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AGGRESSIVE AND CO-OPERATIVE BEHAVIOUR AMONGST INSECTS

It has sometimes been said that it is useless to try to prevent wars since man has an ineradicable combative instinct. The term instinct is very ambiguous in its application to humans, and it may be interesting to see what occurs amongst the insects, many of whose species show the highest development of instinctive behaviour.

Many insect species are predatory, but if they depend on other distinct species, the relation is analogous to hunting or to a crude form of agriculture. Aggressive behaviour to be comparable with war must concern the different members of one species. There are many laboratory experiments which illustrate the effects of competition when a population begins to exceed the capacity of its food supply. In Flour beetles, for instance, the adult beetles and the larvae eat any egg or pupae which they happen to meet in their ceaseless burrowing through the flour. There is thus a fixed population density at which eggs are eaten as fast as they are laid. In Grain weevils, the effect of crowding is to reduce the rate at which eggs are laid by the females who appear to suffer from overstimulation when crowded. Other effects, usually harmful, may be produced by the accumulation of the products of respiration or of digestion. Finally, if the food supply is

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too small, there will be death from starvation. If, for instance, too many blowfly eggs are added to a piece of meat, the flies produced will either be small, weak, and infertile or, if the excess has been too great, the larvae may all starve when half grown. Thus, a piece of meat which could have produced 100 normal flies may produce none at all if a tenfold excess of eggs is laid on it.

Competition of this sort is much easier to detect in laboratory cultures than in nature. It is difficult out of doors to detect any but the more extreme changes in population level, and these usually only occur at rather long intervals. A number of caterpillars which feed on the leaves of forest trees occasionally become several hundred times as common as they are in most years. Under these conditions large areas may be completely denuded of leaves, and the plague destroys itself. A good deal of mortality, perhaps due to micro-organisms, also plays a large part in the destruction. At much lower population levels it is often easy to demonstrate competition for food amongst insect parasites. In many species only a single parasite can develop to maturity inside its host. If two eggs are laid in one host, only one survives, for parasitic larvae destroy their rivals either in actual physical combat or by chemical action or through changes set up in the blood of the host.

These facts are well known to entomologists, but what is less often stressed is that many species which share a single food supply do not seem to compete because the food supply is in most years greatly in excess of their requirements. Large-scale defoliation, for instance, rarely occurs more often than once in ten years. There are reasons for thinking that the social insects may provide a special case in which competition might be expected to be more severe than it is in many solitary species. In a social species, large numbers of individuals are necessarily concentrated in a small area, and this would be expected to increase competition. In many species a suitable nesting site cannot be found everywhere, and this again may lead to severe competition. The high level of organisation exhibited by such creatures as the ants enables their competition to take on more resemblance to struggles between rival nations than does the starvation of caterpillars or maggots which have overeaten their food supply. The largest colonies of ants and termites are so big—hundreds of thousands to millions of individuals—that it is instructive to see how far the colony lives without internal strife and how it manages to do so.

Some of the most spectacular struggles between social insects occur between different species. Wasps often rob and sometimes destroy weak hives of honeybees. Some kind of ants live almost exclusively at the expense of termite colonies whose inhabitants provide their food. The notorious driver and legionary ants live exclusively by raiding and have no fixed homes. They destroy all insects including other social species which live within their foraging area. Ants in general are important enemies of other genera and species of their own kind. The native ant fauna of Madeira was almost completely destroyed when a species of *Pheidole* was accidently introduced. Later the Argentine ant, *Iridomyrmex*, entered the island and replaced *Pheidole*. Slave-making by ants, which will be briefly referred to later, is largely an extension of predatory behaviour. These examples of competition between social insects differ only in scale from the hunting activities of solitary species. They have no more analogy with war than does the organised destruction by human societies of wolves or whales.

The colonies of all social insects seem to be families. Frequently, their members are all offsprings of a single female. In some of the South American wasps in which the colony contains many egg-laying females, these are all sisters. Colony-foundation by what are probably unrelated females is rather frequent in ants, but the offspring are all reared together so that the family atmosphere is maintained. The nest itself is the centre of social activity, and in most groups each individual forages in isolation. Only in some ants and termites is co-operative behaviour exhibited away from the nest.

Social insects do not seem to defend much of the territory surrounding the nest as is done, for instance, by many birds. Usually intruders, whether of the same or another species, are repelled only when they actually attempt to enter the nest. At most a few inches round the colony will be defended territory. Away from the nest social insects from different colonies do not normally quarrel with one another, apart from the examples of predation already mentioned. It is probable that four sorts of competition between different colonies of one species of social insect may be recognised. These are competition for nesting sites, for oviposition sites, for food in the nest, and for food outside the nest.

Competition for nesting sites occurs when new colonies are founded and is especially severe in the subterranean nesting wasps and humblebees. Other social species such as wasps nesting on trees, ants and termites, seem normally to have less exacting requirements, and competition at this point in the life cycle has not been detected. The common wasps and humblebees of Europe usually start their colonies in the deserted nests of

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rodents, and in many localities these are not sufficiently abundant. Queens which are late in the field often attempt to use sites which are already occupied, and severe combats have been recorded, often ending in the death of one or both queens. In some places these combats seem to have some importance in limiting the number of wasps. In both these groups of social insects peculiar 'cuckoo' species have been evolved, probably as a result of this process. The queens of the cuckoo species are better armed for fighting and emerge rather late in the season. They invade incipient colonies of other species and usually kill the queen or at least establish themselves in the nest. Their own eggs are then reared by the workers of the host species, the cuckoo itself lacking a worker caste.

The nest of any insect, whether a solitary bee or wasp or a social species, may be regarded as an oviposition site. Eggs laid in it will be able to develop on the food which has been stored or on the larvae of the host. In social species such eggs are often reared by the worker caste. In most social insects the defence of the nest against intruders partly serves to prevent unwanted eggs being laid. When a cuckoo female invades a nest, after the initial struggle (which is sometimes only perfunctory) much more severe combats occur when the invading female tries to lay eggs. It seems that it is at this point that the rightful queen is often killed. This reaction to oviposition is perhaps an extension of the normal control of oviposition in the nests of most wasps and humblebees. Usually, there is only one egg-laying queen, and oviposition in the workers is suppressed. But if the egg-laying queen dies or is removed, the workers may at once begin to lay. They do this so quickly that it seems that this function has previously been psychologically repressed by the presence of the queen. If the suppression was physiological, egg laying in the workers could not start so quickly after the queen's removal. The well-known rivalry between the young queens of the honeybee may be regarded as an example of the same sort of behaviour. There are, however, a number of exceptions in wasps, ants, and termites, in which some species have several egg-laying queens in each colony. Why this should be so and why it does not lead to disturbances is not well understood.

Nests of social insects are rich stores of food, of honey in the case of bees, or of vulnerable larvae in all species. These stores are defended against almost all intruders and especially against members of other colonies of the same species. It appears that each colony of a social insect has its own smell so that intruders can readily be recognised. The specific colony smell perhaps develops from the habit of widely sharing all the

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food that is brought in. Thus while no two colonies will get quite the same food, the members of one colony will very nearly do so. This, at least, is the best authenticated theory at the moment. Colonies which are split into two acquire different smells in a few months and will then fight if reunited. The robbing of hives by honeybees is a good example of competition for stored food. At times when nectar is scarce, in times of drought, for instance, strong hives will enter and rob the honey of weaker ones. Most examples of raids of this sort in other social insects involve two different species and are not really comparable.

Probably much the most important type of competition is of a more insidious kind, comparable to the replacement of the inhabitants of the Malay Peninsula by Chinese rather than to the replacement of Red Indians by Europeans in North America. A given area can only support a limited number of colonies, and if we consider the ants, in which the nature of the nesting-site is a relatively unimportant factor, it appears that each colony requires a certain minimum foraging area. In fields which are densely populated by the yellow mound-making ant, the nests are found, on the average, to be separated by several feet; the average area required by each nest seems to be about 2.75 square metres. New colonies are founded by queens which are broadcast from the air after the marriage flight, and the spacing out of the colonies is doubtless due to competition. This is not, however, of the obvious kind, and actual combats are rarely witnessed. Probably foraging becomes less efficient as the nest is left farther behind, so that each colony deals with the area it can exploit most efficiently. If the foraging area was too limited, the colony would not flourish and would fail in competition. If two colonies were too close together, the success of one of them might be determined by such factors as differences in the fecundity of their two queens. One colony would either move or die out without any combats necessarily having taken place.

These remarks upon competition might be summarised as follows: Each colony is an isolated defended unit. Intruders of the same or of other species are attacked with varying success. But apart from the attacks of various predatory ants on termites and the raids of driver ants on all forms of insect life whether social or solitary, combats between large groups of workers are rarely observed. Some wasps and bees may be limited by the number of nesting sites, and in them severe combat may occur either between or within species at the time of colony foundation. But perhaps the most wide-spread and effective competition arises from the limitations of food supply which permit only a limited number of colonies to flourish on any area. This means that anything comparable to war in the human sense is rather uncommon since aggressive behaviour is only evoked in the defence of the nest.

The colonies of social insects vary greatly in the number of their inhabitants. The following figures give some idea of the range. Humblebees, up to 500 but often under 100; honeybee, 50,000 to 100,000; social wasps, very variable according to the species, 10,000 to 100,000, but in the common European wasps (*Vespula*) usually 2,000 to 6,000; ants, a few dozen up to half a million, depending on the species; termites, from a few hundred up to several million. Thus apart from the smallest colonies which mostly belong to the less highly evolved types, the colony varies in number of inhabitants from that of a small town to that of a large city. Any sort of quarrelling or civil disorder in the colony is very rare, and we may well enquire what is the system of government which is capable of eliminating civil wars.

The social life of insects always involves a division of labour. Even in some of the least specialised wasp colonies, in which every individual may, perhaps, be capable of the whole range of specific activity, there is nevertheless a diversification of function. Division of labour may be based on either temporary or permanent differences amongst the members of a colony; usually both are present. Clearly some sort of allocation of duties is almost essential if social life is to be at all efficient. Some individuals forage for food or building materials while others guard the nest or look after the young. In European social wasps such division of labour is very marked but is temporary since the same individual may apparently have different functions on different days. In these wasps, in fact, the only permanent division of labour is between the queen who lays most of the eggs and the workers which do the work and lay few eggs. Even this difference is not absolute since in the early stages of colony foundation the queen does all the work of rearing her first brood unaided. It is only after the first workers have emerged that the division of labour can be established; before that the queen has been behaving like one of her remote solitary ancestors.

The queen of the humblebee founds her colony in the same way as the social wasp, doing all the work until the first brood of workers appears. Amongst the workers themselves, however, there is a rather more definite division of labour. On the whole, foraging is done by the larger and older workers and nursing by the smaller and younger ones. The complete picture seems to be rather complicated, since it seems to be 'physiological age' rather than actual age which matters, and small individuals are said to grow old more slowly and therefore keep to the nest longer than the large ones.

In the honeybee new colonies are founded by swarms, that is, by a queen accompanied by a large group of workers. Thus the queen never has to run a young colony unaided and as a result has become considerably more differentiated from the workers. She has lost the apparatus for collecting pollen, and her jaws are less efficient as tools; she could not now survive at all in the absence of the workers. The worker honeybee exhibits a well marked division of labour, based mainly upon age. Foraging is chiefly carried out by the oldest workers, and various duties within the hive by the younger ones. The four or five activities which were at one time thought to succeed one another according to a rigid schedule are now known to be less sharply separated. In particular, in abnormal situations, when, for instance, a particular age-class has suffered a heavy mortality, an age-group may change its functions.

The ants are a much more diversified group than the social bees or wasps and show a variety of types of organisation. Sometimes the workers seem to have no permanent division of labour or only a partial one based on variations in size. In other species, the differences in size become more marked and more associated with differences in colour and structure. In the most specialised species the workers exist in two different forms which do not intergrade and seem to have quite different functions. The larger, large-headed 'soldiers' act either in defence of the nest or, in the harvesting ants, as seed-crushers. They may be unable to feed themselves and have to be looked after by the other workers. In a few species of ant, particularly in the well-known *Oecophylla*, the larva also contributes to the welfare of the colony by producing silk with which the workers can spin together leaves.

The termites are very different from all the other social insects both in their ancestry and in the fact that males and females contribute usually to the caste of sterile workers. The developmental stage of the termite is not very different from the adult, though lacking wings, often blind, and with undeveloped reproductive organs. It would seem that in the early stages of termite evolution, the worker caste developed from the young developmental stages or 'nymphs'. This still seems to be true in the less specialised groups, but often the growing nymph can be deflected into either of two directions, towards a 'soldier' or towards a winged adult. Once a certain critical time has been passed, the deflection is permanent, but sometimes

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an individual which has developed some way in the direction of a soldier may dedifferentiate and take the other direction. In the more specialised termites there may be three or more lines along which a group of initially similar nymphs may develop. Division of labour appears to be related to these various types which, though partly founded on age and number of developmental stages passed through, also involve important differences in structure.

The type of division of labour which is at present least easy to understand is that which is strictly temporary. Where every individual is capable of all the necessary activities and does indeed perform them in relatively quick succession, how is it that the right amount of effort is expended at any one moment? How is it decided that so many workers should build, while some other number should forage? One difficulty is that there has been almost no investigation so far of the efficiency of insect organisations. We do not know in most cases more than very roughly that the right numbers of workers are engaged in various activities. Occasionally, indeed, two workers may be seen acting in what seems opposing ways, e.g., one building and one pulling down, but this does not lead to combats, and the general impression is one of well-organised work. We can form little idea of how much the organisation might be improved and have really no idea of what underlies it. The sort of factors which in one species or another are known to be operative are: (1) inhibition of worker oviposition by the presence of an egg-laying queen; (2) the stimulation of foraging by hunger (and *vice versa*), which may affect the whole colony if all food is shared; (3) control of the oviposition rate by the number of pupae in the nest, i.e., by the number of young nurses which will be present in the near future. Doubtless there are many more unknown relations of this type, but we do not know how they are integrated into a viable pattern of behaviour.

Differences of behaviour involved in the permanent or semi-permanent division of labour are in some ways easier to understand. If individuals of different ages are in different physiological states, it is not unnatural that they should behave differently. In some ants and termites the castes are as different from one another as different species, and it would be surprising if they did not also differ in behaviour. The problem in this case is how are the castes produced and how is a proper balance between their numbers maintained. Division of labour, whether temporary or permanent, involves 'social regulation', a determination of either the amounts of different sorts of activity or of different kinds of individuals.

It is usually thought that only two sorts of eggs are laid, those that will produce males and those that will produce females. Kerr has suggested that a third, worker-producing type of egg is laid by the stingless bees, but this is little more than a supposition; there is no evidence for anything of the sort in the other social insects. In them, everything suggests that it is the treatment given to the larva which determines whether a queen or one or more types of worker will be produced. The facts are best established in the honeybee where the larvae which will produce queens are reared in special, easily recognisable cells. If young larvae are transferred from queen cells to worker cells (or *vice versa*), the appropriate caste is produced. Queen larvae are fed on 'royal jelly', a glandular secretion provided by a particular age-group of the workers. Worker larvae, after the first three days, are mainly fed on honey and pollen. In some ants there is evidence that development into worker or queen (or sometimes soldier) is determined by the amount of food provided or by the ratio between the number of larvae to that of the attendant workers. This is a characteristic example of social regulation, for a colony in which workers are scarce will tend to produce more workers, and queens will only be produced if the proportion of workers is high. The determination of the worker caste in humblebees and wasps is not understood. The first broods produced consist entirely of workers, but at some point towards the end of the life of the colony queens begin to be produced and from then onwards no more workers are reared. This seems to be partly associated with an increase in the worker-larva ratio but is perhaps also associated with the age of the colony. A few queens are usually produced by small, relatively unsuccessful colonies at about the same date as in the larger ones, though the number of inhabitants may be no higher than that of the large colony some weeks earlier. There is at least a hint in the case of the wasps that some glandular product supplied by the workers may be involved.

The most complex situation seems to exist amongst the termites which have the best developed caste system. They provide the best example of social regulation, for groups of identical young nymphs of the same age if isolated in a cage may produce by 'self-differentiation' all the castes, in about the right proportions. It is known in some species that about one nymph in ten develops into a soldier; if the developing soldier in such group is removed, one of the other nymphs becomes a soldier. Similarly, if the fertile sexual forms are removed, substitute sexual forms are developed. Such facts led to the development of a theory of 'social hormones'.

Termites produce cutaneous secretions which they lick up from one another's bodies. It has been supposed that the secretion of one caste, such as the soldier, might inhibit the production of others of the same caste. One individual would only produce enough secretion to inhibit a small number of developing brothers and sisters, so that the proportion of the castes would be kept approximately in balance. It has proved very difficult to demonstrate the existence of such inhibitory hormones, and many students now doubt their existence. There is, however, no other explanation of the facts available so far.

We thus see that a great deal of the social organisation of insects depends on physiological and sometimes also morphological differentiation. Individuals behave differently and do different work because they are different kinds of individuals, sometimes as much so as two species. In examples of this type the problem is not so much the division of labour as the process of social regulation by which the different types are maintained in the right proportions. Some hints have been given of the physiological mechanisms behind social regulation, but investigations are still really at a very early stage.

The apparently more simple situation in which a number of similar individuals apply themselves to different tasks is harder to explain and it is tempting to assume that there must be underlying but so far undetected differences, at least of a temporary and probably physiological nature. It is a well-known fact that if a group of any non-social insect is put in a simple experimental situation, such as a temperature gradient, not all of them behave alike. Sometimes, indeed, their reactions plot something more like the normal curve of error. Thus an appropriate situation reveals a previously undetected diversity. There is some evidence that the variability which is normal in all animal populations has played a special part in the evolution of social forms. Social life allows types which would be eliminated if solitary (e.g., sterile workers) to survive and play an important part in the colony. There is a suggestion that normal variations in size have been selected out and even increased. In humblebees, competition for food amongst groups of larvae leads to the production of workers of widely varying size. The small individuals which in a solitary species would be at a disadvantage may actually be more useful for some purposes in a colony. There may thus be a selection for any factor which leads to greater variability. On the plane of behaviour a similar process could be at work, though this is admittedly very speculative. It would mean that individuals in slightly different physiological states would behave more differently than their solitary ancestors would have done. A normal curve of error in behaviour could in this way be changed into a bi- or poly-nodal curve.

Finally, we may consider certain special types of behaviour which are characteristic of some social insects. Most social insects eat some, and sometimes a high proportion, of the eggs they lay. Possibly, this is especially frequent when nitrogenous food is insufficient. It is also a form of social regulation, allowing some young to develop when there is not enough food or not enough nurses for all. Destruction of larvae is much less usual but sometimes takes place, especially perhaps when the colony is senescent and the behaviour of the workers probably abnormal. Termites destroy any individual which is at all damaged, and this may well be associated with the chronic shortage of nitrogen in their diet. These examples of cannibalism suffice to show that the workers, though assiduous nurses, are little influenced by sentiment. The exclusion of the drones in the honeybee after the young queen is fertilised is a striking example of similar behaviour. The drones do no work and consume much food, so that it is logical that they should be driven out of the hive when the need for them is over. It is certainly highly remarkable that instinctive behaviour of this type should have evolved but it has the cold-blooded rationality of many other processes which have been the subject of prolonged selection.

The keeping of slaves by ants has at first sight a striking analogy with the human institution of slavery, but the resemblance is very superficial. The slave ants always belong to a different species from their masters and the relation would be more properly described as domestication or even as a refined form of parasitism. In the Blood red ant, the relationship is still flexible and the slave keeper is quite capable of looking after itself and in some districts does so. The surviving slave workers run the nest and are replenished by raids which the workers of the Blood red ant make on other colonies. The raiders bring back only larvae and pupae and some of these are used as food; raiding for food may, indeed, have been the origin of this behaviour. In the Amazon ants, however, the workers cannot even feed themselves, and their only function is to raid slave colonies. The worker Amazon has evolved into a soldier caste and all the original worker functions—foraging, distribution of food, nest-building and nursing—are performed by the slaves. It is clear from this brief account that slavery in ants is quite different from what it is in man. The slaves belong to another species, and the process is one of domestication.

The resemblances between the social life of insects and that of man are mostly rather superficial. As far as we know, insect behaviour is almost entirely instinctive. They can only add a little to their innate mental equipment. Most social species can to some extent memorise the topography of their foraging area and some, like the honeybee, can learn to associate particular patterns, colours, or smells with a source of food. Bees and wasps outside their nests always seem to act as individuals. Some ants and termites undertake organised hunting or collection of food but they very rarely seem to attack their own species. Fights between members of one species seem almost always to arise when an attempt is made to invade a nest. This is more often the act of a nest-founding queen than of workers. It seems probable that a species whose instinctive behaviour led it to attack its own species would rapidly become extinct.