Séance de l'Académie des Sciences,*" Paris, 11 juillet, 1898, p. 130.

kept were frequently cleansed with 80 per cent. alcohol, and only distilled water was used in wetting the enclosed sponges. Care was taken to maintain hygienic conditions at all times during the life of the ant. In these experiments a *Stenamma fulvum* worker lived ten days without her head. A *Formica subsericea* worker lived fifteen days without her head. Of seven decapitated *Camponotus pennsylvanicus* workers, three lived five days ; two lived twenty-one days ; one lived thirty days ; and one lived forty-one days. The last two mentioned were the largest, being thirteen millimeters long. After decapitation, they were kept for four days at a temperature of about 10° C. or 50° F. and afterward in the natural summer temperature of the laboratory.[1] The ant that lived forty-one days after decapitation walked about in the cell until two days before her death, and during the last two days gave evidence of life by a twitching of the legs when I touched her.

Submergence.

While making experiments in June, 1904, with a view to ascertaining how long ants could live under water,[2] I came to suspect that the death of ants submerged less than seventy-two hours was caused by bacteria rather than by deprivation of oxygen. Later in the summer I therefore made further experiments, merging the ants in distilled water, and keeping them in the dark at a temperature of about 10° C. or 50° F. Under these conditions the ants survived much longer periods of submergence.

Of eighteen *Stenamma fulvum* submerged four days, seventeen revived and twelve fully recovered.

Of fourteen *Stenamma fulvum* submerged six days, six revived, and one fully recovered.

Of twelve *Stenamma fulvum* submerged eight days in sixty-five cubic centimeters of water, seven revived and fully recovered.

Of seven *Camponotus pennsylvanicus* submerged eight days, four revived, fully recovered, and were returned to their old associates.

[1] Nearly all the experiments recorded in this paper were made at the Marine Biological Laboratory at Woods Holl, Mass., during the summer and autumn of 1904.

[2] "Observations on Ants in their Relation to Temperature and to Submergence," A. M. Fielde, Biological Bulletin, Vol. VII., No. 3, August, 1904, p. 170.

The ants recovering after submergence were those of large stature among their kind.

Dwarf Ants.

The ability of the larva to successfully enter the pupal-stage of development at any time after about half its normal size has been attained, helps to assure the persistence of a harried community. Under propitious conditions the larva grows to the size of an adult ant, expels the contents of the alimentary canal, and eats nothing during the five or ten days preceding pupation. But if suddenly deprived of food it may enter the resting stage when half-grown and may ultimately become a perfectly formed dwarf. I sequestered many fat, healthy, half-grown larvæ of *Stenamma fulvum*, put them in the care of fewer nurses than could regurgitate food to all of them, and supplied but little nutriment to the segregated group. Many of the larvæ soon entered the resting stage and later on became dwarf workers, only three or four millimeters in length, while the length of workers of their species is usually from five or seven millimeters. A corresponding diminution in the stature of a man would take from one to two feet from his height. The dwarf workers were wholly normal in their faculties and activities, and were markedly assiduous in their care of the young. On the other hand, larvæ poorly fed may miserably linger, as if waiting for better times. In one case under my observation, an ill fed larva remained such for one hundred and forty days, although constantly in summer temperature, and it then died without pupating.

Deprivation of Food.

Although ants manifestly suffer and soon die if deprived of water, they can exist for many days without food. In the following tests the ants were kept in Petri cells, ten centimeters in diameter, and not more than five ants were enclosed in any one cell. All the cells were kept in darkness or very dim light. At intervals, never exceeding four days, the cells and the enclosed sponges were cleansed with 80 per cent. alcohol, to prevent microscopic growths which might furnish nourishment to the ants. The cells contained only the ants used in the experiment, and a bit of sponge saturated with distilled water. Care was taken to ensure good ventilation and all other conditions were made hygienic, that there might be no cause of death other than that of deprivation of food. The starving ants did not manifestly weaken after long abstinence but collapsed suddenly and finally, giving no premonitory evidences of exhaustion.

Of thirty *Cremastogaster lineolata*, segregated on July 2, 1904, ten lived so long as ten days and only one lived so long as eighteen days without food.

Of thirteen *Camponotus herculeanus pictus* workers, two lived seven days; two, fourteen days; one, eighteen days; one, twenty-three days; two, twenty-four days; one, twenty-six days; and one, twenty-nine days. On the tenth day of fasting, I found three of these ants killed and dismembered, with an appearance of having been chewed. In all the cells, this was the only group where the ants attacked their companions in tribulation. As ants sometimes quarrel with their mates when food is plentiful, this affray cannot be fairly attributed to a cannibalistic tendency in this species.

Of nine *Stenamma fulvum* workers, two lived eighteen days; one, twenty-seven days; one, twenty-nine days; one, thirty-two days; two, thirty-six days; one, thirty-eight days; and one, forty-six days. The last to die measured seven millimeters.

Of eight *Camponotus pennsylvanicus* workers, one lived fourteen days; two, eighteen days; one, twenty-one days; one, twenty-two days; one, thirty-nine days; one, forty-five days, and one, forty-seven days. The last two mentioned were fourteen millimeters long, and were larger than any of those that died earlier.

Of five *Formica lasiodes* workers, one lived ten days; two, eighteen days; one, thirty-nine days. An isolated queen of this species, lived from July 2 to August 31, just sixty days. During her isolation, she deposited seven eggs, the seventh being laid on the twenty-first day of her fasting. Any egg discovered in the cell was at once removed.

Of nine *Formica fusca subsericea* workers, picked up from a roadside and segregated without feeding on July 3, one lived ten days; one, seventy-one days; and the other seven were all alive on October 18. Possibly the remarkable capability of these ants to live without food, enhances their value in slavery, where other species so often hold them.

Of two *Camponotus castaneus americanus* workers,[1] measuring thirteen millimeters, one lived fifty-four days, and the other lived more than a hundred days.

Two winged queens of *Camponotus americanus*, eighteen millimeters in length, and at least three months old, were established in a separate cell on July 13. One of them dropped her wings on July 31, while the other continued to wear her wings. No eggs were laid by either and both were alive on October 18.

Elimination of Inedible Substances.

The skill with which ants eliminate from their food supply such inedible substances as may be commingled therewith, was shown in the action of *Stenamma fulvum piceum* toward certain dye-stuffs that I mixed with their nutriment. Into each of four similar Fielde nests, C, I, T, and M, I put one queen and fifty workers, with a few half-grown larvæ. During three months no food was given to these ants other than what is hereinafter mentioned. The dye-stuffs were first triturated, molasses was added to make with them a thick paste, and a portion of the paste was then placed in the food-room of the nest. For the C nest, cochineal was commingled with the molasses; for the I nest, indigo; and for the T nest, tumeric; while for the M nest, molasses alone was provided. During the three months hardly any ants died in either nest. There was no evidence that any larva was devoured; and as the introduced larvæ appeared in due time in active life, they must have been nourished solely upon regurgitated food. In only one of the nests were any eggs seen, their absence probably being due to deprivation of insect food.

In all of the nests the finely pulverized inedible substances mixed with the molasses were separated in the mouths of the ants from the nutrient fluid, and were cast out in minute pellets, forming a characteristically colored heap in a corner of each nest, C, I, and T. In the M nest, a smaller pile of brown pellets indicated that non-nutritious particles had been rejected from the unmixed molasses.

[1] These ants were kindly identified for me by Dr. W. M. Wheeler.

Such preclusion of innutrient matter from the alimentary canal must greatly conserve the physical energy of the ants in the processes of digestion.

Avoidance of Poisons.

Ants that had fasted ten days did not partake of sweets in which poisons were incorporated, although their equally hungry mates ate the unpoisoned sweets with avidity.

When the ants were compelled to walk over a mixture of one gram of corrosive sublimate with two cubic centimeters of molasses, they afterward cleaned their feet with tongue and mandibles, and then evinced much distress in cleaning their mouths, but nearly all of them survived the experience.

When one gram of potassium cyanide was dissolved in five cubic centimeters of molasses, and the ants compelled to walk upon the solution, they appeared to die within a few seconds after touching the feet with the tongue, but they all revived some minutes or hours later and continued their normal activities.

When one gram of carbolic acid crystals was dissolved in two cubic centimeters of molasses, the ants compelled to walk upon the solution cleaned their feet with their tongues and mandibles, evinced much distress, and died after some hours or days, with no subsequent resuscitation.

In the experiments with poisons, the ants employed were *Cremastogoster lineolata*, *Stenamma fulvum*, *Lasius latipes*, *Formica subsericea*, *Camponotus pennsylvanicus* and *Camponotus castaneus americanus*. In these experiments the largest ants were latest in succumbing to the effects of the administered poisons. *Camponotus americanus*, about thirteen millimeters in length, lived several days after the administration of the carbolic acid, and in a natural environment might possibly have remedied their ills.

Regurgitation of Food.

Whether the regurgitation of food be a simple reflex or an altruistic act, it was practiced by some of the ants when there was little to confer upon a starving comrade. One *Camponotus pennsylvanicus* worker was seen to make unsuccessful effort to regurgitate food to another on the thirty-first, and also on the thirty-sixth day of fasting.

FIG. 2. *Camponotus castaneus americanus*, slightly magnified, showing five workers engaged in the regurgitation of food to their comrades, and four winged queens. From a photograph by Mr. J. G. Hubbard and Dr. O. S. Strong.

A winged queen of *Camponotus americanus* regurgitated food to her deälated sister queen, on the twenty-fifth, the thirty-fifth, the fortieth and the sixty-second day of fasting, the visible transfer of food occupying several minutes.

The ants cannot, however, be considered to virtually possess a common stomach. There was great difference in the periods within which ants of the same colony and species, in the same cell, perished from deprivation of food.

The feeding of the larva by different ant-nurses doubtless conduces to its vigor, because the nurses forage in diverse localities bringing back nutriment containing unlike chemical elements which they transfer by regurgitation to the growing young.

Doubtless the adult ants also benefit greatly through the habit of regurgitating food to each other. Going afield in many directions, one finds nectar, another berries, another nut-kernels, another insect flesh, another egg-yolk, and many give of their garnered nutriment to their companions in the nest. Variety in the food supply for each individual is in fairly direct ratio to the number of fellow-workers who reach new sources of sustenance. Vigor gained by the adults through varied diet and the assimilation of new chemical compositions, would tend to increase the stamina of the growing young through an improved pabulum as well as through heredity.

There is notable difference in the average size and vigor of the individuals in different colonies of ants of the same species.

Relation of Sex and Food to Tenacity of Life.

Male ants shared all tests here presented, but whatever the test undergone, the males showed far less tenacity of life than did either the queens or the workers.

If, as has long been held, the product of unfertilized ant-eggs are males while the product of fertilized ant-eggs are females, then it may be that the absence of certain chemical elements contained in the fertilized egg is a cause of lesser tenacity of life in the male ants.

In all tests of vitality, ants of largest stature among their species showed greatest tenacity of life. Whether the test applied were endurance of heat,[1] submergence in water, deprivation of food, excision of parts of the body, or administration of poison, the larger the ant, the more probable its survival.

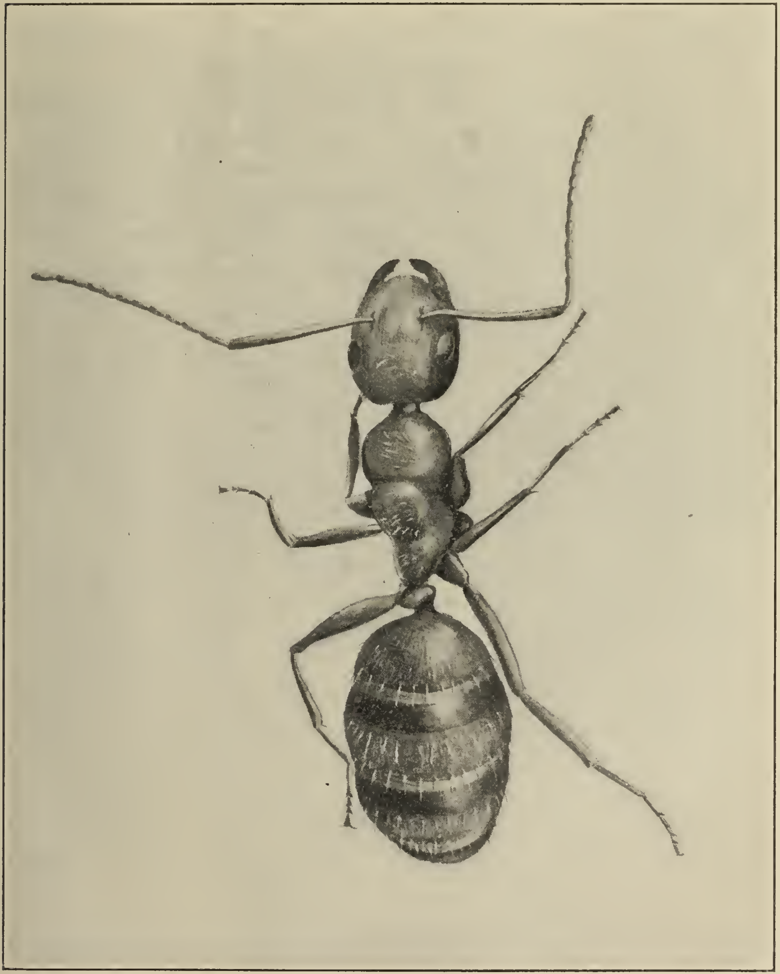

FIG. 1. *Camponotus pennsylvanicus* worker. × 6. From a photograph taken by Mr. J. G. Hubbard and Dr. O. S. Strong, and retouched by Dr. J. H. Macgregor.

There appears to be also a relation between size and natural longevity. Two hundred *Stenamma fulvum piceum* workers,

[1] See paper referred to in previous note, BIOLOGICAL BULLETIN, June, 1904.

majors, minors and minims, were segregated by me in August, 1901, and were kept under observation until August, 1904. At the end of the three years there were eleven survivors, and ten of these were of the largest stature attained by these ants, seven millimeters. Queens, whose longevity probably exceeds that of workers, are ordinarily of larger stature than they.

It has long been known that the size of an ant depends on the quantity and quality of nutriment taken while in the larval stage; but larval nutrition determines not only the size of the ant within the limits of its species; it also determines something of greater influence in the life of the individual and the persistence of the tribe, the probabilities of survival under adverse conditions.

POWER OF RECOGNITION AMONG ANTS

ADELE M. FIELDE

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POWER OF RECOGNITION AMONG ANTS.

ADELE M. FIELDE.

WITH PHOTOGRAPHIC ILLUSTRATIONS BY MR. J. G. HUBBARD AND DR. O. S. STRONG.

When power of recognition is to be tested, appeal for evidence of that power is properly made through the leading sense. We should take evidence from the eagle through its sense of sight, from the mole through its sense of hearing, from the caterpillar through its sense of touch, from the ant through its sense of smell.

That ants have associative percepts which are independent of their chemical sense, is proven by their behavior. Ants learn to be unafraid of the light from which they instinctively withdraw their young.[1] When ants are put into an artificial nest, some weeks are required for their making acquaintance with their domicile, but after such acquaintance has been perfected, they may be transferred to a replica of their abode, whether it be a Petri cell, a glass house, or a wooden box, and they will be wholly at ease in it, and will quietly resume their accustomed routes over its floors or withdraw into it from a strange environment, although it lacks their nest-aura.

I divided a small colony of *Camponotus Pennsylvanicus* into two sections. I fed and fondled the members of the one section until they manifested a sense of safety in my presence, would mount my finger and make a leisurely promenade upon my hand or would return to me after an hour's wandering in my room. These ants not only ceased from biting me when I took them upon my hand, but became so tame that they would

[1] "Supplementary Notes on an Ant," A. M. Fielde, *Proceedings of the Academy of Natural Sciences of Philadelphia*, September, 1903, p. 493.

remain quiescent in their Fielde nest[1] for some minutes after the roof-pane had been lifted.

Upon the ants of the other section I practiced such atrocities as that of lifting them frequently by the leg with a pair of forceps or plunging them for an instant in cold water. The ants of this section quickly acquired such associations with the lifting of their roof-pane, that they fled through the compartments of their house in wild panic whenever I touched the glass.

Preliminary Statements.

Is is the purpose of this paper to show that ants have power to recognize certain ant-odors after months or years of separation from those identical odors, and in order that the evidence presented may be plain, it appears necessary to first restate certain facts, well established by past experiments.

1. Ants of different species in different communities or colonies, and also ants of the same species and variety in different communities or colonies, ordinarily show aversion to each other on meeting, and are especially truculent in defense of their young. The cause of this general and perpetual feud among ants of different colonies, is due to difference of odor, discerned through their antennæ, their organs of smell. Fear and hostility are excited in the ant by any.ant-odor which she has not individually encountered and found to be compatible with her comfort.

2. If ants of different species, or even of different genera or subfamilies, are made pleasantly acquainted with each other within a few hours after hatching, they will thereafter continue to live together in amity, constituting a mixed colony.[2] The acquaintance thus formed is individual, and every ant, in her later behavior, will act in accordance with individual experience. Acquaintance with the odor of one species or colony does not secure from the experienced ant an amicable reception of a representative of any other species or colony.

Among the mixed colonies, formed by me in August, 1903, twenty *Stenamma fulvum* workers lived with a *Cremastogaster lineolata* queen a full year, and the harmony of the nest was as

[1] Described in Biological Bulletin, Vol. II., No. 2, 1900, and Vol. VII., No. 4, 1904.

[2] "Artificial Mixed Nests of Ants," A. M. Fielde, Biological Bulletin, Vol. V., No. 6, 1903, p. 320.

complete as if its inmates had been of one species. Representatives of three subfamilies, *Formica subsericea*, *Stenamma fulvum*, and *Stigmatomma pallipes* lived amicably together five months before the last Ponerine ant died, leaving the Camponotine and the Myrmicine ants to continue together a full year. *Formica lasiodes*, *Lasius latipes*, *Stenamma fulvum*, *Myrmica rubra* and *Cremastogaster lineolata* affiliated through several weeks. All these and other mixed colonies continued until they were disintegrated by me, and friendly treatment was accorded in them to all introduced ants bearing a familiar and therefore an approved odor, while hostile attack was made on every ant bearing an unfamiliar and therefore a disapproved odor. An enlarged acquaintance with ant-odors did not render any ant tolerant of unknown ant-odors, and in no established mixed colony was an ant of any other than the already represented colonies permitted to live, even when the introduced ant was of the same variety.

I have at the present time a mixed colony of *Camponotus pictus*,[1] *Formica subsericea*, *Formica lasiodes*, and *Stenamma fulvum*, and although there are no young of any species in their nest, they have killed every one of several newly-hatched *Cremastogasters* that I have introduced, and they allow none of the latter species to live when hatched in their nest from introduced pupæ.

3. Ants inherit odor from the queen from whose eggs they are developed. That the queen endows her eggs with an odor, and that newly-hatched queens and workers have an odor recognized by their queen-mother, is proven by the fact that an ant may be isolated from the pupa-stage until it is some days old, never having smelled any ant-odor beside that of its own body, and it will instantly snuggle its queen-mother at first meeting, although it may attack other queens, or sister-workers much older than itself. I have known a young worker to identify its mother among five queens of its species presented for its examination. The queen doubtless recognizes her own odor in the callow that she has never before met.

As I have to present the results of several experiments in which the N colony appears, it will be well to here give some

[1] I am indebted to Dr. William Morton Wheeler for kind identification of *Camponotus herculeanus pictus*, and of *Formica pallide-fulva*. A single ant of the last-named species lived for a year in one of my artificial nests with many *Formica subsericea*.

FIG. 1. *Camponotus pennsylvanicus.* Somewhat magnified. Actual length of queen 2 centimeters.

account of that colony. On July 28, 1903, this N colony of *Camponotus pennsylvanicus* was captured on Nonamesset Island, and was housed in a large Fielde nest. It consisted of a queen two centimeters long, some scores of workers, and numerous cocoons. During the first week in August, 1903, the queen deposited about one hundred eggs, and then ceased laying until the following March. The first larva from the August eggs was observed on August 27. From these larvæ the first cocoon appeared on March 13, 1904. On April 8, 1904, there were many large larvæ in the nest, and there were numerous cocoons varying in length from five millimeters to thirteen millimeters. The first cocoon of this brood hatched on April 24, the temperature of the room being 24° C. or 76° F. These cocoons continued to hatch, most of them in carefully segregated groups, until July 14, when the last cocoon rendered its callow.

Experiment A.—Three large workers hatched each in isolation on July 8, 11 and 14, 1904, from the August eggs of the N queen. On August 5, these three worker-ants, ranging from twenty-two to twenty-eight days in age, and never having met any ant-queen, nor any ant older than themselves, instantly affiliated with their queen-mother, and with each other, at the first meeting. The queen manifestly recognized the odor borne by the callows, and at once snuggled with them.[1] They each recognized in her and in each other the only ant-odor they had ever known, that of their own bodies.

Experiment B. — Four N colony workers, the issue of eggs deposited by the queen in August, 1903, were hatched from segregated cocoons, between May 15 and June 15, 1904. On July 6, when the age of these ants ranged between twenty-one and fifty-two days, and they had never met any other ant of their species, I introduced their queen-mother to their nest. The five immediately affiliated and the previously introduced larvæ were brought and placed beside the queen. The queen must have been at least one year older than these workers, and the workers must have recognized in the queen their own odor at hatching time.

Experiment C. — Five Camponotus workers hatched between

[1] The behavior of the ants in these experiments was observed through an orange-tinted roof-pane, under which the ants behave as if in darkness. See "Supplementary Notes on an Ant," referred to in first foot-note.

April 25 and May 10, 1904, out of cocoons from the August eggs of the N queen. They were from fifty-seven to seventy-two days old, and had never met other ants of their species, when on July 6, 1904, I introduced to their nest their queen-mother. Within five minutes the queen had touched antennæ with every worker and had become the center of a friendly group.

Experiment D. — Fourteen Camponotus workers hatched on or after April 24, and on or before May 10, 1904, out of cocoons from eggs laid by the N queen the preceding August. They had never met other ants of their species, when on July 6, 1904, the oldest of the segregated group was seventy-three days old, and I introduced to their nest their queen-mother. There was for an instant great excitement in the nest, and some tentative nabbing of the queen; but in less than one minute the workers had discovered that she was their own. Within a few minutes, four of the workers had licked the queen, one had stood upon her back, and seven others had grouped themselves close about her.

The behavior of these workers toward their queen indicates that her odor is an unchanging one, or that if there be a change in her odor it is but slowly effected.

The behavior of these ants toward their queen was markedly unlike their behavior toward their sisters, when great diversity in ages was represented.

4. Worker ants change in odor as they advance in age,[1] as was shown by experiments made by me in 1902. Further evidence of this fact will be offered later in this paper. Forty days may pass with no change so great as to elicit from former acquaintances any expression of suspicion or antagonism, but in other cases from forty to sixty days so differentiates the known odor as to inhibit association between the ants.[2] This suspicion

[1] "Notes on an Ant," A. M. Fielde, *Proceedings of the Academy of Natural Sciences of Philadelphia*, December, 1902, p. 609. Also "Cause of Feud Between Ants of the same Species Living in Different Communities," A. M. Fielde, Biological Bulletin, Vol. V., No. 6, 1903, p. 327.

[2] All the ants employed in the experiments recorded by me have been under my constant care and my frequent observation. No person beside myself has ever had access to them. They have spent the summers, from the first of June to the end of September, at the Marine Biological Laboratory, Woods Holl, Mass., and the remainder of every year in New York City.

or antagonism is always shown[1] by the younger ants, toward the older, if the ants be of the same colony, and if the young ants have been guarded from association with ants older than themselves.[2]

Experiment E. — On July 18, 1904, I put into the nest of two segregated workers of the N colony, hatched from cocoons taken from the wild nest July 28, 1903, and at the time of this ex-

[1] In all experiments here recorded, unless a contrary condition is indicated, the ants whose recognition of a visitor was in question had in their nest inert young that had engaged their attention during several previous days. The action of resident ants toward a visitor is much more prompt and decisive when there are larvæ or pupæ in the nest.

[2] In experimenting with ants, a third source of individual odor, not set forth in this paper, although always reckoned with in the experiments, lies in the other ants with which the individual associates. This odor appears and disappears with certain external conditions. Ants take on the odor of their associates in a mixed nest, and this incidental odor usually disappears after about ten days of isolation, the inherent odor then reasserting itself. Ants may be smeared with the juices of ants of another species or colony and may thereby become immediately subject to attack from comrades from whom they have been but momentarily removed.

I have lately submerged ants for eighty hours or more in distilled water at a temperature of 10° C., putting two species or two colonies into the same water, using thirty-five cubic centimeters for a dozen ants, and I have found that the ants of each species or colony, when revived and returned to their former nest, were attacked as are enemies, and that ten days proved to be an insufficient time for the reassertion of the inherent over the incurred oder. That these attacks from comrades were due to the alien odor acquired in the water and not to some other cause, was shown by the fact that when similar ants were likewise submerged in unmixed groups, the returned ants were amicably received by their former comrades.

I thus submerged, in thirty cubic centimeters of water, three *Camponotus pictus* and fifteen *Stenamma fulvum*, for eighty hours. One of the Camponotus revived, and a day later I returned it to its three former comrades, employed in the care of cocoons in a small Fielde nest. The three instantly attacked the one, and would doubtless have slain it had I not interfered. Having rescued, I isolated it for ten days in a Petri cell, and then again returned it to its former nest. Two of the three resident ants at once attacked and killed it. Of the Stenammas several revived, and on my returning them to their former nest, they were all killed by their quandam associates.

Of four Stenammas that revived and recovered after eight days submergence in company with five *Camponotus pennsylvanicus*, three were killed by former comrades on my returning them to their nest. One of the four was isolated by me, in a Petri cell, for twenty days before I returned her to the nest, and there the returned ant was for some minutes the center of an examining circle of many ants. A day later she was being dragged by two workers, but she was ultimately restored to good standing in the nest.

It is interesting to observe the puzzled or critical demeanor of an ant engaged in ascertaining whether a new-comer has an incurred or an inherent foreign odor.

periment eleven months old, a callow of the same colony, just seven days old. The callow received careful examination from the older ants, and was then amicably entertained by them. They doubtless recognized in the callow their own early odor.

Experiment F. — On July 6, 1904, after the queen and the fourteen workers mentioned in experiment D were all serenely grouped in the nest there described, I introduced two workers[1] of the N colony, hatched between August 14 and September 3, 1903, and therefore about ten months old, while the resident ants were not over seventy-three days old. The two visitors had affiliated previously with the N queen, and had been approved by her. They were probably the issue of her eggs of the previous year. They were, however, seven or eight months older than the resident workers, and, although they were larger than any worker resident, they were persistently attacked and dragged, sometimes by more than one resident at a time. The visitor-ants did not retaliate. One of them tried to placate her young sisters by offers of regurgitated food, and after a half hour there were signs of diminution in the strength of the attacks. I then removed the visitor-ants. There are all degrees in the hostility shown by ants to one another, as well as many variations in the degree of closeness in their affiliations.

In this experiment, the older ants had met no younger ones during their lives, and the younger ones had never before encountered sisters older than themselves.

Recognition of Odors of Other Species.

The A Series.

Evidence of ability to recognize odors that have not been encountered during many months has been taken from ants of diverse species and of a recorded life history. In August, 1903, I formed a mixed colony of workers of *Camponotus pennsylvanicus*, *Formica subsericea* and *Stenamma fulvum*, all of whom hatched in my artificial nests between August 14 and September 3. Every ant within a few hours after its hatching was

[1] My method, which is also Forel's, of marking ants so as to readily distinguish them from others of their species, is described in a foot-note of "Notes on an Ant," already referred to. Ants were marked whenever an experiment required it.

made acquainted with every predecessor in this mixed colony and no discord appeared in the new nest. This mixed colony was marked A. On September 24, when none of these ants was less than twenty days old, and none more than forty-one days old, I separated them according to genera, putting the Camponotus, the Formicas and the Stenammas each into a Fielde nest that was new and therefore had nonest-aura. The nests were respectively marked A1, A2 and A3. No young was permitted to hatch in any nest, but inert young from the workers' eggs, or introduced larvæ from other nests were always present when tests of recognition were to be made as severe as possible. No ant of any species was admitted to either of the segregated groups except as recorded in the experiments.

Nest A1. — On April 8, 1904, there were in the Camponotus nest,

FIG. 2. *Stenamma fulvum*, with larvæ and pupæ; slightly magnified. Actual length 5 to 7 mm.

marked A1, three large and vigorous workers, without young. I then introduced two Stenammas that the Camponotus had known in the previous September in the A nest. The Stenammas manifested terror and the Camponotus made instant and violent attack upon them, so that I intervened in the ensuing battle, saved the lives of the Stenammas, and returned them to their own nest. It was evident that during the six and a half months of separation these ants had changed in odor, and that the odor borne by them in April was unknown to the ants with whom they had associated in the previous September. I was unable to offer to this group A1 the companionship of young Stanammas having the same odor as had their former associates at the time of association, and young Stenammas taken at a later date from the wild nest in the summer of 1904, were always killed by them. The Formicas were likewise rejected.

Nest A2. — The Formicas that had lived, none less than twenty and none more than forty-one days, in nest A, were domiciled in nest A2. They had been separated from the Camponotus six and a half months, when on April 8, 1904, I introduced into their nest, where there were twenty-six workers and no young, a Camponotus from nest A1, comrade of their earliest days. The Formicas immediately attacked the Camponotus, and I removed the latter to save her life. Six month's progress in odor formation had carried her outside the acquaintance of her former associates. The same antagonism was manifested toward the other two residents in nest A1.

These Formicas continued to reside in their nest and had laid a few eggs, which were under their care when on April 25, 1904, I introduced to their nest three Camponotus newly hatched from eggs that were laid in August, 1903, by the queen-mother of the Camponotus in nest A1. These young Camponotus received amiable welcome from the resident Formicas, and during the next ensuing days, to May 10, I added several more callows. The Formicas, now eight months old, continued to live amicably with the young Camponotus, whose odor had been known to them in their earliest days. They regurgitated food to the young ants, permitted them to carry the egg-packet and care for the larvæ, and in all respects treated them as if of their own colony. There was no death in the nest for twenty days after the introduction of the young Camponotus, but I removed them on June 25. *The Formicas recognized, after seven months of separation from it, an ant-odor previously known to them.*

I was unable to introduce to this nest any young Stenammas that the Formicas would accept, as I could command none of the same lineage and age as those known to them in the autumn of 1903. The individual Stenammas in nest A3, with whom they had formerly associated in the A nest, were now of another odor, and the Formicas refused to affiliate with them.

Nest A3. — The Stenammas in this nest had lived in nest A, none less than twenty and none more than forty-one days, and since September 24, 1903, they had met no ant other than those in their own nest. On April 8, 1904, I introduced into their nest, where, there were forty-one workers, a former comrade, a Formica from nest A2. She was fiercely attacked, and I removed her. Other Formicas from the same nest were likewise attacked. I then introduced Camponotus from nest A1, and they were received with like animosity. It was instantly made evident that the resident Stenammas found in every visitor an unfamiliar odor. I removed each visitor as soon as her status among these Stenammas had been made plain, and the A3 nest remained quiescent until April 24, when I introduced a day-old Camponotus, the issue of an egg laid the previous August by the mother of the rejected individual in nest A1. Within a few minutes after its introduction, three of the Stenammas had licked the Camponotus, and all the Stenammas had viewed it with approval. It was taken care of as tenderly as if it had been a Stenamma callow. On the same day I added two newly hatched Camponotus of the same lineage, and they were kindly entertained until April 27, when I removed them to another nest of Stenammas, the M nest. These M Stenammas were of the same age and colony as were the Stenammas in nest A3, differing from them only in never having lived with Camponotus. There were also about the same number of resident ants. As soon as I introduced the Camponotus into the M nest, the Stenammas attacked them, and although they were double the size of the residents, and of tougher integument, the residents harried them to death. The

FIG. 3. *Lasius latipes*, magnified. Actual length 5 millimeters.

behavior of the M ants indicates that that of the A3 ants was based on a recognition of odor, and that *the Stenamma's power of recognition extends through an interval of at least seven months.*

The B Series.

Another series, marked B, was also established, having its beginning on July 20, 1903, additions of newly-hatched workers being made to the mixed colony up to August 28, or during a period of forty days. The B mixed colony consisted of *Stenamma fulvum* of the C colony, *Lasius latipes* of the F colony, and *Cremastogaster lineolata* of the H colony. On September 24, 1903, I separated these ants according to genera, segregating each genus in a new Fielde nest, marked B1, or B2 or B3, where it remained until the end of the recorded experiments, with no other ants than those here mentioned ever introduced or permitted to hatch in its nest.

Nest B 1. — On April 1, 1904, over six months after their segregation, there were in the B1 nest about sixty Stenammas. I then introduced to their nest two Lasius, their former comrades, taken from nest B2. No fear was evinced by the Lasius, and no aversion by the Stenammas. Residents and visitors perfectly affiliated, and the two Lasius remained safely in the B1 nest four full days. I then, on April 5, removed the two Lasius, and put them into a nest of *Stenamma fulvum* where there were two queens and sixteen workers, all hatched in August, 1902, and therefore a year older than were the ants in nest B1. They were from the same C colony, but had never associated with Lasius. In this nest the Lasius tried to flee or to hide, behaving as do ants when in a nest of recognized enemies. At first they eluded the Stenammas, but when I again examined the nest, on the evening of the same day, both Lasius had been killed and put on the rubbish-heap.

It appears that these very strong-smelling ants, the Lasius, had not so changed their odor during six months that the B1 Stenammas did not recognize it. But on June 11, 1904, I took from the wild nest of the F colony two Lasius workers, of unknown age, and introduced them into the B1 nest of Stenammas. They were soon killed, and two like them were also killed when introduced on the ensuing day.

On August 11, 1904, I introduced a newly hatched Lasius from the R colony, and it was at once killed.

On June 11, 1904, I sought in the old wild nest of the Lasius F colony for a remainder of its population, and secured a few workers and four larvæ. On August 4, three cocoons and one naked pupa had appeared from these larvæ, and from these cocoons the first worker hatched on August 18. It was immediately put into the B1 nest, where it appeared as a yellow pigmy among brown giants. It was much patted with the antennæ, was licked, and was cared for among the eggs, larvæ and pupæ over which the Stenammas were strenuously engaged. *The Stenammas recognized an odor from which they had been eleven months separated.*

The Stenammas of nest B1 met no Cremastogaster from September 24, 1903, until July 7, 1903, when I introduced into their nest, occupied by fifty of the old residents, with larvæ from their own eggs, several newly-hatched *Cremastogaster lineolata* from a wild nest V. Within a day all these young Cremastogasters had been killed and their bodies piled together in a corner of the food-room. Others of their kind met a like fate on July 9.

On the 24th of June, I had happily secured some larvæ, with workers to rear them, from the wild nest of the old H colony of Cremastogasters, and on July 22, I put a dozen callows, newly hatched from this stock, into the B1 nest, where the residents were much engrossed with their own pupæ. Two or three of these introduced callows were killed and dismembered, while all the rest were accepted into close companionship by the resident Stenammas. The Cremastogasters were permitted to walk over or rest upon the pupa-pile, they were gently licked, and none was harmed during the ensuing twelve days. I then removed them to prepare the nest for another experiment.

But while the Cremastogasters were still in the B1 nest, on July 25, I introduced a newly hatched *Formica lasiodes*, in order to see whether these Stenammas would accept a callow of unknown odor. This visitor was immediately killed and carried to the rubbish-pile.

Further evidence that the Cremastogasters were offspring of the queen that laid the eggs from which the B3 Cremastogasters issued, was obtained by putting some of them into K nest with an H colony queen that had never before met any Cremastogaster workers of any colony, having spent her whole life since she was hatched in August, 1903, with Stenamma workers. This queen and the Stenamma workers with her, all accepted the H colony Cremastogaster workers hatched in the latter part of July, 1904, and continued to closely affiliate with them. They were doubtless of the same odor as was the queen in this K nest, being progeny of the same queen in different years, the queen in K nest still retaining her queen-mother's odor, while the worker-callows bore the queen-mother's ordor as yet unchanged by ageing.

Stenamma fulvum in my artificial nests, when they had no young of their own, have many times permitted Cremastogaster pupæ to hatch in their nest and to live there among them. But when engaged in the care of their own young, they have, unless previously acquainted with Cremastogasters, always killed the Cremastogasters as soon as the latter hatched and began to move about. It appears that the Stenammas of nest B1 recognized an old acquaintance in the young Cremastogasters of the H colony, and resumed toward them their accustomed behavior. In other words *the Stenammas recognized an odor after an interval of ten months in which that odor had not been encountered.*

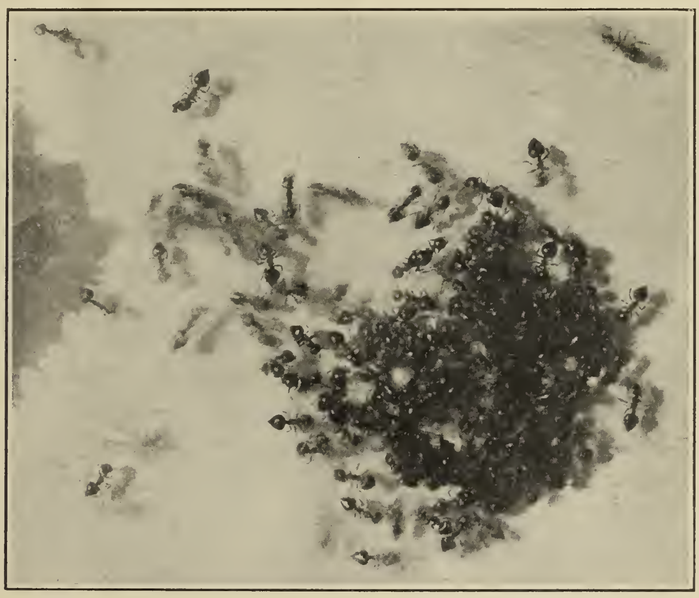

FIG. 4. *Cremastogaster lineolata ;* magnified. Actual length 5 millimeters.

Having removed all Cremastogasters from nest B1 on August 4, there followed an interval of twelve days in which they had met no Cremastogasters. Then on August 16, 1904, I introduced to their nest one of their old comrades in nest B, a Cremastogaster from whom they were separated on September 24, 1903. This visitor was killed by them within a few hours. In less than eleven months she had attained an odor unknown to them.

Nest B2. — There were in April, 1904, so few of the Lasius in this nest that I gave their power of recognition no test within their own nest. All of them were used till their extermination, in the experiments in nests B1 and B3.

Nest B3. — On April 5, 1904, over six months after the segregation of the Cremastogasters, there were about fifty workers in their nest, B3. I then introduced two Lasius, with whom they had lived in amity some forty days, and from whom they had been separated over six months. The residents attacked the visitors from nest B2, and would have slain them had I not rescued them. There was no room for doubt concerning the absence of recognition among the Cremastogasters of the present odor of the Lasius, ants presenting an odor so strong that a single one of them is very impressive to human nostrils. I was unable at that time to introduce to these Cremastogasters any *Lasius latipes* younger than were those with whom they had formerly associated. But on August 12, 1904, when I introduced a newly-hatched *Lasius latipes* of the X colony, they immediately killed it. On August 20, 1904, I introduced a young Lasius from the wild nest of the F colony, a sister of the one put on the 18th into nest B1. This ant was amiably received. *The Cremastogasters recognized an odor from which they had been eleven months separated.* On the same day, August 20, 1904, I also introduced an adult *Lasius*, of unknown age, but also of the F colony, one of the nurses of the newly-hatched ant already accepted. This adult *Lasius* was killed during the ensuing night.

On April 8, 1904, I introduced to these Cremastogasters, in nest B3, two of the Stenammas with whom they had pleasantly lived for forty days, in the preceeding autumn, and from whom they had been separated more than six months. One of the visitors behaved as if in an alien nest, showing fear and attempting to escape. The other fought with a resident. Absence of recognition on either side indicted such change of odor during the period of separation as to render these ants unacquainted with one another.

Early in July, 1904, I was able to introduce to this nest several newly-hatched Stenammas from the wild nest of the C colony, kindred of the ants in nest B1. There were many queens in that wild nest. That the callows might not bear the odor of older ants, I segregated some pupæ, and offered the callows newly hatched therefrom to the ants in nest B3, but these callows were all killed and dismembered within a few days after their introduction. They were doubtless the progeny of other queens than those which produced the early acquaintances of the Cremastogasters in nest B3.

Hypothesis.

From such data as is here presented, correlated with records of past years, it is possible to diagramatically represent the probabilities that an ant, isolated from the pupa-stage, would encounter a known odor at a first meeting with another ant of her colony. If the odor of a queen be unchanging, if she impart odor to all her eggs, if that odor be perceptible in the inert young, and if from the beginning of the active life of the worker there be a progressive change in the inherited odor borne by her, then from each summer's deposit of the queen's eggs there would be in the following summer more than one odor among the workers, because all the eggs of a queen are not hatched during the summer in which they are deposited. We may suppose a young, fertilized queen, the founder of a colony, to deposit eggs in her isolated cell in July, and to have reared her first small brood in not less than sixty days.[1] The eggs laid by her in the latter part of summer or early autumn would reach the larval stage in late autumn, and in that stage would be carried over to the next June, to hatch as ants in summer. While this second brood was developing, the first brood would have advanced to the odor of ants many months old. Their odor would then be unknown to an ant newly hatched from the queen-mother's egg and having the odor of its own body as its only criterion of ant-odor. Succeeding years would bring similar conditions.

In Sir John Lubbock's nests, one ant-queen lived to her fourteenth, and another to her fifteenth year; but the purpose of the diagram is reached by the supposition that the queen lives ten years.

[1] For time of incubation of eggs, larval period and pupa-stage in *Stenamma fulvum*, see "A Study of an Ant," A. M. Fielde, *Proceedings of the Academy of Sciences of Philadelphia*, September, 1901, p. 430. The time of incubation appears to be twenty days for all ants that I have observed; the larval period may be extended to at least one hundred and forty days in a high temperature, and probably to a much longer time in cold weather; and the pupa-stage occupies about twenty days. I have known the larval period to be passed in twenty days.

Diagrammatic representation of the progressive change of odor in worker-ants.

The arabic numerals, in horizontal line, indicate successive years in the life of a queen, the founder of a colony.

The Roman numerals at the left hand, denote successive broods from the eggs of this queen, here supposed to be the only fertile female of the colony.

The letters are used as symbols of the odor of worker-ants of this colony.

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        1      2      3      4      5      6      7      8      9      10
I......a......b+a.....c+b......d+c......e+d.....f+e......g+f.....h+g......i+h......j+i
II.................a......b+a......c+b......d+c......e+d.....f+e......g+f......h+g......i+h......j+i
III............................a......b+a......c+b......d+c......e+d.....f+e......g+f......h+g......i+h......j+i
IV.......................................a......b+a......c+b......d+c......e+d......f+e......g+f......h+g......i+h.....j+i
V..................................................a......b+a.....c+b......d+c.....e+d......f+e......g+f......h+g......i+h......j+i
VI..............................................................a......b+a......c + b......d+c..... e +b......f+e......g+f......h+g......i+h......j+i
VII........................................................................a......b+a......c+b......d+c......e+d......f+e......g+f......h+g......i+h....j+i
```

If all the ants from this queen's seventh year eggs and having the *a* odor were segregated from their pupa stage, onward, the only ants of this colony with which they would affiliate on meeting would be such ants as were hatched in her seventh year from eggs laid by the qeeen in her sixth year. If groups of such ants were segregated they would, if hatched less than forty days apart, affiliate on meeting.

Ants of the *b*, *c*, *d*, *e*, *f* and *g* odors would affiliate with ants of the *a* odor, because that odor was once familiar to them in their own bodies. It would be a recognized odor.

The conditions of odor in her colony during her lifetime are crudely and only approximately represented by the diagram, but the representation conduces to an understanding of certain phenomena observed by me in the C colony, which I have now studied four years, in its natural nest, and in my artificial ones.

When queens, instead of flying away to found new colonies, remain in the colony where they hatched and increase its population by their progeny, there is opportunity for all the members of that colony to receive a liberal education of the chemical sense. Every ant acts on individual experience, and if its experience be narrow it will quarrel with many, while acquaintance with a great number of ant-odors will cause it to live peaceably with ants of diverse lineage, provided the odors characterizing such lineage and age environ it at its hatching. If some of the workers were separated from their colony in their youth, and kept segregated several years, the sequestered ants could amicably meet younger ants from their old home nest only by an act of memory, or a power of recognition spanning the interval of their separation from their colony. Precisely this condition has been created by me with ants of the C colony.

The C colony is a great community of *Stenamma fulvum* that lives under stones scattered at considerable intervals over an area ninety yards in diameter, along a lane and pasture. I have been unable to find any other colony of Stenammas in its vicinage. Many of its young queens appear to mate with their kin and remain in the colony. I have found as many as fourteen deälated queens in a single shovelful of its nest-earth. The queens and workers from its extreme limits always affiliate unhesitatingly on meeting within its domain.

On August 22, 1901, I took from under a central stone of this colony queens, males and workers, and divided them into two sections, each of which was kept segregated in a Fielde nest for two years. No young was permitted to hatch in either section, and when I united the two sections in August, 1903, they affiliated instantly, and also affiliated less perfectly with queens and workers freshly brought from the wild nest.[1] I kept the ants of

[1] Detailed account of these meetings may be found in "Cause of Feud between Ants of the Same Species," already referred to, p. 328.

the two united sections, again without young, another year, until August, 1904, when I introduced to their nest marked queens and workers from their old wild nest. Of the two queens introduced one was at once received into full fellowship. The other was simultaneously licked and dragged by different worker-residents, but was accepted at the pupa-pile within a few hours. The workers introduced had kindly reception. Of one hundred and fourteen callows introduced one by one, or a few at a time, an interval of repose being given between the removal of one and the introduction of its successor, only two were attacked. While it is true that all the accepted callows of the summer of 1904 might have had the odor of the resident queen, it appears more probable that most of them *bore odors that were recognized by the resident workers after the lapse of three years.*

These ants had certainly not within their three years of segregation met a two-year-old or a one-year-old ant of their colony, from outside their artificial nest. In August, 1902, I segregated a queen and workers all hatched during that month, and in August, 1903, I likewise segregated a newly hatched and similar group. All these ants were of the C colony, and no young was permitted to hatch in any of these groups, each in its artificial nest. In August, 1904, I therefore had command of ants of the C colony, one group in the C nest, consisting of ants brought in from the wild nest on June 24, 1904; one group C1, just one year old, one group C2, just two years old, and one group C3, three years old or more. All had been acquainted with their seniors before segregation. In August, 1904, the three-year-old ants received amiably, within their nest, ten of the two-year-old ants, and ten of the one-year-old ants, indicating a perfect recognition of odors no longer represented in their own nest, and from which they had been long separated.

On the other hand, when I introduced the three-year-old ants, queens or workers, into a nest populated with hundreds of workers taken in June, 1904, from the wild nest or hatched within that nest during the present summer, the three-year-olds were always fiercely attacked. *They had become an alien colony to the younger generations of their former wild nest.* The C colony has been much harried in its natural domain, by the rebuilding of stone fences, by repairing of the lane road, and by my own depredations. Ants so old as my three-year-olds have apparently become almost unknown in the wild colony.

The older the colony, the fewer would be the chances that any ant, segregated as a pupa and always kept in isolation, would find its own odor in any ant taken at random from the nest from which said pupa had been taken. In August, 1904, I thus isolated pupæ and the ants hatched therefrom, and from among many experiments made with them, I record the following as typical : I isolated a pupa from the C colony wild nest, and when the ant that hatched from it was eleven days old, never having smelled any ant-odor other than that of its own body, I introduced one by one to its Petri cell, where it was engrossed in the care of introduced larvæ, all the three-year-old ants to the number of twelve, all the two-year-old ants to the number of seventeen, all the one-year-old ants to the number of forty-two, and seven C nest ants of precisely its own age, so that the number of visitors arriving singly and at intervals amounted to eighty. A period of repose was provided after the removal of one visitor before another was introduced. Every one of these visitors was at first meeting violently attacked by this callow, dragged away from the larvæ, and in some cases taken outside the Petri cell, if I lifted its cover. Sometimes a visitor violently attacked the resident callow, and she had to be rescued by me from sudden death. In other like series of experiments with isolated callows the resident callow sometimes found a congenial odor in a visitor and willingly permitted her to share in the care of the larvæ.

Callows having their origin in different parts of the C colony area behaved alike, and it appears improbable that all of those tested could have been the product of eggs, larvæ or pupæ brought in by raids on another colony, especially when the greatness of the C colony is considered and its location studied.

Other experiments with callows from this colony gave support to my hypotheses. On July 11, 1904, there hatched in nest C3, a pupa previously introduced by me from the C nest. I left it seven days with the three-year-old ants, and then transferred it to a Petri cell, giving it a few larvæ to care for. This isolated callow knew only its own odor, that of worker ants at least three years old, and that of a queen. I then, a day or two later, introduced into its cell, one by one, all the one-year-old ants in nest C1, removing each visitor as soon as the action of the resident was decisive, and allowing a period of repose before another visitor was introduced. She affiliated with the first, third, fourth, sixth, seventh, eighth, tenth and eleventh, and attacked the second, fifth and ninth.

I likewise introduced two-year-old workers from nest C2. She affiliated with the first, third, fourth, fifth, seventh, ninth and twelfth, and attacked the second, sixth, eighth, tenth and eleventh. She did not attack the C2 queen, but the queen so persistently avoided her as to make the test undecisive.

In the same manner I tested a callow, hatched on July 11, in nest C2, where all the ants beside herself were two years old. When this callow had spent seven days in the C2 nest, and one day in isolation with larvæ to care for, I introduced into her cell workers from the C3 nest, where all the ants were three or more years old. She affiliated with the second, fourth, fifth, eighth, eleventh and twelfth, and attacked the first, third, sixth, seventh, ninth and tenth visitors. I then introduced one-year-old ants from. nest C1. She affiliated with the first, second, third, seventh, eighth, ninth, tenth and twelfth, and attacked the fourth, fifth, sixth and eleventh visitors.

I intended to likewise test a callow reared in nest C1, and I expected to find that this callow would reject all three-year-old ants; but I unfortunately dropped an unmarked three-year-old ant into nest C1, and thereby so vitiated the nest as to make it useless for this experiment.

A comparison of all the tests made gave a consensus of testimony that the C3 ants, *the Stenammas, recognized and adapted their behavior to ant-odors that they had not encountered during three years.*

As the workers are not supposed to reproduce colonies, and as the queens are not supposed to change their own odor, how then would queens of diverse odor originate through the ageing of the workers?

In 1901 I segregated winged queens of the C colony,[1] putting

[1] "Notes on an Ant," previously referred to, p. 605.

some of them into nests with kings of their own colony and others of them into nests with kings of alien colonies, and believed that I ascertained that the progeny of sister queens affiliated, regardless of paternal influence in the egg from which the ants issued. I then supposed that queen-ants captured before swarming must be virgin queens. I now know that virgin queen-ants often mate with the males within the maternal domicile, and that neither the possession of wings nor an early capture guarantee the virginity of a queen. Only by sequestration of the queen from her pupa-stage can her virginity be secured. I have had *Lasius latipes* queens drop their wings and lay eggs soon after being brought from the wild nest from which they had not yet swarmed. In my artificial nests, I have observed the persistent avoidance, by queens, of kings of alien colonies and their manifest preference for kings of their own colony. Mating in captivity, in artificial nests, is not uncommon, and it must be frequent in the wild nests before the swarming.

We know that the eggs of workers often produce sturdy males, and it appears probable that such males impart to the fertilized eggs of the queen something of the odor attained by the worker-mother at the time when the egg, producing the male, was deposited. This would differentiate odors in the progeny of sister queens, and cumulative differentiation would account for ultimate differences in the odor of queens of the same species and variety. When queens remain in the mother-nest after mating, and there rear their broods, that colony must become one of much mixed odors, as is the C colony described in this paper. Fertilized queens, departing from the maternal nest, would found colonies whose issuing queens would have an odor depending on the age of the workers who were mothers of kings hatched in the season in which their founder-queens mated.

Besides discerning the aura of the nest and other local scents and the track laid down by its feet,[1] an ant perceives in other ants the *incurred* or incidental odor which appears with conditions and disappears in course of time ; the *inherited* odor derived from the queen-mother, apparent in the eggs, larvæ, pupæ and newly

[1] "Further Study of an Ant," A. M. Fielde, *Proceedings of the Academy of Natural Sciences of Philadelphia*, November, 1901, p. 521.

hatched young, and probably strengthening as size increases through the three inert stages of development; the *progressive* odor, that distinguishes the worker and changes or intensifies with her advancing age; and the *specific* odor which pertains to the species or tribe. Adding to these perceptions the power of recognizing familiar odors after a lapse of months or years, the ant appears to be well equipped for life in her world.[1] If she has not reason and imagination, she has at least the ground on which to exercise both, cognoscence of past experiences.

[1] The organ discerning the nest-aura and probably other local odors lies in the final joint of the antenna, and such odors are discerned through the air; the progressive odor or the incurred odor is discerned by contact, through the penultimate joint; the scent of the track, by the antepenultimate joint, through the air; the odor of the inert young, and probably that of the queen also, by contact, through the two joints above or proximal to those last mentioned; while the next above these by contact also discerns the specific odor. It is probable that the size of the queen determines the amount of odor diffused by her. The amount of odor diffused by or discerned in the larvæ and pupæ may be the determining factor in the assorting of the young according to size, as is common among ants. The results of many experiments whereby the function of many joints in the antennæ were determined by me in 1901–1903 in *Stenamma fulvum* are recorded in "Further Study of an Ant" and "Cause of Feud among Ants of the same Species," above referred to. The joints in the antennæ vary in different species, from four to thirteen.