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Original article

The silent dances of the Himalayan honeybee, *Apis laboriosa*

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Summary — Comparative studies of the mechanisms of information transfer in the dance language of honeybees have recently led to an evolutionary scenario, assuming that acoustic signals replace visual communication signals in species that are forced to communicate in the dark, either because of nesting in dark cavities like *Apis mellifera* and *Apis cerana* or because of nocturnal activity like *Apis dorsata.* To test this idea, the dance language of the giant honeybee *Apis laboriosa,* which is closely related to *Apis dorsata,* but exclusively diurnal, was studied. We observed the dances, determined the flight range and recorded and analyzed acoustic signals emitted by worker bees. The dances of this species do not contain any acoustic signals, indicating that acoustic signalling of the location of food sources is indeed restricted to species which need to dance under low light intensities. The evolutionary implications are discussed.

communication / sound / Asian honeybee / *Apis laboriosa*

Honeybee foragers communicate distance and direction of profitable food sources to their nestmates by means of their dance language (von Frisch, 1965). In *Apis mellifera*, it has been shown that the information is transmitted in the darkness of their nests through airborne sounds (Kirchner and Sommer, 1992; Michelsen et al, 1992; Dreller and Kirchner, 1993a), which are perceived by the dance attenders through Johnston's organ, an auditory sense organ located in the antennae (Dreller and Kirchner, 1993b).

Dance communication is found not only in *A mellifera* but in all species of honeybees studied so far (Lindauer, 1956). Among the open nesting species of Asian honeybees, the dwarf honeybee *Apis florea* does not produce information coding dance sounds and presumably communicates the location of food sources by means of visual signals (Towne, 1985), whereas the giant honeybee *Apis dorsata* does emit dance sounds which contain the information about the location of the food source (Kirchner and Dreller, 1993). However, the probability of sound production, which is close to one in *A mellifera*, turned out to be substantially lower in *A dorsata*, indicating that this species might be able to use both visual and acoustic signals. *A dorsata* forages and dances not only during the daytime, but also during moon-lit nights (Dyer, 1985). Observations of nocturnal dances of *A dorsata* revealed that the probability of dance sound production was significantly higher at night time than during the day (Kirchner and Dreller, 1993), supporting the hypothesis of Towne (1985) that acoustic dance communication signals might have evolved in honeybees when they were forced to dance at low light intensities.

The giant honeybee, *Apis laboriosa*, a close relative of the lowland giant honeybee, *A dorsata,* can be found in the Himalayan range at altitudes of 1 200 m to 3 500 m (Sakagami et al, 1980; Roubik et al, 1985; Underwood, 1990). The species was first described by Smith in 1871, but there was some discussion on the species status of this bee (Maa, 1953; Sakagami et al, 1980; McEvoy and Underwood, 1988; Ruttner, 1988, 1992; Smith, 1991), which was mostly considered as being a subspecies of *A dorsata* until quite recently. Many aspects of the biology of this bee, which lives in quite inaccessible places, are still entirely unknown. This is especially true for the dance language of *A laboriosa.*

A laboriosa has never been found to be active at night and nocturnal activity would seem to be quite unlikely because of low temperatures at night time. The dance language of this species is therefore especially interesting, because it should allow a test of the hypothesis that acoustic communication of the location of feeding sites is an adaptation to foraging at low light intensities. If, on the other hand, acoustic communication of food sources already evolved in a common ancestor of the genus *Apis* and the silent dances of *A florea* were a derived trait, one would expect acoustic dance signals to be present in *A laboriosa.*

The purpose of the present study was therefore to observe the dances of *A laboriosa*, compare the dance language of these bees with the dances of other honeybee species and to clarify whether *A laboriosa* uses sound to communicate the location of feeding sites.

METHODS

The study was conducted in March 1995 in northeast Nepal, close to the 8 586 m high Mount Kantchenjunga (87’45”N, 27’30”E) at an elevation of 2 100 m. A large colony of *A laboriosa* Smith 1871 (width and length of the comb both about 1.2 m) was found under an overhanging cliff ledge about 150 m high in a vertical cliff of a deep river valley. In this area *A laboriosa* is geographically separated from *A dorsata*. Furthermore, measurement of the cubital index of the wings revealed an extremely high cubital index of 17.5 ± 6.2 ($n = 13$), which is typical for *A laboriosa* and different from the cubital index of *A dorsata* as reported by Sakagami et al (1980).

Dances were observed through binoculars from a distance of about 30 m. The dance tempo was determined by measuring the duration of dance circuits with a stop watch, the directions indicated in the dances were estimated with a resolution of 15°. Individually marked bees were trained to forage at an artificial feeding site, where 2 M sucrose was provided. Sound was recorded using a pressure-sensitive and a velocity-sensitive microphone (previously used to record dance sounds of *A mellifera* (Michelsen et al, 1987)) on a digital audio tape recorder (Sony DAT recorder TCD-D3). Sounds of flying bees were recorded at a distance of 1 m from the comb. Sounds emitted by bees standing on the comb were recorded at a distance of 1–2 cm from the comb. Recorded sound signals were analysed in the laboratory using a CED 1401 laboratory interface and an IBM-compatible computer.

RESULTS

During 8 days of observation of the colony we observed intense foraging and dancing activity. The main activity time of the bees was between 900 and 1600 hours, depending on the weather conditions. Returning forager bees advertised a number of different feeding sites, mostly nectar sources, at different distances and directions. The pattern of feeding sites indicated in a sample of 93 dances recorded on three consecutive days is indicated in figure 1a. The durations of the dance circuits ranged from 2.0 to 11.1 s with a mean of 4.8 ± 1.8 s. Figure 1b shows the distribution of circuit durations in this sample of dances. Compared with the distribution of circuit durations found for *A dorsata* in India in a previous study, there was a significant difference in that the dance circuits of *A laboriosa* lasted longer on average. As it turned out to be impossible to train the bees to an artificial feeder at distances further than 50 m, we could not determine the distance dialect of *A laboriosa*. Assuming the distance dialect is similar to the distance dialect of *A dorsata*, we can calculate the distances inferred by the dancers. The mean distance would then be about 700 m, the longest distance indicated by the dancers about 2 km.

In all species of honeybees found to produce dance sounds studied so far, the frequency of the dance sounds is similar to the frequency of wing beat in flight. Therefore, we determined acoustically the wing beat frequency of flying workers of *A laboriosa*. We found a mean wing beat frequency of 133 ± 18 Hz ($n = 20$). This is significantly ($P < 0.01$) lower than in the wing beat frequency of *A mellifera*, but not significantly different from the wing beat frequency of *A dorsata*.

A sample of 40 vigorous and long-lasting dances was observed from a short distance and all sounds produced by the dancer and the dance attendance recorded on digital audio tape.

None of the dancers produced any dance sounds. The dances were entirely silent. Just short squeaking sounds similar to those which have been described as stop signals in *A mellifera* could be heard from time to time. An example of such a signal is shown in figure 2. This signal was produced by bees standing close to the dancer, presumably emitted as a begging signal.

DISCUSSION

The main result of the present study is the lack of dance sounds in the dance communication system of *A laboriosa*. As the recording system used in *A laboriosa* was the same as in previous studies of the dance sounds of other honeybee species, it was obviously suitable to detect dance sounds, and as stop signals and background noise were recorded and of similar amplitude as in other species of honeybees, the system was also operating during the recordings. Therefore we can exclude the possibility that the lack of dance sounds is due to inappropriate, insensitive or malfunctioning equipment. Dance sounds have been described independently in *A mellifera* by Esch (1961) and Wenner (1962). These sounds are produced by dorsoventral vibrations of the wings in round and wagging dances (Kirchner et al, 1988) and are exclusively airborne sounds (Michelsen et al, 1986), perceived by the dance follower bees through Johnston's organ, located in the antennae (Kirchner et al, 1991; Dreller and Kirchner, 1993b). The dance sounds provide the dance attenders with the information about the location of the food source (Michelsen et al, 1992; Kirchner and Sommer, 1992; Dreller and Kirchner, 1993a). Similar dance sounds have also been found in the Asian bees *A cerana* (Towne, 1985) and in *A dorsata* (Kirchner and Dreller, 1993), whereas *A florea* does not produce dance sounds (Towne, 1985). Both open nesting species, *A florea* and *A dorsata*, however, can perceive those sounds like *A mellifera* (Dreller and Kirchner, 1994). Therefore, we assume that *A laboriosa* might also be able to per-

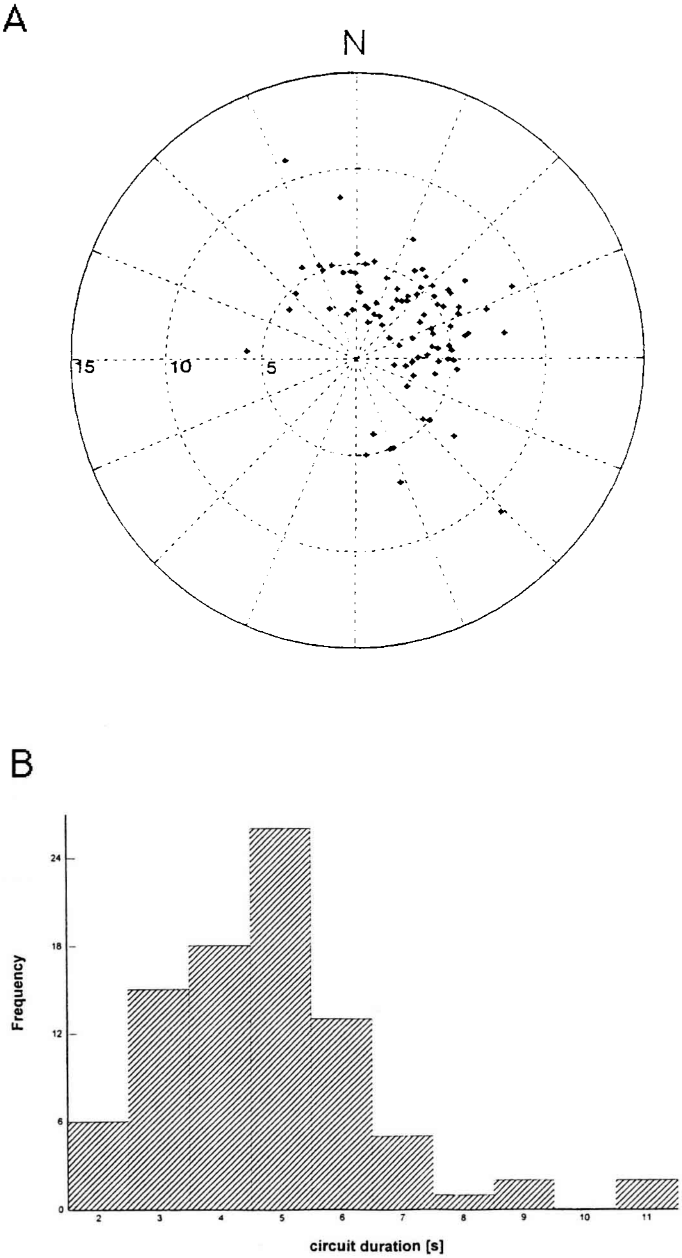

Fig 1. A: Pattern of feeding sites indicated in a sample of 93 dances of *A laboriosa* recorded on three consecutive days. Distance is expressed in terms of circuit duration (s), the magnetic north compass directions is indicated. **B.** Distribution of circuit durations (s) in the same sample of dances. The mean circuit duration is 4.8 ± 1.8 s.

that *A laboriosa* might also be able to perceive sound.

Dance attenders in *A dorsata* are able to pick up the information about the location of the food source acoustically. However, only a fraction of the dances of *A dorsata* for natural food sources contains dance sounds. This finding supported the hypothesis of Towne (1985) that acoustic signalling of the location of food sources evolved when ancestors of recent honeybees began to forage at low light intensities. In this scenario *A dorsata* reflects an evolutionary stage in which acoustic signals can be used, and are used during nocturnal foraging, but are probably not essential for successful dance communication during the day.

This idea was tested in our study of the dance language of *A laboriosa*. The rough climate at the high altitudes where this bee lives excludes nocturnal foraging. If giant honeybees are able to communicate the location of food visually during the daytime, a species that is dancing exclusively diurnally does not need additional acoustic signals. Our result that the dances of the Himalayan honeybee *A laboriosa* are entirely silent thus supports this hypothesis.

The squeaking sound (fig 2) is basically similar to the stop signal of *A mellifera* (Esch, 1964; Nieh, 1993). The frequency is substantially lower, corresponding to the lower wing beat frequency of the much larger *A laboriosa*. A stop signal has also been described in *A dorsata* by Towne (1985). It is similar in signal duration. Sound frequency was not analysed by Towne (1985).

The distribution of dance circuit durations indicates that the observed colony foraged in a wider area compared to a colony of *A dorsata* observed in a previous study in India (Kirchner and Dreller, 1993). The lack of a calibration of circuit durations by train-

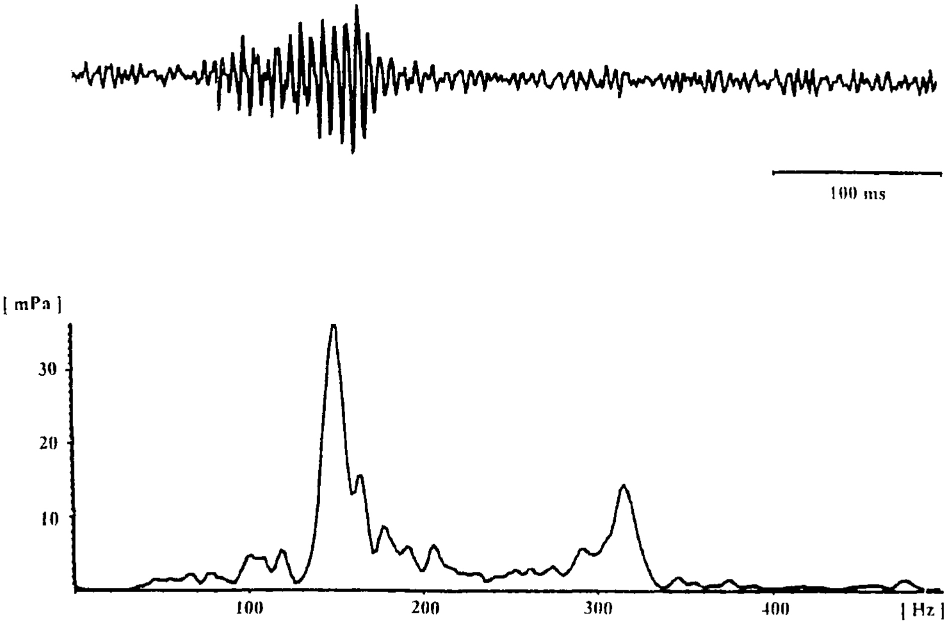

Fig 2. Temporal structure and frequency spectrum of the stop signal of *A laboriosa*. The signal duration is about 130 ms, the main frequency is about 150 Hz.

ing bees to artificial feeders at different distances prevented us from calculating a flight range of the observed colony. However, the topography of the area where these bees were studied, which is characterized by high mountains and deep and steep valleys, would limit the value of a distance dialect curve so long as we do not know exactly how bees calculate distances. Whereas in most places slope can be ignored in calculations of distances, they may become significant in mountainous areas. In *A mellifera* indication of distance seems to be affected by the topography of the landscape (von Frisch, 1965).

Our result that *A laboriosa* dances silently, whereas *A dorsata* produces dance sounds, supports, as discussed above, the hypothesis that acoustic signalling of the location of food sources is an adaptation to dancing at low light intensities. In an evolutionary perspective the silent dancing of *A laboriosa* could either reflect a primitive trait or a derived trait. The phylogeny within the genus *Apis* is not yet fully clarified (see Koeniger, 1976; Smith, 1991). However, one can assume that *A laboriosa* is quite closely related to *A dorsata*, the lowland giant honeybee. According to Sakagami et al (1980), it is most likely that the origin of *A laboriosa* is interglacial or postglacial. The first giant honeybees appeared already in the Miocene and lived under a warm Tertiary climate. If the silent dancing in *A laboriosa* was a primitive trait, we would have to assume that *A dorsata* and the *A mellifera* group have independently developed acoustic signals in the dances. The facts that *A mellifera* and *A cerana* use sound signals that are quite similar to those of *A dorsata* (Towne, 1985; Kirchner and Dreller, 1993) and that *A mellifera*- and *A dorsata*-like bees are known since Tertiary times, whereas *A laboriosa* is much younger, make it unlikely that the silent dancing of *A laboriosa* is a primitive trait. We assume instead, that the common ancestors of *A dorsata, A laboriosa, A mellifera* and *A cerana* did use acoustic signals in their dances. On the other hand, we can ask whether the use of visual signals for the transfer of information in the dances of *A laboriosa* is a primitive or a derived trait. In *A dorsata* dance sounds are found in only a fraction of the dances performed during the daytime and it seems likely that *A dorsata* can communicate the location of food sources without the aid of sound signals. Therefore, the common ancestor of both giant honeybee species should have been able to use both channels of information transfer, sound as well as visual cues.

However, the question remains whether this is also true for the common ancestor of the giant honeybees and the *A mellifera* group. The dwarf honeybee *A florea* nests in the open, dances silently and uses visual cues to transfer dance information. If we assume, as did Lindauer (1956), that this represents the ancestral mode of information transfer in the dance language of honeybees, the next step must have been the evolution of the acoustic channel of communication in the common ancestor of the *A mellifera* group and the *A dorsata* group. However, it is also possible, as Koeniger (1976) pointed out, that the common ancestor of the recent species in the genus *Apis* was a cavity-nesting species. In this case we have to assume that the use of visual signals in the dance communication system has evolved twice, in the ancestor of *A florea* and independently in the ancestor of the giant honeybees, whereas the *A mellifera* group would have conserved the primitive trait of an exclusively acoustical transfer of information. This hypothesis can be tested: *A mellifera* has been observed to dance in the open under experimental conditions (von Frisch, 1965). If *A mellifera* could communicate the location of food sources without the aid of sound signals when they are dancing in the open, it would be possible to conclude that visual transfer of information must be a primitive trait and that the latest common ancestor of all recent honeybees was nesting in the open.

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Zusammenfassung — Die stummen Tänze der Honigbiene aus dem Himalaya, *Apis laboriosa*. In der Tanzsprache teilen Honigbienen ihren Nestgenossinnen Richtung und Entfernung lohnender Futterquellen mit. In der Dunkelheit ihrer Nester benutzt die westliche Honigbiene *Apis mellifera* akustische Signale zur Weitergabe dieser Informationen. Unter den im Freien nistenden Arten, die auch mit Hilfe optischer Signale kommunizieren können, benutzt *Apis florea* keine Schallsignale für die Tanzkommunikation, während *Apis dorsata* Tanztöne produziert, die Information über die Lage der Futterquelle enthalten. Diese Töne treten allerdings nicht wie bei *Apis mellifera* in allen Tänzen auf. Bei nächtliche Tänzen ist die Wahrscheinlichkeit der Schallproduktion erheblich höher als am Tage. Diese Beobachtung führte zu der Hypothese, daß die Evolution akustischer Signale in der Tanzsprache eine Anpassung an die Notwendigkeit ist, bei geringen Lichtintensitäten zu kommunizieren. Diese Hypothese wurde an der Riesenhonigbiene des Himalaya, *Apis laboriosa*, die eng mit *Apis dorsata* verwandt, aber nicht nachtaktiv ist, getestet. Die Tänze von *Apis laboriosa* wurden an einer Kolonie in Ost-Nepal in 2100m Höhe beobachtet. In einer Stichprobe von 93 Tänzen (Abb 1) wurde die Umlaufdauer und die Tanzrichtung bestimmt. Im Mittel betrug die Umlaufdauer 4,8 ± 1,8 s, die längste beobachtete Umlaufzeit war 11.1 s. Unter der Voraussetzung, daß der Entfernungscode dem von *Apis dorsata* gleicht, entspricht das einer mittleren Entfernung der Futterquellen von etwa 700 m, als größte beobachtete Entfernung von Futterquellen ergibt sich etwa 2 km. Da die Tanztöne anderer Honigbienenarten in ihrer Frequenz der Flügelschlagfrequenz im Flug entsprechen, wurde diese in 1 m Entfernung von der Wabe an vorbeifliegenden Bienen bestimmt. Sie beträgt im Mittel 133 Hz ± 18 Hz. Bei einer Stichprobe von 40 lebhaften und langanhaltenden Tänzen wurden alle Geräusche aus einer Entfernung von 1-2 cm von der Wabe aufgezeichnet und analysiert. In keinem der Tänze traten Tanzlaute auf. Während die Tänzerinnen von *Apis laboriosa* völlig stumm sind, konnten gleichzeitig kurze piepende Signale, die den bei *Apis mellifera* und *Apis dorsata* auftretenden Stop-Signalen ähneln, registriert werden (Abb 2). Die Tatsache, daß die Tänze von *Apis laboriosa* stumm sind, unterstützt die Vorstellung, daß sich akustische Kommunikationssignale bei Honigbienen als Anpassung an die Notwendigkeit von Tanzkommunikation bei niedrigen Lichtintensitäten entwickelt haben.

Tanzkommunikation / Schallproduktion / asiatische Honigbiene / *Apis laboriosa*

Résumé — Les danses silencieuses de l'abeille de l'Himalaya, *Apis laboriosa*. Par le langage dansé les abeilles mellifères (genre *Apis*) communiquent aux congénères du nid la direction et la distance des sources de nourriture à exploiter. Dans l'obscurité de son nid l'abeille mellifère occidentale, *Apis mellifera*, utilise des signaux acoustiques pour transmettre ces informations. Les espèces qui nidifient en plein air peuvent aussi communiquer par signaux visuels. Parmi celles-ci, *Apis florea* n'utilise

pas de signaux sonores alors qu'*Apis dorsata* produit au cours des danses des sons qui contiennent l'information sur la situation de la source de nourriture. En fait ces sons ne sont pas présents, comme chez *A mellifera*, dans toutes les danses. Leur probabilité est considérablement plus élevée la nuit que le jour. Cette observation a conduit à émettre l'hypothèse selon laquelle l'évolution des signaux acoustiques dans le langage dansé serait une adaptation à la nécessité de communiquer dans les cas de faible intensité lumineuse. Cette hypothèse a été testée sur l'abeille géante de l'Himalaya, *Apis laboriosa*, qui est étroitement apparentée à *A dorsata* mais n'est pas active la nuit. Les danses d'*A laboriosa* ont été observées sur une colonie située à 2 100 m d'altitude dans le nord-est du Népal. La durée et la direction de la danse ont été déterminées sur un échantillon aléatoire de 93 danses (fig 1). La durée moyenne a été de 4,8 ± 1,8 s (maximum observé 11,1 s). À condition que le code de distance soit le même que celui d'*A dorsata,* la distance moyenne des sources de nourriture a été évaluée à 700 m environ (maximum observé : 2 km environ). Puisque chez les autres espèces d'abeilles mellifères la fréquence des sons des danses correspond à la fréquence des battements d'ailes en vol, on a déterminé celle-ci sur des abeilles qui volaient à 1 m du rayon. Elle était en moyenne de 133 ± 18 Hz. Sur un échantillon aléatoire de 40 danses vigoureuses et de longue durée on a enregistré et analysé tous les bruits à une distance de 1 à 2 cm du rayon. Aucune de ces danses n'a été accompagnée de sons. Les danseuses d'*A laboriosa* sont restées totalement silencieuses, mais on a pu enregistré de temps en temps des petits cris aigus qui ressemblaient aux signaux d'arrêt déjà décrits chez *A mellifera* et *A dorsata*. Le fait que les danses d'*A laboriosa* soient silencieuses conforte l'idée que les signaux acoustiques chez les abeilles mellifères sont le résultat d'une adaptation de la communication par les danses dans les cas de faible intensité lumineuse.

***Apis laboriosa* / communication sonore / danse**

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