
*An Interpretation of the Slave-Making
Instincts in Ants.*

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Article I.—AN INTERPRETATION OF THE SLAVE-MAKING INSTINCTS IN ANTS.

By WILLIAM MORTON WHEELER.

Few animal instincts have excited keener interest among naturalists than the slave-making instincts of certain ants. This is due, no doubt, partly to the human connotations of the word "slave-making," and partly to the unique and highly specialized nature of the instincts themselves. Hence it is not surprising that conservative naturalists have regarded the accounts of these instincts as more or less incredible. Darwin was inclined to be somewhat skeptical of the magnificent pioneer observations of Pierre Huber¹ till he had himself observed a slave-making expedition of the sanguinary ant. Later the elaborate observations of Forel² brought full confirmation of the facts, with a wealth of additional details. Darwin was the first to attempt an explanation of the slave-making, or dulotic, instincts in a well-known passage in the eighth chapter of the "Origin." Forel and, later, Lubbock found Darwin's conclusions to be in full accord with their own observations. More recently the Jesuit father, E. Wasmann,³ whose work on this subject is, to a large extent, compilatory and critical, has put a peculiar and, in my opinion, unwarrantable construction on the views advanced by Darwin. I sought to place the subject in a clearer light,⁴ but succeeded only in eliciting from Wasmann a repetition of his misrepresentations of Darwin's views.⁵ Since my article was written I have had many opportunities to study the habits of all the known species of North American slave-making ants.

¹ Recherches sur les Moeurs des Fourmis Indigènes. 1810.

² Les Fourmis de la Suisse. Zürich, 1874.

³ Die zusammengesetzten Nester und gemischten Kolonien der Ameisen. Münster i. W., 1891.

⁴ The Compound and Mixed Nests of American Ants. Am. Nat., XXXV, 1901.

⁵ Neues über die zusammengesetzten Nester und gemischten Kolonien der Ameisen. Allgem. Zeitschr. f. Ent., 6, 1901; 7, 1902.

The full presentation of these observations would fill a voluminous paper, the writing of which must be postponed till a later day. At present I wish to attempt an interpretation of the slave-making instincts along somewhat more general lines and to suggest a view to which I am led by reflecting on some observations recently published in the Bulletin of the American Museum of Natural History.¹

The ants which may be said to exhibit slave-making, or dulotic, instincts are the following:

1. *Formica sanguinea* Latr., the sanguinary ant, an holarctic species, represented by a single form in Europe, and in North America by numerous subspecies and varieties, several of which have not yet been described. In Europe the slaves of this ant are members of the *Formica fusca* group, namely, *F. fusca*, *rufibarbis*, and *gagates*. In America the number of forms which furnish the different subspecies and varieties of *sanguinea* with slaves is much greater, embracing the following members of the *fusca* group: *subsericea*, *argentina*, *subænescens*, *neorufibarbis*, *neoclara*, *subpolita*, *neogagates*, and *neocinerea*²; and the following members of the *pallidefulva* group (not represented in the European fauna): *schaufussi*, *incerta*, *nitidiventris*, *fuscata*.

2. *Formica pergandei* Emery, a rare and exclusively North American species allied to *sanguinea*. Slaves: *F. pallide-fulva*, *subpolita*, and *subsericea*.³

3. *Polyergus rufescens* Latr., the amazon ant, an holarctic species, represented in Europe by the one typical form, in North America by four subspecies (*lucidus*, *breviceps*, *bicolor*, and *mexicanus*) and probably several varieties. The European form enslaves *F. fusca* and *rufibarbis*, more rarely *cinerea*. The American *P. lucidus* enslaves only members of the *F. pallide-fulva* group, namely, *schaufussi*, *incerta*, or *nitidiventris*; *P. breviceps* enslaves *argentina*, *subsericea*, and

¹ A New Type of Social Parasitism among Ants. Bull. Am. Mus. Nat. Hist., XX, Oct., 1904, pp. 347-375.

² Although I am unable to detect any morphological differences between our American *cinerea* and the European form, it is probable that the former should be regarded as a distinct ethnological variety, which I would call *neocinerea* var. nov. Professor Emery calls my attention to the fact that the European *cinerea* nests only in pure sand. Its habits have been recently described by Piéron in the following words: "les *formica cinerea* vivent dans un sable de dunes, très mouvant, que le vent déplace perpétuellement, avec les aiguilles de pin qui, à peu près seules, le recouvrent." (Du Rôle du Sens Musculaire dans l'Orientation de Quelques Espèces de Fourmis. Bull. de l'Inst. Génér. Psych., 4. Année, No. 2, 1904, p. 168-185.) How different are the habits of our American form, which as I have shown (The Occurrence of *Formica cinerea* Mayr and *Formica rufibarbis* Fabricius in America. Am. Natur., XXXVI, Dec., 1902, pp. 947-952) constructs rather conspicuous mounds in the damp, black soil of grassy meadows! *F. neocinerea* is very common in certain parts of Illinois and Colorado. In the latter state I found it near Colorado Springs, nesting along the shores of Prospect Lake and in the irrigated meadows about Broadmoor.

³ The occurrence of a mixed colony of *F. pergandei* with *pallide-fulva* was noted by Pergande, but he failed to show that the former species is dulotic. Some years ago Rev. P. J. Schmitt, O. S. B., sent me specimens from Colorado, mixed with *subsericea* workers. Aug. 3, 1903, I found at Broadmoor, near Colorado Springs, a small colony of *F. pergandei* comprising four winged females and about fifty workers living with an equal number of *subpolita* workers. This observation, taken in connection with the close taxonomic affinities of *pergandei* with *sanguinea*, forcibly suggests dulosis.

neocinerea; *P. bicolor* only *F. subænescens*. The slave of *P. mexicanus* is unknown.

4. *Tomognathus sublævis* Nyl. of Northern Europe. Slaves: *Leptothorax acervorum* or *muscorum*.

5. *Tomognathus americanus* Emery of the Atlantic States. Slave: *Leptothorax curvispinosus*.¹

6. *Strongylognathus*, a genus represented, so far as known, only by the European and North African species *huberi*, *cæciliæ*, *christofi*, *ajfer*, and *testaceus*. The slave of *huberi*, *testaceus*, and *ajfer*, the only forms of which the habits are known, is *Tetramorium cæspitum*. It is doubtful whether any of these species are truly dulotic. They are probably all permanent social parasites.²

It thus appears that only the sanguinary and amazon ants furnish us with unmistakable dulotic instincts. Until the much rarer species of *Tomognathus* and *Strongylognathus* have been more thoroughly studied, we may omit them from the discussion, especially as they are known to present no peculiarities that would contradict the conclusions reached in this paper. The sanguinary and amazon ants represent, however, two very different subtypes of dulosis. The former is not dependent on its slaves, as it is an active worker, able to excavate its own nest, care for its young, and obtain food without assistance from other ants. *Polyergus*, on the other hand, has reached a highly specialized stage of dulosis: it is unable to feed itself, excavate the earth, or care for its own offspring. Hence it is absolutely dependent on its slaves and exhibits a high degree of precision and proficiency in obtaining the larvæ and pupæ that will become slaves

¹ I have recently had the good fortune to find three *T. americanus* + *L. curvispinosus* colonies in hollow twigs of elder bushes in rather damp, shady woods near my home at Bronxville, N. Y. One of these colonies contained only a single *Tomognathus* worker, another six and the third eight workers and a *Tomognathus* queen. The latter insect is not at all ergatoid, like the female *T. sublævis* described and figured by Alderz (Myrmecologiska Studier. III *Tomognathus sublævis* Mayr. Bihang till K. Svenska Vet. Akad. Handl., XXI, 4, No. 4, 1896, 76 pp., 1 pl.), but decidedly larger (3.5 mm.; the worker measures only 2.5 mm.) and has three ocelli and a typical female thorax, showing distinct traces of having borne wings. All of the colonies contained larvæ and pupæ, presumably of both species, but no queens of *L. curvispinosus*. I am not at all convinced from my brief study of one of these colonies in an artificial nest, that our American species is dulotic. For that matter, Alderz failed to establish this fact beyond question for the European species. Both may be trueinquilines or permanent social parasites. In the same locality in which I found the three above-described colonies, I found a mixed, queenless colony of the yellow *L. curvispinosus* and the black *L. longispinosus*, inhabiting a hollow elder twig. Now if a dealated *T. americanus* queen should establish her colony in such a nest as this, we should have a case like Alderz's case of *T. sublævis* living with two species of *Leptothorax*, but the inference that the latter indicated repeated slave-making expeditions on the part of the *Tomognathus* would be erroneous.

Since the female *T. americanus* is so very different from the female of the European species, it may be well to regard the former as belonging to a distinct subgenus, for which I would suggest the name *Protomognathus* subgen. nov., for the purpose of indicating that the American is less advanced phylogenetically than the European *Tomognathus*. This is, of course, frequently the case with American as compared with allied European forms. Compare, e. g., the parasitic ant *Symmyrmica chamberlini* with the allied European *Formicoxenus nitidulus*.

² I find that the term "social parasitism," employed by Forel and myself to designate the parasitism of one colony of organisms on another colony, has been used in a very different and purely sociological sense by Massart and Vandervelde (*Parasitisme Organique et Parasitisme Social*. Bull. Scientif. France et Belg. Tome XXV, 1893, 68 pp.) The authors restrict the term to human society in which certain individuals become parasitic on others of the same species.

on hatching. In any attempt to interpret the dulotic instincts we are therefore compelled to centre our attention on the sanguinary ant; this is the crucial form, on an accurate understanding of which must depend any satisfactory explanation of dulosis.

In all previous attempts to explain dulosis, authors have gone at once to the most salient instinct of *sanguinea*—its tendency to make forays on other species, kidnap their young, and permit these to develop into auxiliaries. This is undoubtedly the striking character of the whole phenomenon. But a too exclusive interest in this matter has, in my opinion, withdrawn attention from certain other instincts of considerable importance. Foremost among these are the instincts relating to the founding of the *sanguinea* colony. In a question which involves the phylogeny of the instincts exhibited by adult colonies of ants, it is necessary to study the instincts of young and incipient colonies; inasmuch as a colony, being an individual of a higher order, may reasonably be expected to conform more or less closely to the biogenetic law. To my knowledge no accurate and irrefutable observations on the founding of *sanguinea* and *Polyergus* colonies have ever been made either in Europe or America. We do not know how the *sanguinea* colony comes into possession of its first batch of auxiliaries. Two alternatives suggest themselves. The *sanguinea* queen may be able to establish a formicary and bring up her first brood of workers all by herself, after the manner of the majority of ants, and the first batch of slaves may be acquired by dulosis. On the other hand, it may be impossible for the *sanguinea* queen to bring up her own young. For this purpose she may have to enter a small or depauperate colony of the auxiliary species. In this case the sanguinary ant in the earlier stages of colony formation would be a true social parasite, and dulosis would be due to the manifestation of later, superadded instincts. The little evidence that can be produced is indirect, but I am inclined nevertheless to accept the latter of these two alternatives as the more probable, for the following reasons:

1. Although isolated *sanguinea* queens are often seen running about on the ground and seeking suitable nesting sites, no one, to my knowledge, has been able to show that these insects can found colonies without the assistance of alien workers.¹

¹ Wasmann (Die zusammengesetzten Nester, etc., p. 201) does, indeed, make the positive statement: "Eine befruchtete Königin von *Formica sanguinea* kann allein, ohne Mitwirkung eigener oder fremder Arbeiterinnen, eine neue Kolonie gründen," but when we turn to the passage to which he refers in Blochmann's paper (Ueber die Gründung neuer Nester bei *Camponotus ligniperdus* Latr. und anderen einheimischen Ameisen. *Zeitschr. f. wiss. Zool.*, XLI, 1885, p. 725) we find only the following remark: "Ich will darum auch nicht auf weitere Einzelheiten eingehen, sondern nur noch die Arten nennen, von denen ich einzelne Weibchen mit Eiern, Larven etc.,

2. Near Rockford, Ill., I found two colonies each containing seven to twelve callow *sanguinea* workers, whereas the *subsericea* workers in the same nests, numbering not more than a dozen in either case, were very large and mature. The latter could not, therefore, have been kidnapped as larvæ or pupæ by the *sanguinea* workers.

3. These two, as well as several other small *sanguinea* colonies I have seen, are very similar to the incipient colonies of *F. consocians-incerta*. As I have shown,¹ the small yellow female of the former species seeks out and enters, as a convenient place in which to start her own formicary, some depauperate and probably queenless nest of *F. incerta*. The *consocians* young are reared by the *incerta* workers and when the latter have sufficiently increased in numbers they emancipate themselves from the workers of the host species and eventually become a pure and independent colony of considerable size. The *sanguinea* would differ from the *consocians* colony in becoming dulotic instead of emancipating itself. That the colonies of other dulotic ants, like *Polyergus* and *Strongylognathus*, are founded in the same manner as the *consocians* colony, is hardly open to doubt.²

4. The fact that in its structure *sanguinea* is much more closely related to ants of the *rufa* group, like *F. consocians*, than to other species of *Formica*, may also suggest a tendency towards temporary parasitism at least during the period of colony formation.

5. Like *F. consocians*, *F. sanguinea* shows a tendency to emancipate itself from the auxiliary species when its colonies become old and populous. It has been repeatedly observed that the smallest *sanguinea* colonies contain the greatest number of slaves, whereas those of large size tend to become pure *sanguinea*. Wasmann attempts to minimize the number of slaveless colonies and claims that

im Freien vorfand, theils auch solche zu Hause hielt. Es waren das: *Formica fusca, sanguinea; Lasius niger, umbratus*." This remark is rather general and vague, since it omits the very "Einzelheiten" that would justify Wasmann's statement. Moreover, the accurate identification of single dealated females of *Formica*, especially of the forms with red thoraces and black abdomens, is a delicate matter, and it is by no means impossible that Blochmann may have mistaken a *F. rufibarbis* for a *sanguinea* queen, notwithstanding the clypeal notch which is so distinctive a character of the latter species. So careful and experienced a myrmecologist as Wasmann recently mistook for *rufibarbis* two *F. truncicola* queens which he found in *F. fusca* nests (Neues über die zusammengesetzten Nester, etc., p. 77).

¹ A New Type of Social Parasitism, etc.

² I attribute very little value to Wasmann's conception of "alliance-colonies" as distinguished from "adoption-colonies." It is highly improbable that in a state of nature, two colonies of different species, both containing adult workers, ever fuse to form a mixed colony. Such an appearance is produced by a colony of one species adopting a dealated queen of another species plus the young of the latter after they have been reared. A superficial observer would interpret the young *consocians-incerta* colony as an "alliance," but he would be very wide of the mark. Wasmann's table, therefore, again requires revision and readjustment to the facts. His classification is clearly vitiated by his using as *differentia* sometimes the method of colony formation (i. e., the behavior of the isolated queen), sometimes the behavior of the adult workers or colony as a whole. Thus *Polyergus* and *Strongylognathus* would belong in two categories, since they are adoption-colonies in their younger stages and later on "Raubkolonien."¹ A more natural classification would recognize three groups of cases: temporary parasitism, dulosis, and permanent parasitism; the first comprising such forms as *F. consocians, F. dakotensis*, etc.; the second, *sanguinea* and *Polyergus* and possibly also *Tomognathus* and *Strongylognathus huberti*; and the third, *Anergates, Strongylognathus testaceus*, etc.

in an examination of 410 *sanguinea* colonies occurring over an area of four square kilometres near Exæten, Holland, he found only one in forty to be without slaves. And he proceeds to extend his conclusions to the American forms. In the first place he doubts whether the subspecies *aserva*, described by Forel from Canada, is really as slaveless as its author supposed. Forel saw only one large colony of this subspecies, which is closely related to the common European form and appears to be largely confined to British Columbia and the mountains of the northern United States. I have seen some eight or nine colonies of *aserva*, in Colorado, Wisconsin, and Connecticut, but in only one of these did I find a few slaves, although none of them were very large. I have also recently received numerous *aserva* workers without slaves from a colony collected in the Porcupine Mountains, Michigan, near Lake Superior.

F. aserva, however, is not the only North American form of *sanguinea* which shows that Wasmann has been too hasty and confident in his generalizations. July 26, 1903, I made an excursion to Woodland Park, Colo., which is located in the Ute Pass at an altitude of about 8500 feet. At this place I came upon an enormous number of colonies of a form of *sanguinea* closely related to the common subspecies *rubicunda*. These colonies, small, of medium size, and very large, were everywhere in the woods—in and under pine logs and stumps, under stones, about the roots of plants, etc.. I devoted an entire day to their examination and excavated 106 of them by actual count, but succeeded in finding slaves (*F. subsericea*) in only two medium-sized colonies! I may have overlooked a few slaves in some of the nests, but I feel confident that less than one per cent of the colonies contained auxiliaries. That this condition of the species was not due to any lack of the requisite auxiliaries was proved by the fact that there were many nests of *F. subsericea* and *F. subpolita* in the immediate neighborhood. The *sanguinea* workers were, of course, doing all their own work, collecting dead insects, attending aphides on the aspen leaves, and visiting the large fimbriated nectaries on the green petals of the strange gentianaceous *Frasera speciosa*, which is not uncommon in the Ute Pass at an altitude of over 7000 feet. These observations show, first, that *sanguinea* is a highly variable species in respect of the slave-making instinct; second, that this instinct is by no means so firmly established in heredity as Wasmann would have us believe, and third, that there is an unmistakable suggestion of something like the temporary parasitism of *F. consocians* and other forms of *rufa*, *exsectoides*, etc. The Ute Pass *sanguinea* may

emancipate itself from the species (*subsericea*) in whose nests its colonies are probably started, very much sooner than the European *sanguinea* or the subspecies and varieties of the Eastern and Middle States of the Union.

We come now to the vital point of dulosis. As I have said before, there is this striking difference between colonies of *sanguinea* and *Polyergus* on the one hand, and those of such species as *F. consocians* on the other, that in the former we have additional instincts which lead the colony to add to its personnel by robbing the young from other colonies of the auxiliary or host species. It is clear that a specialized instinct or group of instincts cannot arise from nothing; but must be traced to pre-existing instincts of a simpler, more generalized and primitive nature. If successful such tracing amounts to an explanation in a scientific sense, although we may still be unable to account for instinct as such. Now this tracing of dulosis to more general and better understood instincts was exactly what Darwin proposed to do in the well-known passage, which I again quote for the sake of the argument:

“By what steps the instinct of *Formica sanguinea* originated I will not pretend to conjecture. But as ants, which are not slave-makers, will, as I have seen, carry off pupæ of other species, if scattered near their nests, it is possible that such pupæ originally stored as food might become developed; and the foreign ants thus unintentionally reared would then follow their proper instincts, and do what work they could. If their presence proved useful to the species which had seized them—if it were more advantageous to this species to capture than to procreate them—the habit of collecting pupæ originally for food might by natural selection be strengthened and rendered permanent for the very different purpose of raising slaves. When the instinct was once acquired, if carried out to a much less extent even than in our British *F. sanguinea*, which, as we have seen, is less aided by its slaves than the same species in Switzerland, natural selection might increase and modify the instinct—always supposing each modification to be one of use to the species—until an ant was formed as abjectly dependent on its slaves as is the *Formica* [*Polyergus*] *rufescens*.”

Darwin here traces the specialized slave-making instincts to the more primitive and general, and therefore better known hunger and foraging instincts, or rather to a somewhat modified form of these instincts as they are widely, if not universally, exhibited by ants. The slaves are a by-product which is conceivably useful, though their

présence in the colony is the result of activities not undertaken with a view to their acquisition. The explanation is analogous to that often used in morphological derivation, as, for example, in accounting for animal pigments as due in the first instance to a detention of excretory by-products in the integument. In the case of *sanguinea* the "survival value" of the colony may be increased by the presence of the auxiliaries and the instinct to acquire them may therefore be supposed to have been perpetuated and intensified by natural selection. This view was accepted by Forel and Lubbock after a much more searching study of *sanguinea* than Darwin had been able to make, and I had come to the same conclusion in my paper on the compound nests and mixed colonies. The many observations which I have since been able to make on these ants, both in the field and the laboratory, have only confirmed me in the opinion that Darwin's interpretation is in close accord with the facts. Wasmann, in commenting on my paper, misses the whole point of the discussion and runs full tilt at sundry wind-mills of his own construction. Neither Darwin, Forel, nor myself ever stated that natural selection created the dulotic instinct. It has long been evident to every thinking zoölogist that selection cannot account for the origin of an instinct variation, any more than it can account for the origin of a structural variation; but given the variation, whether it arise by mutation, continuous variation, in a definite or indefinite manner, or what not, it is perfectly conceivable that it may be strengthened by natural selection.¹ At any rate, Wasmann has failed to show that this is impossible either in dulosis or in any other case. The merit of Darwin's explanation lies in the fact that he did not in this instance seek to explain the origin of a variation by means of natural selection, but sought to show how a given instinct—namely, that of robbing larvæ for food—could be modified by other impulses till it became what we call the slave-making instinct.

Wasmann's objections, however, really come down to a question of fact. He maintains that the *sanguinea* rob the larvæ and pupæ of other ants, in obedience to a special inherited instinct, for the sake of rearing them. He concludes: "dass in dem sinnlichen Vermögen der Raubameise eine bestimmte Verbindung bestehen müsse zwischen den Vorstellungen welche auf die Hilfsameisen, auf deren Puppen und

¹ As de Vries (Die Mutationstheorie, Bd. 2, p. 667) tersely says: "Die natürliche Auslese ist ein Sieb, sie schafft nichts, wie es oft fälschlich dargestellt wird, sondern sichtet nur. Sie erhält nur, was die Variabilität ihr bietet. Wie das, was sie sibt, entsteht, sollte eigentlich ausserhalb der Selectionslehre liegen. Eine Frage ist es, wie der grosse Wettkampf sibt, eine andere, wie das Gesiebte entstanden war. In beiden Hinsichten ist auch jetzt noch die ursprüngliche Ansicht Darwin's die beste von Allen, doch ist die Sachlage von späteren Schriftstellern vielfach getrübt worden."

auf die Puppenjagt sich beziehen." He is not such a bad psychologist, however, as to pretend that these "Vorstellungen" or images (of the nature of contact-odors, in this case) could be inherited as such, for he, of course, recognizes the fact that the *sanguinea* workers must carry out their very first slave-making foray successfully, if we are really dealing with an instinct. "Es bleibt also nichts übrig als die Annahme, dass die jungen Raubameisen bereits eine instinktive Neigung zum Sklavenraub mit auf die Welt bringen. Dasselbe gilt auch für die Erziehung der Sklavenpuppen, kurz für die ganze Sitte Sklaven zu halten." He does not see that he here begs the whole question: the *sanguinea* make slaves because they are gifted with a slave-making instinct!

A more satisfactory result is reached when he tries to resolve the dulotic instincts into a catenary reflex, although he fails to notice that in so doing he is practically restating in ontogenetic terms Darwin's view of the phylogeny of the instincts in question: "Die instinktive Neigung zum Sklavenraub regt sich erst nur als unbestimmte Beutelust; der Geruch der Hilfsameisenart lenkt diese Beutelust auf die richtige Fährte, auf die Plünderung eines benachbarten Sklavennestes; die geraubten Arbeiterinnenpuppen erregen in den Raubameisen die Neigung zur Pflege derselben, bis schliesslich die ersten Hilfsameisen in dem Räubernest das Tageslicht erblickt und ihren Chitinpanzer ausgefärbt haben und sich als angenehme Gefährtinnen thatsächlich bewähren." Of course, it is only after the first dulotic expedition that associative memory and habit could come into play to strengthen the instinct.¹

Now the point on which I continue to differ from Wasmann is his too restricted view of the behavior of the existing forms of *sanguinea* toward the kidnapped young. The statement, "die geraubten Arbeiterinnenpuppen erregen in den Raubameisen die Neigung zur Pflege derselben," implies a very partial interpretation. In my opinion, it refers to a secondary instinct, variable in its intensity even in the existing forms of *sanguinea*, and by no means supplanting the primitive larva- and pupa-eating instincts of the species. It is probable that the auxiliary species are doubly useful to the *sanguinea*: both as food and as helpmates in the colonial activities. In other words, *sanguinea* may owe its survival quite as much to the adroit utilization of a rich and convenient food supply, which feebler ants are compelled to

¹ Wasmann is not at liberty to construe Darwin's words "for the very different purpose of raising slaves" in conformity with his own views, inasmuch as the word "purpose" is often used in a different and more general, albeit still teleological connotation, as, for example, when we say "the plant unfurls its petals for the purpose of exposing its pistils and stamens and of attracting insects."

forego, as to the keeping of auxiliaries. The question is, therefore, whether there are any facts that support this contention. I believe that they exist and have been, moreover, in great part enumerated in my former paper, though ignored by Wasmann in his reply:

1. Ants are very generally fond of appropriating the larvæ and pupæ of other ants whenever there is an opportunity. Such larvæ and pupæ are not killed at once, but kept in the chambers of the nest and eventually either partly or wholly eaten. These instincts are so universal among the different species that they cannot be said to be absent in *sanguinea*. On the other hand, many ants besides *sanguinea* occasionally neglect some of the foreign young and permit them to hatch and become active members of the colony. Whenever these instincts are tested, either in natural or artificial formicaries, by giving ants larvæ or pupæ of another species, we find that, in comparison with the number of alien young appropriated, the number of surviving auxiliaries is remarkably small.

2. We know that certain ants, like the smaller species of *Eciton* of tropical and subtropical America, make a regular business of robbing the larvæ and pupæ of other ants indiscriminately. In this they are quite as expert and intrepid as *Polyergus*. The kidnapped larvæ and pupæ, often of several species, are stored up in the nest as fresh food in a convenient form to be eaten at leisure. But in this case, even if some of the pupæ were permitted to hatch, there could be no slaves, since the *Ecitons* do not occupy permanent nests, but lead a nomadic life.

3. Some of our northern ants at times display the same instincts as *sanguinea* and as a consequence form mixed colonies with other species. Adlerz maintained¹ that *Lasius niger* occasionally appropriates the larvæ and pupæ of *L. flavus*, and that the latter may hatch and function as slaves in the nests of the former species. Wasmann seeks to discredit these observations on what seem to me to be very inadequate grounds. He suggests that such mixed colonies, if they exist at all, probably result from the "accidental alliance" of two fertilized queens of the different species. During the past three summers I have found altogether six mixed colonies, each consisting of two species of *Lasius*. Two of these, found near Rockford, Illinois, consisted of *L. myops* and *americanus*, and four found at Colebrook, Connecticut, consisted of *L. latipes* and *americanus*. In none of these cases was there any doubt about the "mixed" character of the colonies, as the insects were taken alive and kept for some time in arti-

¹ Myrmecologiska Notiser. Entomol. Tidskr., XVII, H. 2, 1896, p. 131.

ficial nests. All of these colonies were small and in none of them was it possible to find a queen of either species. The simplest explanation of such cases is certainly not by alliance of fertile queens but, as Adlerz has maintained, by dulosis.¹

4. Even *sanguinea* shows a tendency to lapse into the ancient instinct of plundering the nests of different species of ants indiscriminately. Forel (*loco citato*, p. 363) has described forays of *sanguinea* on *Lasius niger* and *L. flavus*, and similar observations have been made by Wasmann. I once witnessed a ridiculous foray of a large *rubicunda* colony on a colony of a woodland variety of *Myrmica scabrinodis*. In this instance the foray was carried out exactly as if it had been directed against one of the normal auxiliary species. After killing or putting to flight the *scabrinodis* the *rubicunda* returned to their nest with the small larvæ and pupæ of an ant, which belongs to an entirely different subfamily. In another *rubicunda* nest under a log in the same wood, I found two of the flat chambers full of uninjured pupæ of *Myrmica scabrinodis*. They had evidently been set apart from the *sanguinea* young and from those of the normal auxiliaries (in this case *F. subænescens*). Forel made a similar observation on a *sanguinea* nest in which *Lasius niger* and *L. flavus* cocoons had been stacked up in a chamber by themselves. A large colony of *F. subintegra*, near Rockford, Ill., was seen one morning to make a normal assault on a *Lasius americanus* colony and return to the nest with a number of larvæ and pupæ in their jaws and many *Lasius* workers hanging to their legs and antennæ. These forays, which are probably not at all infrequent and are, moreover, undoubtedly undertaken by *sanguinea* colonies of considerable size and of some experience in capturing the normal auxiliaries, point directly to something very closely akin to hunger as the impulse which compels the workers to undertake their expeditions. We can hardly suppose that the *sanguinea* workers, even after some practice in making slaves, have any definite association between the kidnapped young and the slaves to be reared from them or they would not make forays on such unsuitable species. The contact-odor sensations of a *sanguinea* worker that is kidnapping *Lasius* and *Myrmica* larvæ and pupæ must be of a very different nature from the corresponding sensations experienced in a foray on the normal auxiliaries.

5. Although a *sanguinea* colony kidnaps great numbers of larvæ

¹ The mixed colonies of *L. latipes* and *americanus* are especially remarkable on account of the great difference in the odoriferous secretions of the two species. The workers of *L. americanus* have a faint and rather indifferent odor whereas those of *latipes*, like all our species of the subgenus *Acanthomyops*, have a very striking odor like oil of citronella.

and pupæ during the course of a summer, there is no commensurate growth in the number of its auxiliaries. I observed during the greater part of a summer a large *subintegra* colony in Mr. Ralph Emerson's garden at Rockford, Ill. The ants made almost daily forays on the numerous *subsericea* colonies nesting in different parts of the lawn and carried home thousands of larvæ and pupæ. Some of these forays extended over two whole days. But when I came to examine the *subintegra* colony in the autumn, it contained, if anything, fewer slaves than early in the summer. What became of all the larvæ and pupæ carried home if they were not eaten or thrown away? Similar consumption and neglect of larvæ and pupæ may be readily seen in artificial nests, although such observations are open to the objection that the ants may be compelled to feed on the young of the auxiliary species, just as they sometimes feed on their own young, through lack of proper animal food. It is not impossible that in cases like the Ute Pass colonies above described, where a great many *sanguinea* colonies inhabit a comparatively small area, the slaveless condition may be due to a complete consumption of all the kidnapped larvæ and pupæ.

6. The fact that the largest and oldest *sanguinea* colonies contain fewer or no slaves cannot be explained on Wasmann's assumption, since this would lead us to expect a stable or constantly increasing dulotic instinct as the colony grows in size. The fact is, however, readily explained on the view that even our existing forms of *sanguinea* really rob, not for the purpose of making slaves, but for food. Under these circumstances the chances of survival of alien larvæ and pupæ would naturally tend to diminish and even to disappear with an increase in the number of the *sanguinea* workers.

The above phenomena are all readily explained if we adopt Darwin's view of dulosis, but on Wasmann's they are isolated, incomprehensible anomalies.

The fact remains, however, that *sanguinea* is, as a rule, *discriminatively* predatory, and this peculiarity neither Darwin nor Wasmann have been able to explain. In other words, why does *sanguinea* normally confine its forays to colonies of ants belonging only to the *pallidifulva* and *fusca* groups of *Formica*, with a pronounced predilection for the typical *fusca* in Europe and its variety *subsericea* in America? I believe that we may account for this instinct by reverting to previous considerations. The *sanguinea* queen, as I have stated, very probably establishes her colony in a depauperate nest of the auxiliary species. She is a parasite, like *F. consocians*, and as such seeks adop-

tion in the nest of a particular species. The same explanation will account for this instinct that will account for the association of any parasite with its host. Now the *sanguinea* workers are, of course, abortive females, and may be supposed to inherit in some degree the instinct to seek out nests of the same species on which the queens are parasitic. If we do not wish to assume such an inherited instinct on the part of the workers, we may, perhaps, regard the discriminative tendency as acquired by habit-association, since the worker *sanguinea* is from the first brought up in nests containing the auxiliary species. This instinct or habit has merged in the workers with the more ancient and more universal formicid instincts to rob the young of other ants and to forage in files or companies. The result of this fusion of various instincts, combined with an enterprising and pugnacious disposition, leads to the typical dulotic foray. If this view of the matter is correct, the discriminative character of the foray has its root in the discriminative parasitism of the queen.

To complete the interpretation of the dulotic instincts and account for the presence of the slaves in the *sanguinea* colony we have to admit the existence of still another set of instincts, which are also nearly if not quite universal in ants. These are manifested in part by the adult *sanguinea* and auxiliaries already in the colony and in part by the callows hatching from the kidnapped pupæ. The adult workers permit or even assist the alien young to leave their cocoons and pupal envelopes, and the callows remain in the colony and mature with a sense of being its regular component members. The instincts thus manifested on the part of two different species towards each other are obviously the same as those which render colonial life possible in either of the species by itself. Wasmann seems to think that *sanguinea* has much more highly developed philoprogenitive instincts than other species of *Formica*. At any rate, such a conclusion is implied by his assumption that these ants really go out of their way to raise slaves. I am not prepared to entertain this view. The young are reared and cared for by the more recently hatched workers of *both* the species, for in *sanguinea*, as in many other ants, the callows serve an apprenticeship in the nursery before they leave the nest to forage. We may designate the various instincts, which relate directly to the rearing and care of the young and influence the attitude of the young towards the remainder of the colony, as threptic instincts.¹

¹ Some such term seems desirable for use in a purely ethological sense. It is, of course, derived from the same root as *trophic*, but this word is more properly used with a purely physiological connotation.

Some remarkable experiments recently performed by Miss Fielde¹ throw a flood of light on the formation of mixed colonies in general and on the formation of the dulotic colonies in particular. The ease with which she succeeded in making artificial mixed colonies of ants belonging to the most different subfamilies shows how plastic are the threptic instincts even in species which under natural conditions are never known to live in symbiosis. The simple conditions under which such colonies were formed are thus described by Miss Fielde: "If one or more individuals, of each species that is to be represented in the future mixed nest, be sequestered within twelve hours after hatching, and each ant so sequestered touch all the others with its antennæ during the three ensuing days, these ants will live amicably together thereafter, although they be of different colonies, varieties, species, genera, or subfamilies. For sequestering the ants, I used artificial nests, made in watch-glasses so small that the natural movement of the newly-hatched ants would bring each of them into contact with all the others. In no case did the callows quarrel, and those of most diverse lineage sometimes snuggled one another. The ant's sense of smell appears to be perfectly acquired, and its standards of correct ant-odor to be established during the first three days after hatching. Any two species or any number of species that I captured for use in these experiments became accustomed to each other's odor, and therefore friendly, if the early association was close and continuous. This association is more perfect when no inert young distracts the attention of the callows from one another, and when the arrangement of the nest offers no place of seclusion for any of its inmates." By these methods Miss Fielde succeeded in producing among others such starting mixed colonies as the following:

Lasius latipes + *Stenamma fulvum*;

Formica sanguinea + *Cremastogaster lineolata*;

Stigmatomma pallipes + *Formica subsericea* + *S. fulvum*;

L. latipes + *F. lasioides* + *S. fulvum* + *C. lineolata*;

Camponotus pennsylvanicus + *F. sanguinea* + *S. fulvum* + *C. lineolata*; etc.

In these colonies "there is a close affiliation of ants of different species. Those of different subfamilies sometimes lick one another. Introduced young is carried about and taken care of without regard to its origin. Ants of one genus accept regurgitated food from those of another genus."

To sum up, in conclusion, it would seem that the slave-making, or dulotic, instincts of *sanguinea* may be resolved into a number of

¹ Artificial Mixed Nests of Ants. Biol. Bull., V, No. 6, Nov., 1903, pp. 320-325.

instincts which are unique in their combination, but as single elementary activities are of much more universal occurrence and hence of greater phylogenetic antiquity and importance. These instincts fall into three groups:

1. The *discriminative parasitic instincts* of the queen. These may have originated by the "method of trial and error" from a condition of more indiscriminate parasitism.

2. The *discriminative kidnapping instincts* of the workers. These, too, have probably developed out of indiscriminative activities of a similar nature undertaken, like those of *Eciton*, for purely predatory purposes, through the influence of and in conjunction with the discriminative parasitic instincts of the female.

3. The *threptic instincts* which are apparently universal among ants and depend on simple conditions that readily permit of the survival, hatching, and rearing of alien species.¹

If this interpretation of the dulotic instincts is correct, we must admit that dulosis has grown out of temporary social parasitism and tends towards a form of permanent and abject social parasitism through such a series as is represented successively by *Polyergus*, *Strongylognathus huberi*, *S. testaceus*, *Anergates*, etc. This interpretation is in part at variance with that of previous authors, who suppose that dulosis has grown out of the "abnormal mixed colonies." In so far as these colonies are regarded as fortuitous alliances of ants belonging to different species, the interpretation is incorrect. I have shown² very good reasons for supposing that such "abnormal mixed colonies" are in reality normal cases of temporary social parasitism, and only as such would I admit that they represent an initial stage in the development of dulosis. While it will be necessary, therefore, to abandon the older interpretation in so far as it relates to the phylogenetic origin of dulosis, we may still accept it in so far as it relates to the developments that are supposed to have succeeded the *sanguinea* stage.

I am well aware of certain shortcomings in the interpretation offered in the preceding pages. A particularly weak point is our ignorance of the first beginnings of the *sanguinea* colony. The interpretation I have given, however, has the very great advantage, even as an hypothesis, of avoiding unnecessary psychological assumptions and drawing into the discussion any instincts that are not well

¹ I have not considered the obscure and interesting question of the absence of the sexual forms (males and females) of the auxiliary species in dulotic colonies, since the same condition obtains also in cases of temporary (*Formica consocians* + *incerta*) and in permanent social parasitism (*Anergates* + *Tetramorium*).

² A New Type, etc., *loco cit.*

known and readily observable in many ants besides the dulotic species. It is certain that these instincts, both individually and in combination, are subject to great variation in intensity, especially in our American ants, many of which, like our species of *Formica*, seem to have emerged from a mutation period only within comparatively recent time. That these variations are subject to modification and development through natural selection is an opinion to which I incline, and against which I fail to see that Wasmann has adduced any valid arguments whatsoever. I need not waste many words on his "innere gesetzmässig wirkende Ursachen," to which he resorts whenever it suits his convenience. Such expressions are merely scholastic formulæ, which in one sense may be regarded as obvious, in another as specious phrases that explain everything, while they demonstrate nothing.