NOTES AND COMMENTS

EVOLUTION OF COMMUNICATION IN BEES AND ITS ROLE IN SPECIATION[1]

WARWICK E. KERR

Faculdade de Filosofia, Ciências e Letras de Rio Claro, Rio Claro, Est. S. Paulo, Brazil

Several families of bees have species that are either social or subsocial. Only the subfamily Apinae, however, possesses species that are known to have reached a social level sufficiently high as to have developed some method or methods of communication among their workers.

The Apinae social tribes, in phylogenetic order, are the following: Bombini (bumblebees), Meliponini (stingless bees), and Apini (honey bees). In these bees, the evolution of communication systems is indicated by the order of their increasing complexity, and by the parallel evolution of other characters of the species in which a given system of communication is found.

Ribbands (1953) suggested that exchange of food among adult bees was the first step toward communication. In fact, *Bombus* species neither engage in food exchange nor have a system of communication (Brian 1952, Free 1951). As far as nest structure is concerned, they are the most primitive Apinae (Kerr and Laidlaw, 1956).

A first evolutionary step may have occured when foraging was so intense that a field bee gave nectar to a house bee instead of delivering it directly to the storage pots. Such house bees, when they became foragers, may have been more attracted to flowers having the same odor as the nectar they received. Indeed, workers of the most primitive Meliponini known, namely *Trigona silvestrii,* alert their mates to look for an artificial source of food only when a drop of scent is added to the feeder (Lindauer and Kerr, 1958). The nest structure of these bees resembles very much the one found in *Bombus.* The communication of the location of either a source of food or a place to live by odor is a method found in all species of Meliponini and Apini.

A further step was reached when returned bees, while delivering nectar, ran excitedly in zig-zag movements knocking bees not engaged in field work with their heads or bodies. Such a method was discovered first by Lindauer (1956) in the Indian meliponid *Trigona iridipennis* and later by Lindauer and Kerr (1958) in ten species of Brazilian meliponids. By further work, I found this same mechanism to be present in eight other species, namely: *Trigona (Scaptotrigona) xanthotricha, Trigona (Scaptotrigona) postica II, Trigona (Scaptotrigona) postica III, Trigona (Trigona) hyalinata, Trigona (Trigonulla) muelleri, Trigona (Partamona) testacea,* and in the African species *Trigona (Hypotrigona) araujoi* and *Trigona (Meliponula) bocandei.*

One other method of alerting, either developed anew or brought from *Bombus,* is found in several (or all) species of meliponids. It is a special buzz that is perceived as vibration by the legs (Lindauer and Kerr, 1958). I found that the frequency of this sound varies with the species. Usually it lies between 464 and 484 vibrations per second for *Melipona quadrifasciata,* 326 and 348 for *T. (T.) jaty,* and is approximately 391 for *T. (S.) postica I.* These are only the frequencies of the most common sounds, the total range being greater than these presented. For instance, *Melipona quadrifasciata* sounds vary from 348 to 588 v.p.s. It may be that the ability to use sounds for communication has been lost in *Apis mellifera,* although it is very interesting to know that Hansson (1945) and later Frings and Little (1956) were able to stop activity of bees by subjecting them to simple sounds. Frings and Little (o.c.) caused bees to cease movement by subjecting the colonies to sounds between 300 and 1000 v.p.s. (Sounds between 300 and 800 v.p.s. were most effective.) *Apis mellifera* workers, therefore, have maintained the nerves (Shön, 1911) for perceiving vibrations similar to the ones perceived by stingless bees, but seem to have lost the ability to use them for communication. These sounds may not provide information concerning distance or direction, but are excellent for alerting other individuals.

It seems likely that the primitive Apini had three simple methods of communication: odor of the crop, zig-zag runs, and alerting buzzes. As far as we can see, further evolution of communication in the Apis species proceeded mostly from the zig-zag runs to the specialized dances. But even in these communicatory dances, three evolutionary levels were disclosed by Lindauer (1956). He found that *Apis florea* (which is morphologically the most primitive *Apis*) dances only in the horizontal

---

[1] Research reported in this paper was done with the help of the Conselho Nacional de Pesquisas (Brazilian Research Council) and the Rockefeller Foundation.

plane pointing straight toward the food source. *Apis dorsata* workers perform the dance on the vertical comb, but need to see the sun during the dance. *Apis mellifera* performs the so-called circle, sickle, and wagging dances (von Frisch, 1950), that are of amazing precision, inside the dark hive.

The species within the Meliponini have developed along two different paths. The *Melipona* species are the ones with the stronger buzz. In addition, *Melipona* species and some *Trigona* (for instance, *Trigona testacea*) release in the air great quantities of odor from their mandibular gland which attract other bees to a food source. The *Trigona* species are strikingly variable. Many of them remained primitive insofar as communication is concerned since they utilize only the three simple methods mentioned above. One group, however, has developed a particularly interesting method of communication. The scout bee, after having collected nectar or pollen for some time, acts to bring newcomers to this spot. To do this, as she flies from the flowers toward the hive, she stops frequently leaving on each stop an odor mark. The newcomers follow this odor path, which in *Trigona trinidadensis* can be as long as 900 meters, and reach the flowers in great numbers. Lindauer and Kerr (1958) found this method in the following species: *Trigona* (*Trigona*) *ruficrus, Trigona* (*Scaptotrigona*) *postica, Trigona* (*Geotrigona*) *mombuca, Trigona* (*Cephalotrigona*) *capitata.* Recently, in our laboratory, the following species were found to have the same communication method: *Trigona* (*Trigona*) *trinidadensis, Trigona* (*Trigona*) *hyalinata, Trigona* (*Scaptotrigona*) *postica II, Trigona* (*Scaptotrigona*) *postica III, Trigona* (*Scaptotrigona*) *xanthotrica.* The odor producing substance for the marks comes from a pair of mandibular glands (Lindauer and Kerr, 1958). This method is very precise and works better than the dances of *Apis.* Colonies of species having this mechanism occur in greater number than the others.

The average interval between two odor marks varies from species to species. In *Trigona ruficrus,* it is about 8 meters; in *T. capitata,* around 5 meters; in *T. trinidadensis,* 20 meters; and in *T. postica,* it is approximately 1 to 2 meters.

For the species of the subgenus *Scaptotrigona,* the odor mark system of communication, besides improving fitness of the species, has had a further evolutionary effect. Since the distance between two odor marks is around 1 or 2 meters, any river about ten meters wide would be big enough to constitute a geographic barrier for one of these species facilitating its break up into several new ones. Variability in the species of this subgenus is very great indeed. Two subspecies of *T. postica I* have been ascertained to belong to two different reproductively isolated sibling species, not crossing with each other nor being attracted to the odor marks of the others (they are called *T.* (*S.*) *postica II* and *III* for the time being). In addition *T. postica I* is extremely variable. It is very difficult to decide which of its varieties are species and which are subspecies, at least without a test of interbreeding. Recently Kerr and Stort (unp.) found that populations occurring North of the river Piracicaba are indistinguishable from ones located 40 kilometers apart; however, they are different from ones located in the South side, about 100 meters apart.

I wish to thank Dr. Walter Rothenbuhler very much for the trouble he had to put this paper in readable English.

LITERATURE CITED

BRIAN, A. D. 1952. Division of labour and foraging in *Bombus agrorum* Fabricius. J. Animal Ecol., **21**: 223–240.

BUTLER, C. G. 1951. Bee Department. Rept. Rothamst. Exp. Sta., 7 pp.

FREE. (In Butler, 1951.)

FRINGS, HUBERT, AND FRANKLIN LITTLE. 1956. Reactions of honeybees in the hive to simple sounds. Science, **125** (3238): 122.

FRISCH, K. v. 1950. Bees, their vision, chemical senses and language. Ithaca, N. Y.

HANSSON, A. 1945. Lauterzeugung und Lautanffassungsvermögen der Bienen. Opusc. ent. Lund. Suppl. 6.

KERR, WARWICK E., AND H. LAIDLAW. 1956. General genetics of bees. Adv. Genetics, **8**: 220–354.

LINDAUER, M. 1956. Über die Verständigung bei indischen Bienen. Z. f. vergl. Physiol., **38**: 521–557.

LINDAUER, M., AND WARWICK E. KERR. 1958. Die Gegenseitige Verständingung bei den stachellosen Bienen. Zeits. f. vergl. Physiol., **41**: 405–434.

RIBBANDS, RONALD. 1953. The behaviour and social life of honeybees. 352 pp. Bee Research Ass. Ltd., London.

SCHÖN, A. 1911. Bau und Entwicklung der titialen Chordotonalorgane bei der Honigbienen und der Ameisen. Zool. Jb., Abt. 2, **21**: 439–472.