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## Problems in the Development of Social Behavior and Communication among Insects<sup>1, 2</sup>

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*Man has long been fascinated by the life of social insects, probably because we see in insect life the reflection of many human antics in miniature. As Dr. Michener points out, however, it is not wise to trust the ancient adages resting on the observation of insect behavior selected for the lessons they are supposed to teach.*

*The author is professor of entomology and chairman of the department at the University of Kansas. Dr. Michener, a graduate of the University of California, joined the University staff in 1948.—The Editor.*

When one is searching for the causes of evolutionary change, investigations are usually most fruitful if comparable developments can be studied in as many different groups of organisms as possible. Such parallelisms are instructive because one may be able to select the common causes or factors from among the many factors concerned. Such common factors may be assumed to be among the important ones influencing the developments which are parallel. It has been suggested that a study of the causes of social evolution, including the improvement of communication, among certain insect groups may result in a better understanding of the causes of these same developments in man and his ancestors. If so, we may possibly obtain a better insight into man's social behavior.

Before going further, I wish to emphasize that I do not belong to that school which believes that information of practical importance for improving our own social organization can be obtained by observing the ants or the bees. True, their societies and ours are in many ways similar, as will appear below, but they differ in so many vital ways that it is foolish to look to these insects for wisdom in social economy. We might as well

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<sup>1</sup>Part of this material was prepared for the Thirteenth Conference on Science, Philosophy and Religion in their Relation to the Democratic Way of Life held in New York City, September, 1952. No claim of originality is made for most of the ideas presented in this paper. As the bibliography suggests, the data come from previous publications, and many of the ideas have evolved through years of consideration and discussion by numerous students of social behavior. The most that can be claimed is that the thoughts are here presented in a new framework.

<sup>2</sup>Contribution No. 816, Department of Entomology, University of Kansas.

[1]

Hymenoptera - Aculeata  
Social insects

expect the insects to learn from us! Moreover, any morals that might be drawn from the insects are likely to cut two ways. Solomon advised the sluggard to the "Go to the ant . . .," but we now know that he might see there the companion sluggards among the ants (see Chen, 1937; Combes, 1937). Or he might learn that among honeybees at the height of summer activity, the life of the worker is only some six weeks; but if by some mischance there is no brood to feed and little work to do the worker may live two or three weeks longer (Rockstein, 1950). If we still wish to draw a moral it could be pointed out that bees in the winter cluster indulging only in the apparently easy work of heat production live for as long as six months.

*Definition of Social Behavior.* Allee and others have used the word "social" in a very broad sense to include virtually all intraspecific relationships among animals (see Allee, 1938, 1950). The significance of their investigations and outlook is unquestionable, but to me such broad usage makes that term nearly meaningless. I prefer to follow students of social insects (e. g. Wheeler, 1928) in considering as social only those organisms which occur in groups or colonies, in which one or both parents survive to cooperate with their young when the latter are mature, and in which division of labor occurs. So restricted, the only thoroughly social animals are man, the termites, the ants, some wasps, and some bees<sup>3</sup>.

*Prerequisites for the Development of Subsocial Behavior among insects.* Insect societies are families in the sense that they consist of a queen or mother (sometimes also a king) and her progeny. The progeny are the sterile castes, workers and soldiers. Young reproductives usually leave the nest instead of becoming part of the parent colony. There can be no doubt that the social insects arose from subsocial ones, that is, from insects in which family life exists but in which the families break up, usually with the death of the mother, before the progeny reach maturity<sup>4</sup>. Therefore the prerequisites for subsocial behavior are of necessity among the prerequisites for the establishment of fully social behavior. Fortunately, for our purposes, subsocial behavior has arisen in numerous groups of insects and true social insects have arisen independently from subsocial ones several times (see Table I). These parallel developments provide clues which help us to decide which of the characteristics of the various groups

<sup>3</sup>Marginal cases occur in flocks of certain animals in which rudimentary cooperation and division of labor are demonstrated, e.g., by the existence of guards and sentinels. Also hydroids actually fulfill the qualifications given above, but for all practical purposes should be excluded because of their sessile plantlike habit, asexual production of the cooperating individuals, etc.

<sup>4</sup>Most birds and mammals are subsocial by this definition, for their families break up before the young are mature.

of insects may be prerequisite to the establishment of subsocial and social behavior.

Obviously even the most rudimentary society is impossible if the mother dies soon after laying her eggs, as is the case in many insects. One prerequisite for both subsocial and social life, then, is that the mother must live long enough to be with her offspring.

Examination of Table I, and consideration of insect groups *not* found in it, leads to the conclusion that each time subsocial behavior has arisen, it has been in a group of insects in which the food of immature and adult individuals is the same. Whole great orders of insects (*e.g.*, Diptera, the flies; Lepidoptera, the moths and butterflies) have no known social or subsocial members. This lack of social behavior can readily be explained, for in these orders larvae and adults ordinarily have entirely different foods. Young and old would have to separate to feed. The simplest group in which to understand the development of subsocial behavior is the Hemiptera, especially the Pentatomidae (stinkbugs). In some subsocial species of this family, eggs are laid in groups on leaves, and young as well as adults obtain their food by sucking it from the leaves. If the mother guards the eggs and young, food is available for all of them beneath their feet. An apparent exception to this principle is found in the subsocial and social wasps in which the larvae are fed on insect tissue while

**Table I. Subsocial and Social Behavior among Insects.**

(The figures give an estimate of the number of times that subsocial and social behavior have arisen.)		
	Estimated number of origins of subsocial behavior	Estimated number of origins of social behavior
Blattaria (roaches, termites) <sup>5</sup>	3	1
Dermaptera (earwigs)	1	---
Embioptera (webspinners)	1	---
Hemiptera (true bugs)	8	---
Coleoptera (beetles)	10	---
Hymenoptera		
Vespoidea (wasps)	3	1
Formicidae (ants)		1
Sphecoidea (wasps)	2	
Apoidea (bees)	3	3

the adults feed largely on sweets, such as nectar. This case is not really an exception, however, for the adults also eat insect juices. This behavior is a widespread habit in other Hymenoptera and is characteristic of the adults of the parasitic groups from which the ancestral wasps presumably arose.

*Prerequisites for the Establishment of Social Behavior Among Insects.* If parental longevity and similarity of food for various stages are prerequisites for development of subsocial behavior, what further factors are prerequisite to social behavior? Obviously greater parental longevity is

<sup>5</sup>It is customary to place roaches in the Orthoptera, termites in a separate order Isoptera. There is little merit to this tradition, however, in view of the relationship of the termites to the roaches.

usually necessary. Furthermore, Table I shows us that societies have arisen only among insects that have jaws with which they can manipulate their environment to construct nests and with which they can transport food and young. Insects with piercing and sucking mouthparts have never gone beyond the subsocial stage. This point should be considered in connection with the importance of the human hand in making possible our society.

It is also interesting to note that social insects usually arise from nest making subsocial ones. Almost all subsocial Hymenoptera have some sort of nest or home to which periodic return must be made. Subsocial insects like the lacebugs (Tingidae) and the stinkbugs (Pentatomidae) seem to have no such home from which they leave and to which they return. They suck their food from the leaves beneath their feet. They may wander from leaf to leaf but never need return to the starting point and perhaps are unable to orient themselves to this extent. In contrast, the various social groups of Hymenoptera all arose from ancestors (the non-social and subsocial wasps and bees) in which nestmaking was well established. This is a significant point, for such an insect must possess the nervous mechanism to enable it to undergo conditioning to numerous land marks if it is to be able to find its way back to the nest after locating a food supply. Familiar examples of this sort of behavior among nonsocial insects are found in the mud dauber wasps (*Sceliphron*) which carry load after load of mud from considerable distances to construct the cells of the nest and forage over a wide area to collect the spiders with which the cells are provisioned. This behavior is similar to that seen in most birds and mammals. A possible exception to the idea that nestmaking and the associated ability to leave and return to the nest must precede establishment of social behavior is found in the termites, where there is little evidence of learning. Most termites, however, live permanently inside their nests or in tunnels leading from them, so that there is not much opportunity for them to wander away from the nest and get lost. They probably arose from ancestors such as the wood-eating roaches which likewise spend most of their lives in wood and have little need to return to nests.

To become social, insects must be capable of evolving more numerous and more refined reflexes than their nonsocial ancestors, and they must respond to more complex and perhaps more subtle stimuli. They must possess the potentiality of expanding their form of communication beyond that usually needed by solitary and subsocial forms as will be discussed in greater detail later.

As social behavior arises, mechanisms must develop to hold the members of the colony together. This matter has been extensively

treated by many authors. The most important factor in maintaining the colony as a group seems to be exchange of food or chemical stimuli among the members of the colony. Thus wasps feed their larvae and in return receive certain secretions from the larvae; or again, worker termites feed the queen, and receive exudates which they lick from her body surface. Indeed the best fed and most licked termites are those which have the largest mass of exudate tissue. Plainly feeding is not altruistic but is correlated with hunger for exudates (see Holmgren, 1909). Escherich (1911) points out that termite workers may even strip pieces of cuticle from their queen in their eagerness for her exudates.

Wheeler (1918) called this exchange of food among members of an insect society, "trophallaxis." Exchange of food is well known in all groups of social insects except the bees. Among the specialized social bees (honeybees, bumblebees) there is little evidence of trophallaxis, but as Wheeler says, they may well have evolved through a stage in which reciprocal feeding of larvae and adults occurred. This contention is supported by the recent report of trophallaxis in the scarcely social small Australian carpenter bee, *Exoneura* (Rayment, 1951). Although this bee is certainly not ancestral to honeybees and bumblebees, it may exhibit this characteristic of the ancestor.

Schneirla (1946) has expanded the concept of trophallaxis to include tactile and other sensory sensations, for example, the agreeable stimulation which the human mother receives from the suckling infant. The reciprocal nature of this relationship and its similarity to the relationship among individuals of a colony of social insects was appreciated by Bonnet as early as 1764 and received attention from Wheeler (1918) when he coined the word trophallaxis. Reciprocal stimulation of various sorts, including that involved in copulation, is akin to trophallaxis; but I prefer to use the word in a somewhat restricted sense to include only those instances in which there is exchange of materials (foods, secretions, etc.) in both directions. If not so limited, the meaning of the word will doubtless further expand to include such reciprocal stimulation (usually mutually beneficial either in a material or psychologic way) as is obtained from conversations\*. At this point the word trophallaxis, like the word social in its broadest sense, has acquired such broad meaning as to be nearly useless.

Division of labor is a matter of importance among all social animals.

\*Dr. T. C. Schneirla, to whom must be attributed many of the thoughts repeated in this paper, has recently published an additional paper (1952, Basic correlations and coordinations in insect societies with special reference to ants, *Colloques Internationaux du Centre National de la Recherche Scientifique*, vol. 34, *Structure et Physiologie des Sociétés animales*, pp. 247-269) of much general value which should be consulted by those interested in social behavior. In the comments printed at the end of this paper, Dr. Schneirla states that he regards certain discussions of a conference as "intellectual trophallaxis". As indicated above, I feel that Schneirla's broad concept is sociologically and psychologically valuable but I question the use of the word trophallaxis in such a broad sense.



Division of labor, if it can be so called, occurs between sexes in all animals except hermaphrodites and those which are obligately parthenogenetic. Probably biologically (and morphologically) differentiated castes are not possible in social groups in which all individuals are reproductive (man). Differentiation of individuals of one or both sexes into morphologically recognizable castes (*e. g.*, queen, worker, etc.) by means of complicated trophic (nutritional) interrelationships (Light, 1942), or perhaps by genetic means (Kerr, 1947, 1950) is certainly not a prerequisite to social behavior in insects. Obviously there would be, under most circumstances, 100 percent selection against non-reproductives (*e. g.*, workers) in non-social and subsocial forms. Caste differentiation, however, has occurred in every major social group of insects. It is, of course, associated with division of labor and may be prerequisite to highly developed division of labor among insects, hence to highly developed societies. As more insects are discovered which are living in the borderline region between subsocial and social, more light will be shed on this matter (see Rayment, 1951).

*Advantages of Social Behavior.* Most discussions of the origin of social behavior emphasize the obvious advantages of well established societies: many stings and jaws for defense, ability to control temperature and other environmental conditions as a single insect could never do, ability to escape competition and to feed a large biomass (weight of a species population per unit area) by using widely dispersed food supplies (*e. g.*, nectar, pollen) or food supplies ignored by most other organisms (*e. g.*, wood). These are important points in explaining the success and abundance of social groups, but their importance in the actual origin of social behavior is uncertain, for such behavior must be established or at least started before these advantages take effect.

In studying the origin of subsocial or social behavior, as in other evolutionary considerations, one must remember that evolution is a population phenomenon. It is easy to understand the advantages of subsocial life over nonsocial. To return to the example of the stinkbugs already mentioned, most species survive without subsocial behavior. Yet within a species, if mutant forms arise which protect their eggs and young by resting on them and even by buzzing their wings at intruders, these forms will be at an advantage because of the greater chance of survival of the eggs and young. There will probably be a selection for these forms, as a result of which subsocial behavior may come to characterize the species. Actually many mutations may have been involved in each such change in habits. The biological basis for the selection is evident, however, for egg

masses too large to be protected by the mother's body often have the marginal, unprotected eggs parasitized.

In the noncolonial Hymenoptera, subsocial behavior probably permits rearing of young in places and at seasons when nonsocial forms could not find enough food to provision and seal their cells. The subsocial forms feed their young progressively and so need to provide only for the day to day demand. An African wasp of the genus *Synagris* is particularly plastic in this regard, exhibiting nonsocial behavior when food is abundant, subsocial behavior when it is scarce.

Additional examples illustrating the advantages of subsocial over nonsocial behavior could be easily found. The advantages of the step from subsocial to social behavior are less obvious. Perhaps the matters of defense, ability to control the environment, and ability to use relatively unpopular food supplies, already mentioned, do play a part even in the initial stages of the transition to true social behavior. Perhaps, also, as soon as the caste system is established, the reproductives are hidden and protected most of their lives; most of the individuals killed are workers whose loss does not directly result in a loss of germ plasm for the next generation.

*Communication among Social Insects.* Communication is involved in the lives of all insects except the strictly parthenogenetic. Common and simple examples of communication involving signs among nonsocial insects are the liberation of odors by females which attract males, the chirping of male crickets which attracts females, the flashing of fireflies, and other sorts of displays among many groups of insects which serve to get the sexes together for mating. Similar signs are used, of course, by all social insects. For example young female termites, after the dispersal flight, break off their wings; then each turns up the tip of her abdomen. Apparently in this position she liberates an odor attractive to males, for pairing (but not mating) occurs at this time.

When insects become subsocial, an increasing number of contacts occur and communication becomes more important. This is obvious, for example, from what is known of the habits of certain subsocial lacebugs (Tingidae). The eggplant lacebug is reported to guard her eggs and later shepherd her flock of over two hundred young as they move from leaf to leaf. The mother hurries about, apparently guiding the young with her long antennae, and has been seen to dart at a predator as though to frighten it off. Obviously there is considerably more communication among individuals in such a familial relationship than among ordinary solitary (nonsocial) insects.

The establishment of subsocial behavior among wasps and bees adds



to the amount of communication between adults and larvae, but it has no obvious influence on the development of communication among adults. By contrast, as soon as a family of adults is produced and social behavior is established, the advantage of communication between adults is clear. Natural selection will obviously favor colonies in which there is sufficient communication that when a large food source is discovered, other individuals from the colony can be not only stimulated to activity but directed to the new source.

It is this matter of directing individuals in a colony to a previously discovered food source that will occupy most of our attention in the remainder of this paper. Obviously there are many other sorts of communication in insect colonies (*e. g.*, food exchange with larvae), but so far as known none of them lead to anything which can be called a language, involving symbols, even by the most enthusiastic observer.

Quite consistently among social Hymenoptera, the return of an individual carrying food excites other individuals in the nest. Spieth (1948) has described this behavior for *Polistes*, a wasp far less advanced along the line of social behavior than ants or the honeybee. In *Polistes*, when a worker returns to the nest carrying food, there ensues a wave of activity involving virtually all of the few dozen adult individuals of the colony. The returning worker is accosted as she arrives at the nest. Whatever she has brought back is divided among others of the colony, larvae are fed, and activity continues until all of the material is disposed of. Individuals which have not shared in the food brought in nevertheless respond by visiting larvae for their secretions, cleaning themselves, or merely moving about. Thus in *Polistes* the return of a forager, while stimulating activity, does not cause other foragers to go afield.

Among certain ants (*Formica*) that forage as individuals not employing trails, the return of an individual with food likewise excites others in the colony, and some of them will leave the nest on foraging excursions. The returning *Formica* apparently gives other foragers no clue as to the source of her find, for they may go in any direction although they tend to visit places where they have been accustomed to finding food.<sup>6</sup>

Among many ants communication has reached a point where the discoverer of an important food source can direct other ants to it. The layman's usual supposition is that the discoverer leads others to the food, and this method is indeed reported for a South African termite-eating ant (*Megaponera*) in which groups of workers are led by a single scout which

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<sup>6</sup>Schneirla (1929) who summarized much of what was known until that date about ant orientation, points out that *Formicas* do indeed make some use of odor in orientation, but this behavior apparently does not invalidate the general truth of the above statement.

has supposedly discovered the termite nest to be plundered. If this leader is removed, the whole group returns to its nest.

Far more usual among ants is a type of communication in which the discoverer of a good source is able to stimulate others to follow an odor trail to the food without herself leading them. Among ordinary trail-making ants some of the workers, perhaps the older ones, leave the nest as individuals. These must be the ants having sufficient experience with the landmarks (visual or olfactory or both, according to the kind of ant) near the nest that when they find a food source they can take some of the food and then find their way back to the nest. Usually the route back is a more or less direct one, not following the circuitous course followed before the food was located. Discovery of a good food source apparently excites the forager, and one of the results is that on her homeward trip she lowers her abdomen and seems to drag it, presumably liberating a secretion wherever she walks, thus leaving an odor trail that can be followed by other ants. On reaching the nest, the discoverer of the new food supply apparently gives some of the food to other ants and excites them further by means of movements, antennal tapplings and the like, or in some ants by stridulatory vibrations<sup>7</sup> (Eidmann, 1925). Some of these stimulated individuals leave the nest and are able to follow the fresh odor trail to the food. By analogy with what is known of honeybee behavior, it seems likely that if the food source is large, the workers stimulated to go to it by the finder (scout) are also much excited and on their return stimulate many more ants to go to the same food source. But if the source is small, or when it becomes well covered by ants, the excitement is less and fewer ants, or none, are stimulated to go to the same source. If this is true it accounts for the fact that food sources are rarely much overburdened by an excess of ants.

There remain a number of unanswered questions, such as what determines which odor trail a worker leaving the nest is to follow. In spite of such matters about which we are ignorant, it is obvious that a form of communication of great importance to the ants has arisen. It enables the ants to make relatively efficient use of food supplies by getting approximately the right number of workers to each source, and it probably permits the numerous young and relatively inexperienced workers, that are unable to orient themselves as individuals in the field, to help in bringing in food by merely following odor trails.

Among honeybees the problem of directing individuals to a source of food is more difficult than in ants because, being flying insects, the bees can leave no odor trail. It is perhaps for this reason that it is among the

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<sup>7</sup>Communication among termites also involves vibrations (see Emerson, 1928).

bees, which have the most highly specialized social behavior of any insects having winged workers, that we find signs used in a manner that has caused certain students to speak of a language among bees. Part of bee behavior, however, is closely comparable to that of the trailforming ants discussed above. If a bee discovers a rich food source less than fifty to one hundred meters from the hive, she is excited and liberates there an odor which, like that of the ant, comes from an abdominal gland. The bee flies in a more or less direct line back to the hive. Again, this is the counterpart of the direct route home taken by the scout ant. In the hive, the bee gives some of the syrup or nectar she has collected to other bees, then starts a dance (round dance) in which she circles alternately to the right and to the left. Other bees seem excited by the dance, just as ants are excited by the antics of a successful scout. The other bees follow the dancer, keeping their antennae close to her. During pauses in the dance, they receive droplets of nectar regurgitated by the dancer. One by one these bees turn, leave the dancer, and fly from the hive. They fly at random about the area near the hive. When they approach the food source they are guided to it by the odor of the flower, learned both from that which clings to the dancer's body (perceived by sensory organs on the antennae) and from droplets of nectar given them by the dancer. They are further guided by the odor left by the dancer on the flower. Experimental evidence for the behavior summarized above cannot be presented here, but it is given in detail by Frisch (1923) and in simplified form by the same author (1950).

The similarity of this behavior to that of trailforming ants is most remarkable when it is recognized that it evolved independently in ants and in bees, for these groups of insects arose from quite different non-social ancestors. There is one important difference between the bee behavior described above and that of the ants. The type of dance described is a sign indicating that the food source is less than fifty to one hundred meters from the hive. So far as known, comparable ant behavior conveys no such information.

Except for this one characteristic all communication so far discussed apparently involves signs which transmit excitement from individual to individual, but there is no real evidence of information being transmitted. If the excitement produces activity useful to the colony, it is because of associated chemical stimuli (other signs), as with ants that use odor trails, or because of previous learning, as with the ants which do not use odor trails but have learned the places where food is likely to be found.

By contrast, language as we know it in man has (1) symbolic and

conventionalized character, (2) a directive function (i.e., symbols are used to influence others), (3) an intentional use in social situations, and (4) a capacity for rearrangement according to the requirements of meaning (paraphrased from Schneirla, 1946). The first two of these characteristics seem to apply also to the signs described below used by the bees; the last two find no counterpart among insects. Like the language symbols of man, the signs used by bees are not all mimetic. Those of vertebrates lower than man are generally mimetic, as for example, the dog that learns to curl its lips and growl instead of actually fighting. The use of "language" by bees is strictly limited in that, so far as known, it involves only one sort of activity, namely, the directing of bees to fly to a place where another has already been, and this is accomplished with extremely few signs.

Bees often collect nectar and pollen from sources two or more miles from the hive. It is obvious that mere odor or taste guides, such as those provided in connection with the round dance, could not be practical at such distances. A bee would have to fly for hours or days to cover in detail the area within two miles of its hive and locate a certain source of food. If the dances transmitted no information concerning the location of the food source, the bees would be in the same category as *Formica*; successful foragers could return to the food supply known to them by means of learned landmarks but their dance would only stimulate others to foraging activity without indicating the source of the food.

Actually the dances indicate both the distance and the direction to the food supply. The round dance, as already stated, indicates a food source close to the hive but does not indicate direction. For distances above fifty to one hundred meters from the hive the dance changes abruptly to a "wagging dance." The bee makes a short straight run on the comb while wagging the abdomen rapidly from side to side. Then she turns to the right and returns to the beginning point, repeats the straight run over the same course, then turns to the left and returns to the beginning point. This pattern is repeated over and over. This dance indicates a rich source of food far away.

The speed of the dance, that is, the number of turns per unit time, indicates the distance. A food source one hundred meters from the hive is indicated by a very rapidly turning dance, seven to ten complete cycles of the dance in fifteen seconds. A food source 6,000 meters (six kilometers) from the hive is indicated by a dance having only two cycles in fifteen seconds (Frisch, 1946, 1950). Actually the effort or time required to reach the food, not the ground covered, determines the speed of the

dance. For example, a head wind on the way to the feeding place slows the dances, having the same effect as increased distance (Frisch, 1948).

The direction to the food source is indicated in relation to the position of the sun by the direction of the straight run in the wagging dance. It is dark in the ordinary hive and the bees cannot perceive the direction of the sun from inside, but they evidently can detect the force of gravity, for they dance on the vertical faces of the combs. They use a downward run as a symbol for away from the sun. Of course, it follows that an upward run indicates that the food source is toward the sun; a run sixty degrees to the left of straight up indicates food situated sixty degrees to the left of a line toward the sun's position in the sky, etc. (Frisch, 1946, 1948, 1950).

Bees excited by a dancer are presumably able to detect with their antennae the direction of her straight run in the dark hive, or rather, the angle of that run relative to the force of gravity. On emerging into daylight they must remember this angle and are able to relate it to the direction of the sun's rays well enough so that few of them make errors of over fifteen degrees in direction. Having flown the distance and direction indicated by the dance, the bee is helped to locate the particular source by the odor of the flowers and the odor left on them by the excited dancer when she found them. These clues are the same as those that guide bees working close to the hive after stimulation by the round dance.

It seems possible that the use of the direction of the run in indicating direction of the food is ultimately of mimetic origin. A run directly toward the food is impracticable on the vertical combs of true honeybees (*Apis*). If a honeybee comb is artificially turned so that it is horizontal, the bees perform their dances with the straight run directly toward the food source, providing there is sunlight visible for orientation. Furthermore, the nearest relatives of honeybees are the tropical stingless honeybees of the genera *Melipona* and *Trigona*, which build horizontal combs. Dr. W. E. Kerr (in litt.) has reported dances among these bees suggestive of those of the honeybees. It is not difficult to imagine how dances on such combs or at the nest entrances, with the direction of the run indicating the true direction toward the food, could evolve into dances like those of the honeybee as nestmaking evolved and produced vertical combs.

The question arises as to whether we should call anything in bee behavior intelligence. Since the behavior pattern is presumably hereditary and transmitted by the reproductives (which, however, do not participate in the behavior concerned), I do not believe that their behavior indicates intelligence.

*Discussion and Conclusions.* Social habits in insects have been



evolving for 30,000,000 years or more. They have arisen at various times in different groups of insects. As a result we can find among insects now living virtually every stage in the development of social behavior. For this reason we can determine some of the prerequisites to and some of the advantages of social habits, as summarized in Table II.

It is noteworthy that most birds and mammals have fulfilled the prerequisites mentioned for the establishment of social life, but not, or only to a slight degree, those suggested as important for the maintenance of social groups. Thus family groups, flocks, and herds of these animals are common but often temporary (seasonal) in nature. Only in man, among vertebrates, has a really specialized division of labor, and a highly evolved society, arisen.

Advantages of the subsocial and social behavior patterns are important to consider, for such patterns will evolve only if there are advantages.

**Table II. Some Factors Related to Social Development among Insects.**  
(A sequential relationship exists in each series of numbered items.)

Status	Some Prerequisites (Items in this column are shown under the "status" groups in which they must appear to make possible evolution to next status group.)	Some Advantages	Communication having to do with directing others to a food supply
1. Nonsocial	1. For establishment of sub-social behavior — Longevity of parents — Food of young and adults similar		None
2. Subsocial	2. For establishment of social behavior — Ability to carry and manipulate objects (e. g., young, food, materials for nest) — Sensory and nervous mechanisms permitting orientation for return to nest and permitting considerable communication	— Protection and care of young — Among nestmakers, sub-social behavior permits progressive feeding rather than mass provisioning	None
3. Social	3. For maintenance of social behavior — Trophallaxis (usually) — Division of labor (usually also caste formation)	— Defense (especially of re-productives) — Ability to control environment — Ability to feed large biomass on dispersed food supply	1. Forager excites nest mates to various activities. 2. Forager excites nest mates to go in search of food. 3. Forager excites nest mates to go in search of food and directs them by: a. leading them b. odor trail c. signs indicating distance and direction.

Most birds and mammals share with subsocial insects the advantages listed for subsocial behavior, and many animals which occur in herds share with social insects one advantage of social behavior, that concerned with defense. Unless reactions like bedding down together for warmth constitute an ability to control environment, only man shares with the social

insects the second and third advantages listed. The prerequisites and advantages listed are obviously remarkably similar to those which have influenced vertebrate social evolution.

Problems of communication are not well suited to tabular treatment, but for comparative purposes some material has been included in Table II. A striking point immediately evident is that while complex social relationships in vertebrates (man) are made possible largely by a language, this is not the case among insects, and communication in human ancestors did *not* pass through the stages (1 to 3) listed in the table. Presumably in man the development of complex social behavior and of language were more or less concurrent; among insects social behavior exists with no language.

No doubt the great difference in evolution of communication between insects and man is due to the manner of transmission of behavior characteristics from generation to generation. In insects this is primarily a biological process; evolution in such characteristics must be due to mutations and subsequent selection. A learning capacity is present but stereotyped and limited to the individual, so that information learned by one individual ordinarily dies with it. As Emerson (1942), Sinnott (1945), Simpson (1949), and others have said, man has developed an additional mechanism supplementing biological heredity. He can transmit behavior patterns from generation to generation with the aid of language. On the other hand, again unlike insects, man is capable of a high degree of plastic learning and reasoning. Aspects of the social heritage can therefore be changed or displaced rather than passed on intact. These great differences in communication between the social insects and man are not diminished by the fact that the honeybee has evolved a sort of stereotyped, automatic "language".

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