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6. Ants as models for mimicry.

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Many naturalists, of whom Father Wasmann is one of the most distinguished, have made a special study of the insects which mimic ants — a study so comprehensive and varied that a large and ever-growing mass of literature has grown up around it. It is probably correct to say that all who have contributed to this subject believe that ants possess special qualities which are associated with their appearance in the minds of enemies; so that many of these enemies recognise and avoid ants because they object to the qualities; that therefore the superficial resemblance to ants is advantageous and has developed by natural selection. This conclusion is confirmed by a consideration of the widely different methods by which the mimicry is brought about. The argument was stated thirty years ago by the present writer in the following paragraphs:

“. . . The means by which the resemblance to ants are brought about are diverse, the end — the resemblance itself — is uniform. Furthermore, the likeness is almost always detailed and remarkable, however it is attained, while the methods made use of differ absolutely. Such a result, it would seem, is the most complete proof of the operation of natural selection that can be attained, short of the actual demonstration of its action by observation and statistics . . .

“When one insect resembles an ant by the superficial alteration of its whole body-form, another by the modification of a shield-like structure which conceals its unaltered body, another by having the shape of an ant painted, as it were, in black pigment upon its body while all other parts are concealed; another by a further modification of its body, so that it represents not an ant only, but the object which the ant is almost always carrying — when the effect of all these results is heightened by appropriate habits and movements, we are compelled to believe that there is something advantageous in the resemblance to an ant, and that natural selection has been at work. The phenomena do not merely disprove all other suggested causes of change, but they constitute the most powerful indirect proof of the operation of natural selection.” (Linn. Soc. Journ., — Zool., 1898, Vol. XXVI, p. 595.)

So far as I am aware, no dissent from this conclusion was expressed until 1922 when Dr. J. Bequaert published an interesting and valuable account of the enemies of ants (Bull. Am. Mus. Nat.

Hist., Vol. XLV, p. 271—331, New York, 1922). From the facts there collected the author inferred that the mimicry of ants, which he fully admitted at least in some cases, was useless as a protection against enemies. "Because ants have many enemies the resemblance to ants cannot protect against enemies" is I believe a fair although condensed statement of his argument. Similar reasoning would, with even more justification, lead to the conclusion that the danger would far outweigh the advantage of the well-known longitudinal stripes and green colour borne by grass-feeding larvae. It might be pointed out that the development of an important section of the larger Mammalia has been due to the food-supply provided by the ever-spreading and conquering grasses. How dangerous to resemble grass when such quantities are eaten at a single meal by these huge animals!

It is a mistake to suppose that naturalists, with the single exception of Haase (Bibliotheca Zoologica, 1891—93, Stuttgart), have ever supposed that even the most formidable or the most distasteful insects are immune from attack. If it were so, such species would speedily succumb to the most deadly enemy of all, — their own unchecked population. They would quickly exhaust their food-supply and die of starvation.

Dr. G. D. H. Carpenter in a paper read before the British Association in 1913 has clearly stated the reasonable belief of most zoologists:

"Supporters of the theory of mimicry believe that certain insects escape being eaten by vertebrates generally on account of distastefulness, the possession of a sting, spines, &c. Such are said to be protected insects. This is not meant to imply protection against every enemy, or even against every vertebrate enemy. Such a state of affairs would soon bring itself to an end by the unlimited increase of such an insect. There is evidence that bee-eaters, for instance, prey especially upon such a typically protected insect as the honey-bee; that cuckoos prey especially upon hairy caterpillars shunned by other birds." (Rep. Brit. Assoc., 1913, p. 516.)

The following sentence states one chief conclusion from all the experiments I was able to make or find recorded, up to the year 1887: "The likes and dislikes of insect-eaters are purely relative, and if pressed with hunger the most disagreeable and highly conspicuous insects may be eaten." (Proc. Zool. Soc., London, 1887, p. 267.) The attacks upon ants' nests made by certain birds, in winter, the time of stress, is a good example of this principle.

How tremendous the attacks upon ants must be is proved by an indirect line of reasoning. "If each ant-community, when it came to an end, were replaced by another, the average number of communities would be maintained. But this means that, out of all the vast clouds sent forth by each community in all the years of its existence, only a single female will, upon the average, succeed in founding a community to take the place of the parent one." (Proc., 1924, p. lxix)[1]. And this indirect argument is supported by direct observations; for the winged, sexually mature individuals of ants and termites are known to be attacked on a vast scale. Thus H. W. Bates, writing of the males and females of the Saüba ant (*Oecodoma cephalotes*), records that "They are so eagerly preyed upon by insectivorous animals, that on the morning after their flight not an individual is to be seen, a few impregnated females alone escaping the slaughter to found new colonies[2]."

The attacks on winged termites appear to be even more indiscriminate. A striking example of the gathering together of the most varied insectivorous forms attracted by a flight at Barrackpore is recorded by the late Mr. G. A. James Rothney (Proc., 1918, pp. lxiv—lxvi).

Such are the attacks upon the flying sexual stages of ants and termites. Why then are there not equally marked attacks upon the immature forms in the nest and upon the workers always abundant in its vicinity and issuing in multitudes upon the least disturbance? The enemies which devour the flying ants could also obtain any number of workers by disturbing the nest. That, with certain exceptions, these attempts are rarely made is to be reasonably explained by the fact that the workers are specially protected against most insectivorous enemies. And, as we should expect, it is the workers and not the winged forms which are mimicked by other insects and by spiders. It must be added that the great relative size of the winged forms, especially the females, is doubtless an additional reason for the severity of the attacks upon them.

Strong confirmatory evidence of the special powers of defence possessed by worker ants is provided by the associated warning characters which so many of them possess, such as the holding up of the abdomen by an irritated *Cremastogaster*, the loud hissing

[1] The Proceedings and Transactions of the Entomological Society of London are to be understood by "Proc." and "Trans.", respectively, throughout this paper.

[2] "Naturalist on the River Amazons" 5th. Ed., Lond, p. 15.

made on the slightest vibration of the ground by the termite-raiders (*Megaponera foetens* F.) on the march, and the disgusting smell emitted on the same provocation by *Paltothyreus tarsatus* F. The late Mr. C. O. Farquharson has given the following brief description of the aggressive tactics of some of the African ants: "A Driver (*Dorylus*) soldier will bite at one's bootlace or puttee in impotent fury and even the relatively tiny soldiers of a *Cremastogaster* colony make for the enemy at sight. *Odontomachus* hasn't got such a name for nothing. He lives up to it. As for *Oecophylla*, at the first alarm the whole crowd come out on to the surface of the nest ready for action, all facing the enemy . . . *Oecophylla* inspires respect, and so does *Megaponera*." (Trans., 1921, p. 424.)

Major R. W. G. Hingston has also given a graphic description of the pugnacity of the Oriental *Oecophylla smaragdina* F., and how the workers communicate alarm by attitude and movement as well as by tapping on the nest, when "they pour out in thousands, rush down the branches, drop from the foliage, and in a minute one's body is covered with ants. They attack the skin, cut it with their jaws, then squirt poison into the wound. Also they shoot poison through the air which smarts severely if it gets in the eyes. The attack . . . is fierce enough to protect the ants even from the largest mammals." (Proc., Vol. II, 1927, p. 92.)

In my own limited experience the most evident reliance upon powers of defence was exhibited by the workers of *Myrmecia vindex* Sm., which I had the opportunity of observing on the bank of the Swan River near Perth, W. Australia, in August 1914. "This species is one of the well-known 'Bull-dog' ants of Australia . . . The number of nests in a small area seemed to be a definite habit and is probably advantageous on the Müllerian principle. An enemy having experienced the defensive powers at the mouth of one nest would carefully avoid disturbing others. Thus each nest would help in guarding the rest. The behaviour of the ants was different from any I have seen. Around and just inside the entrance, which appeared to descend vertically into the earth, was a little group of ants. The head of each ant was always facing outwards in the direction of possible attack. When disturbed, the ants walked slowly, with widely opened mandibles, towards the enemy. I have never seen suggested, in the bearing of an insect, so firm a confidence in the possession of terrible powers of defence and such relentless determination to use them. . . . Retreat of any kind or the avoidance of danger by rapid movement was quite foreign to their nature."

(Ent. Monthly Magazine, 3 rd. Ser., Vol. VIII, 1922, p. 119.) I do not think that anyone who has seen these insects in life would be surprised by Mr. Rowland E. Turner's observation that a Fossorial wasp, *Aphelotoma tasmanica* Westw., is a mimic of two species of *Myrmecia*. When disturbed this wasp will often pick up a bit of stick or leaf and carry it about, thus adding the habits of an ant to its ant-like appearance (Ann. Mag. N. H., Ser. 8, Vol. XV, 1915, p. 64.)

It is obvious that all the methods of intimidation and display referred to above would be worse than useless, would in fact be a serious danger, if they were not associated in the minds of enemies with special powers of defence or aggression.

The difference between lizards and birds as enemies of ants is well brought out in the following note by Dr. G. D. H. Carpenter, an extract from a letter written 15 May 1927, at Guimara, W. Madi, Uganda. "Ant mimicry is very interesting because it is so obviously quite useless against lizards, particularly Agamids, which often sit by an ant-run for quite a long time, picking up the ants one after another. My wife saw one day a small Lacertid, longitudinally striped, with blue tail, eating ants vigorously one afternoon, while she was lying down. On the other hand, one day at tea we were vigorously 'swotting' flies and the corpses were being carried away by ants. We watched a black and white Wagtail (I think *M. capensis*), to see whether it would pick up any of the ants. It wandered about, seizing the freshly killed flies, but when one of these had an ant already on it, the Wagtail shook it vigorously until it got rid of the ant which it obviously didn't like." (Proc., Vol. III, 1928, p. 9.)

An interesting observation made by Dr. W. A. Lamborn proves that the predaceous fly *Bengalia depressa* Walk., gets rid of a Driver ant, *Dorylus nigricans* Illig., by a similar but more elaborate method. The fly swoops down on a column of marching Drivers carrying their pupae, and flies off with a pupa, the ant hanging to it. These it drops on the ground, and if the ant is not sufficiently disconcerted to let go, the performance is repeated until it does so, when the fly carries off the pupa and sucks it in safety. (Proc., 1913, p. cxxv; 1919, p. li; 1924, p. lxix n.)

Mr. C. F. M. Swynnerton, as the result of a very long and intimate experience, has come to the following conclusions: "In my experiments on many species of insectivorous birds I found that some ate ants generally, including *Dorylus*, far more readily than

others. Of these others some shewed a strong repugnance to them, and it is doubtless in relation to this latter class of enemy that ant-mimicry finds its main use. Yet even the birds that prey on ants show caution in attacking *Dorylus* in column, merely (in my observations) dropping down to stragglers and hastily returning to their perch." (Trans., 1915, p. 318.)

Another very different criticism of a striking example of mimicry was advanced by Dr. A. JACOBI[3]. Referring to the resemblance of certain S. American Membracidae to ants, he argued that it can only be "Pseudomimicry" because the insects usually sit motionless and when disturbed escape by leaping. But a succession of different methods of escape from enemies is common in insects: one method, in this case the resemblance to an ant, for as long as it is effective; then another and quite different method when the first no longer avails.

The deeply interesting and important investigations upon ants and their guests with which the name of WASMANN will always be associated, lead directly to the conclusion that it is advantageous to insects and other forms to be associated with ants — that, whatever constant attacks are made by exceptional enemies and whatever exceptional attacks, under the stress of hunger, by other enemies, ants are, on the whole, remarkably well protected and owe to this, in combination with their communal life, the fact that they are the most successful insects, and probably, except for man, the most successful animals in the world. In the nests of British ants Mr. H. ST. J. K. DONISTHORPE has since 1891, discovered 150 species of insects, spiders and mites new to the country, including 70 new to science. Of these guests 28 are mimics of ants and would thus be protected outside the nest or in a disturbed nest by enemies which fear the ants[4]. He has also recorded 34 mimics living independently of ants, and 15 possibly guests, possibly independent. Such results obtained by patient research upon the comparatively scanty fauna of my country prepares us for the extraordinary profusion of guests and mimics of ants in more favoured latitudes.

We also gain some idea of the strength of the stronghold when we consider the subtlety of the means adopted by parasitic enemies in order to enter it. H. W. BATES concluded that certain flies lay their eggs on the insects pursued and carried by Brazilian Driver ants *(Eciton)* to their nests. Dr. CARPENTER, who observed the employ-

[3] "Mimicry und Verwandte Erscheinungen". Braunschweig, 1913, p. 106.
[4] "Guests of British Ants". London, 1927.

ment of apparently similar methods against the African Drivers (*Dorylus*), remarks — "Isn't it extraordinarily interesting that two such different species of ants, but of precisely similar habits, should be attacked by parasites in the same way in South America and Uganda? If one thinks of it there is very little chance for an enemy to attack these ants, which are so active and ferocious and of wandering habits. . . . But what an extraordinarily fine adjustment to the habits of the ant! The method of gaining an entrance into the inaccessible nest reminds one rather of old stories such as the wooden horse of Troy, &c!". (Proc., 1914, p. cix.)

In the wonderful association discovered by Lamborn between the Lycaenid larva *Euliphyra mirifica* Holl., and the African so-called "Tree-Driver" *Oecophylla,* the caterpillar living in the nest was defended by armour against attack and yet had to obtain food by thrusting its head and slender neck into the jaws of an ant which "made movements as if feeding it. Sometimes, too, when a large ant was feeding a small one, the latter retired in favour of a caterpillar." In spite of all this solicitude the armour is certainly necessary, for Lamborn found that larvae which "happened to fall on their backs were immediately seized by the ants." (Trans., 1913, pp. 450—456.) In attempting to understand such puzzling differences of behaviour on the part of the ants "the most helpful consideration is probably that suggested in conversation to the present writer by Prof. W. M. Wheeler, viz., that the ant community is so successful and affords so safe a retreat from the attacks of enemies, that ants are liable to be overwhelmed by the numbers of forms living under their protection. The uncertainty of their temper is probably one means by which this danger is prevented from becoming too great; for a species that seeks the shelter of the ants' nest is itself taking terrible risks." (Trans., 1913, p. 446.)

I have attempted in this brief sketch of a vast subject to bring together a few important observations[5], nearly all brought to my notice by friends, keen naturalists who are convinced by their experience of animal life in the tropics that ants are specially protected insects and that the widespread mimicry of ants is advantageous. The observations here quoted are but samples of an immense mass of records consistent with these conclusions and I do not know of a single one opposed to them; for, as I maintained at the outset,

[5] References to further observations of the same kind are given in Proc., 1924, pp. lxviii—lxxi.

the fact that ants are attacked by many and varied enemies is in no sense opposed, but rather focusses attention upon those special qualities which, in spite of all attacks, have made the ants what they are — the most powerful of insects, ever-present and aggressive in all habitable parts of the earth.

We may feel the utmost confidence in the strength of the foundation on which Father WASMANN has built the interpretation of his classical discoveries — discoveries upon which we unite to offer him our warm congratulations and to express the earnest hope that he may for many years continue to find happiness in the pursuit of researches as fruitful as those we celebrate to-day.