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Original article

Sounds in *Melipona costaricensis* (Apidae: Meliponini): effect of sugar concentration and nectar source distance

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Abstract – The principal finding presented here is that *Melipona costaricensis* produces sounds that vary significantly in relation to varying sugar concentrations. Several components of the sounds produced, during the bees' stay inside of the hive, were positively correlated with sugar concentration: song duration, probability of sound production, duration of the long pulses and the relationship between short / long pulsed sound. Number of pulses per song was negatively correlated with sugar concentrations. The duration of all sound pulses was significantly correlated with the distance of the food source. Duration of the short pulses and interpulses were significantly affected by the distance of the food source. Sounds may contribute to the recruitment of nestmates to increasingly rich food supplies during the day. It is clear that aspects of the sound signals are correlated with profitability of food sources.

sound production / sugar concentration / distance / food source /stingless bees

1. INTRODUCTION

When a foraging social bee (Apidae: Meliponini) finds food, it returns to the hive and may recruit nestmates to that source. Through recruitment, which implies some mechanism of communication, newly available food sources can be exploited more efficiently (von Frisch, 1967). The known mechanisms for recruitment vary considerably between species of Apidae. They include olfactory, taste and acoustic cues (Lindauer and Kerr, 1958; Esch et al., 1965). It has been found that honey bees give information about direction and distance of food sources by performing dances on the vertical combs in the hive (von Frisch, 1967). Esch (1964) and Esch et al. (1965) demonstrated that sound signals are also an important element of honey bee dances and apparently they are an adaptation to dancing at low light intensities inside the nest (Kirchner et al., 1996). These signals are airborne sounds of high intensity produced by dorsoventral vibrations of the wings (Michelsen et al., 1987; Kirchner et al., 1988). Their sounds consist of short pulses at a repetition rate of 15 Hz (Kirchner, 1993), they do not have a long continuous pulse sound.

The duration of sound pulses during each performance of both the round dance and the waggle dance increases with distance between the hive and the feeder (Esch et al., 1965; Waddington and Kirchner, 1992; Kirchner and Dreller, 1993). Sounds produced during round and waggle dances are necessary for successful communication (Michelsen et al., 1989;

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Kirchner and Sommer, 1992). It has been suggested that both dances additionally may contain useful information about profitability of the food source (Spangler, 1991; Waddington and Kirchner, 1992; Kirchner and Dreller, 1993) and sound signals emitted in the round dances of *Apis dorsata* may contain useful information about direction (Michelsen et al., 1992; Waddington and Kirchner, 1992; Kirchner, 1993). In *A. mellifera* the duration of sounds was positively correlated with the sucrose concentration (Waddington and Kirchner, 1992) and the probability of sound production was correlated with the profitability of the food source in *A. dorsata* and *A. mellifera* (Waddington and Kirchner, 1992; Kirchner and Dreller, 1993).

The communication systems for recruitment adopted in the eusocial stingless bees, differ from those of honey bees (Lindauer and Kerr, 1958; Kerr, 1959). Stingless bees use several cues to locate food sources: scent marks along the route to the food source, odour of nestmates and of the food source (Kerr, 1959). They may also be guided to the source by an individual worker bee. Scent trails allow them to indicate not only distance and direction but also height, whereas honey bees only communicate distance and direction (Wilson, 1971; Nieh and Roubik, 1995).

Not much information is available about the intranidal behaviour of foragers and recruits of *Melipona* or *Trigona* species. Observations in some species showed that foragers, once they reach a good food source outside the nest, made irregular excited movements inside the hive associated sometimes with sound production (Kerr, 1959; Lindauer and Kerr, 1958; Esch et al., 1965). Returning foragers of *M. scutellaris* (Lindauer and Kerr, 1960), *M. quadrifasciata*, *M. merillae* (Esch et al., 1965) as well as *M. panamica* (Nieh and Roubik, 1995) produce sound pulses. A distance related signal is produced in the hive by forager bees of *M. quadrifasciata* (Esch et al., 1965; Esch, 1967), *M. merillae* (Esch, 1967) and *M. panamica* (Nieh and Roubik, 1998). Nieh and Roubik (1998) found that sound signals were correlated likewise with height. Although communication of distance by sound signals seems to be clear (Nieh, 1998b; Nieh and Roubik, 1998), Hrncir et al. (2000) did not find a significant correlation with distance to the food source for either *M. quadrifasciata* or *M. scutellaris*.

It is unclear if quality of the food source (sugar concentration) is communicated by sound signals in stingless bees. There are indications that *M. panamica* behaviour varied depending on the sugar concentration: foragers appeared to produce lower amplitude sounds at 1.0M sugar concentration, although this was not quantified, and they turned 36% more slowly than foragers at a 2.5M (Nieh, 1998b). As the concentration of the sucrose solution decreased, the rate of recruitment decreased. Nieh (1998b) also noted that at artificial food sources, more foragers produced sounds as the concentration increased. Jarau et al. (2000) observed in *M. quadrifasciata* and *M. scutellaris* that foragers collecting food from a source 0.75M did not show any kind of specific behaviour nor did they produce any kind of sounds when entering the hive. These observations suggest that there may be variation among stingless bee species in the use of sound for the recruitment of foragers.

The objective of this paper is to provide information on whether sound “signals” (pulse duration, interpulse duration, song duration, long and short pulses, number of pulses per song and probability of singing), produced by trained *M. costaricensis* foragers inside the hive change in relation with different sugar concentration and with different distances to the food sources.

2. MATERIALS AND METHODS

2.1. Study site and colony

The study was carried out in Costa Rica during January, August 1998 and April 1999 at the Centro de Investigaciones Apícolas Tropicales (Heredia province) and Universidad de Costa Rica (San José province). Data were obtained from a colony of *Melipona costaricensis* of about 600 individuals collected in Horquetas de Sarapiquí, Heredia province. It was installed in a wooden observation box (70 × 20 × 20 cm) and brought to our building in 1998.

2.2. Effect of the sugar concentration on sound production

Foragers of *Melipona costaricensis* ($N = 5$) were trained to an artificial food source containing 2.0M sucrose solution, which was placed 10 m from the hive according to the experimental set up used by von Frisch (1967). The bees were marked individually with paint on the thorax. The feeder station with the sucrose solution consisted of a removable paper yellow plate on a 65 cm iron stake and a drinking cup with 6 holes glued on the plate. The concentration of sucrose solution was changed between series, varying the order of the concentration from 2.0M, 1.0M and 0.5M (total: 17 series), with about 15 min observation per concentration. We offered the sugar solution ad libitum on the top of the feeder into the plastic cup. We refilled the cup at the feeder table with fresh sugar solution before each observation with the corresponding sugar concentration, after having removed residue of the former solution. Returning *Melipona costaricensis* foragers produced sounds inside the hive. Sounds and behaviour of bees were video recorded each time the trained bee returned from feeding station.

Songs, defined as multiple long and short sound pulses produced while the forager was inside the hive, began when the singing forager entered the hive, and ended only when it has finished dispensing its nectar load to nestmates. A returning forager performed only one song, and some foragers may perform none. Here, the "rate" of song production was the number of songs performed by an individual nectar forager per observation period.

To analyze the probability of sound production, we considered only the returning foraging flights within the first six minutes, after the bee started to visit the feeder table. The probability of song production was calculated by dividing the number of visits during which the returning foraging bee ($N = 4$) produced sounds inside the hive by the total number of returning foraging flights.

The behaviour of the returning bees was recorded inside a clear plexiglass chamber (11 × 10 × 4 cm) located between the hive and the entrance exit tube, using a Video Camera (CCD V-801) equipped with +6 close up lens so that a single bee filled the screen. The sound was recorded through a Senheiser MZK 80 ZV microphone inserted into the Plexiglas chamber from above (3.5 cm).

Recordings of sounds were imported from video recordings into a Pentium II 350 MHZ computer using a 32 bit card. The mean duration of pulses and interval between pulses were measured using the real time display in the program Avisoft®. The standard deviation of these measurements was determined by measuring the duration of 10 pulses and intervals in each of 10 different songs. The average differences were 2.0 ms in pulse duration and 2.2 ms in interval duration. *N* refers to number of bees; n to the number of songs and *n* to the number of sound pulses analyzed.

2.3. Effect of the distance of the food source on sound production

Bee foragers of *M. costaricensis* were trained to an artificial food source with a 2.0M sugar solution (von Frisch, 1967). The bees were marked individually by different spots of paint and trained to collect the food offered at a feeder placed at distances of 1 m ($N = 5$), 10 m ($N = 3$), 30 m ($N = 5$), 50 m ($N = 5$), 55 m ($N = 5$), 70 m ($N = 5$), 90 m ($N = 5$), 100 m ($N = 10$), 130 m ($N = 3$) and 150 m ($N = 3$) from the hive. The training procedure, bee behaviour and sound analysis were conducted as described above.

2.4. Statistical analysis

The statistics are based on the average of all pulses in a song, obtained for a specific parameter (sound duration, interpulse duration, song length, relation between long and short pulses and probability of pulsed sounds) for each respective concentration and distance. We estimated the relationship between the mentioned parameters and both the concentration and the distance to the food source by expressing one in terms of a linear function of the other through a regression analysis. Significant differences among the three different concentrations were analyzed for long pulses with a non-parametric Mann-Whitney U-test. We used the Friedman Two-Way analysis of variance to test if the repeated measures on the same bees were significantly different in probability of sound production. Likewise, we used the coefficient of determination as an estimate of the proportion of the variation of probability of sound production determined by the variation of the sugar concentration. We selected an alpha level of $P < 0.05$.

3. RESULTS

3.1. General patterns of sound production by foragers

The carrier frequency and temporal structure of a typical song of returning bees is shown in Figure 1 (A and B). Returning nectar foragers of *M. costaricensis* perform a song which consists of multiple long and short pulses of relatively loud sound (Fig. 1). The song of *M. costaricensis* has acoustical properties similar to songs produced by other stingless bees (e.g. *M. quadrifasciata*, *M. scutellaris* and *M. panamica*). The carrier frequency of the signals in *M. costaricensis* (Fig. 1A) ranged from 429 up to 588 Hz (493 ± 50 Hz, n = 30). We also found up to eight peaks in the spectrum generated by other bees humming inside the hive. We did not attempt to analyze in detail the frequency of songs.

M. costaricensis did show a sequence from long pulsed to short pulsed sounds (we will refer to pulses shorter than 0.1 s as "short pulses" and to pulses longer than 0.1 s as "long pulses") (Fig. 1B). During each performance (one return of the trained forager bee inside the hive) a long pulsed sound was made first. The trained forager bee continued this long pulsed sound until she found a nestmate or nestmates to give her load. Then she produced long and short pulsed sounds while unloading food (trophallaxis). Soundless periods were noted during trophallaxis, and more frequently while the trained bee returned to the feeder place. Trained bees did not always produce sounds at a 0.5M sugar solution. Returning pollen gathers did not produce sounds at any time during the period they were recorded.

Recruitment was observed during our experiments. A total of 10 new bees landed at the feeder table during the sugar concentration experiments. From these new bees, six arrived at the feeder when it contained 2.0M sugar solution. We also observed recruitment at the feeder table during distance experiments (1 m, $N = 65$; 10 m, $N = 5$; 30 m, $N = 13$; 50 m, $N = 5$; 70 m, $N = 1$ new bees). We did not observe the arrival of new bees at 100 m and 150 m.

3.2. Effect of the sugar concentration

We observed variations in the songs of bees trained at different concentrations (Fig. 2) in a feeder 10 metres North from the hive. The song duration of 2992 sound pulses (long and short combined) was analyzed from bees visiting a food source of 0.5M (number of songs, n = 41), 963 pulses at 1.0M (n = 60) and 4566 pulses at 2.0M (n = 38). The duration of all sound pulses was correlated with sugar concentration ($P = 0.0000001$, $r = 0.232$) (Fig. 3). In addition, the duration of the *long pulses* was positively correlated with sugar concentration ($P < 0.0001$, $r = 0.150$). At 0.5M, long pulses averaged 0.164 ± 0.1 s ($n = 134$), at 1.0M they averaged 0.262 ± 0.225 s ($n = 219$), and at 2.0M they averaged 0.343 ± 0.381 s ($n = 1230$). Also, significant differences between the *long pulses* among different food concentrations were found (1.0M vs. 2.0M, $P < 0.0016$; 0.5M vs. 1.0M, $P < 0.00001$; 0.5M vs. 2.0M, $P < 0.000001$, Mann-Whitney two-tailed test).

The percentage of long pulses increased with the increase in sugar concentration (4.4%, 22.7% and 26.9% respectively). Likewise, the proportion of short to long pulses increased considerably with the increase on sugar concentration (0.0468, 0.280 and 0.368 at 0.5M, 1.0M and 2.0M respectively) ($P < 0.000001$, $r = 0.61$) (Fig. 4). The number of pulses per song was negatively correlated with the sugar concentration of the food source ($P < 0.000001$, $r = -0.69$).

A positive relation between the duration of a complete song (one visit of a trained bee inside the hive) and sugar concentration of the food source was also found ($P < 0.0000001$, $r = 0.69$). A negative correlation between total interpulse duration and sugar concentration also was found ($P = 0.000001$, $r = -0.13$) (Fig. 5).

The probability of sound production increased with the increase of sugar concentration in each trained bee ($N = 4$). Different sugar concentrations had an effect on the observed behaviour. There was a significant difference in probability of sound production at different sugar concentrations ($df = 3$, $x_r^2 = 29.34$, $\alpha = 0.001$). Sugar concentration may explain 97% ($r^2 = 0.970$, n = 125 songs, pooled data) of the variation in probability of song production.

During some trials at low sugar concentrations, some bees did not visit the feeder table at all, but stayed in the nest receiving food from other foragers. Other bees stayed outside making a few visits to the feeder until food was again substituted with sugar solution of either 1.0M or 2.0M.

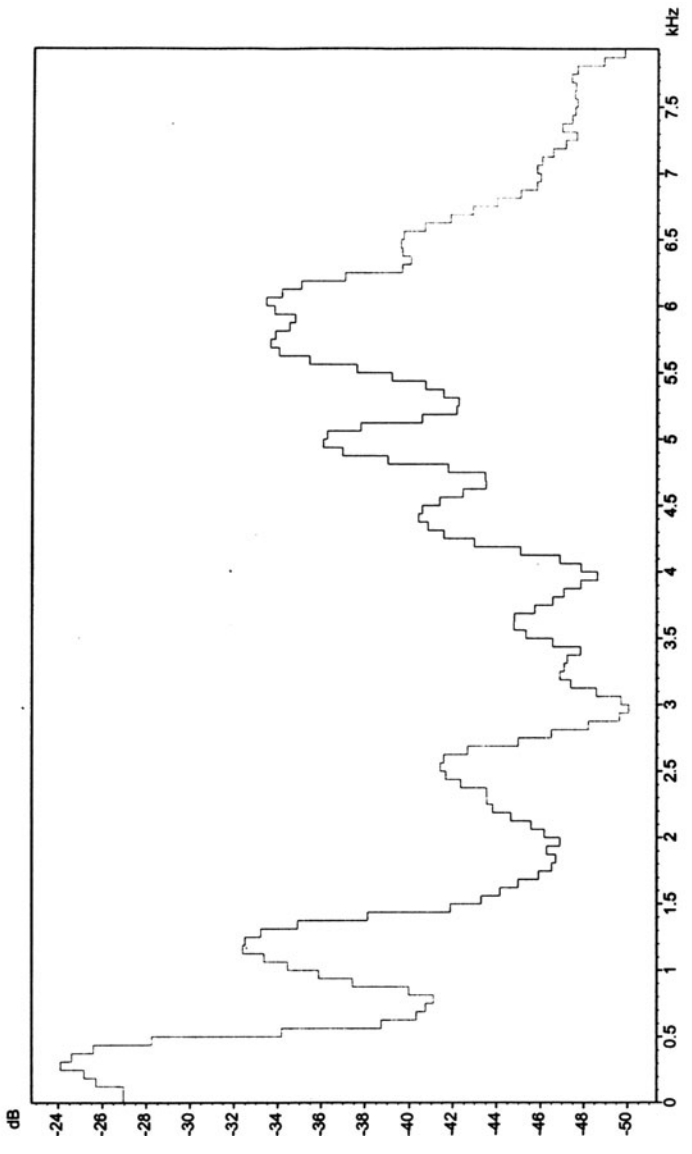
dB
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Figure 1A

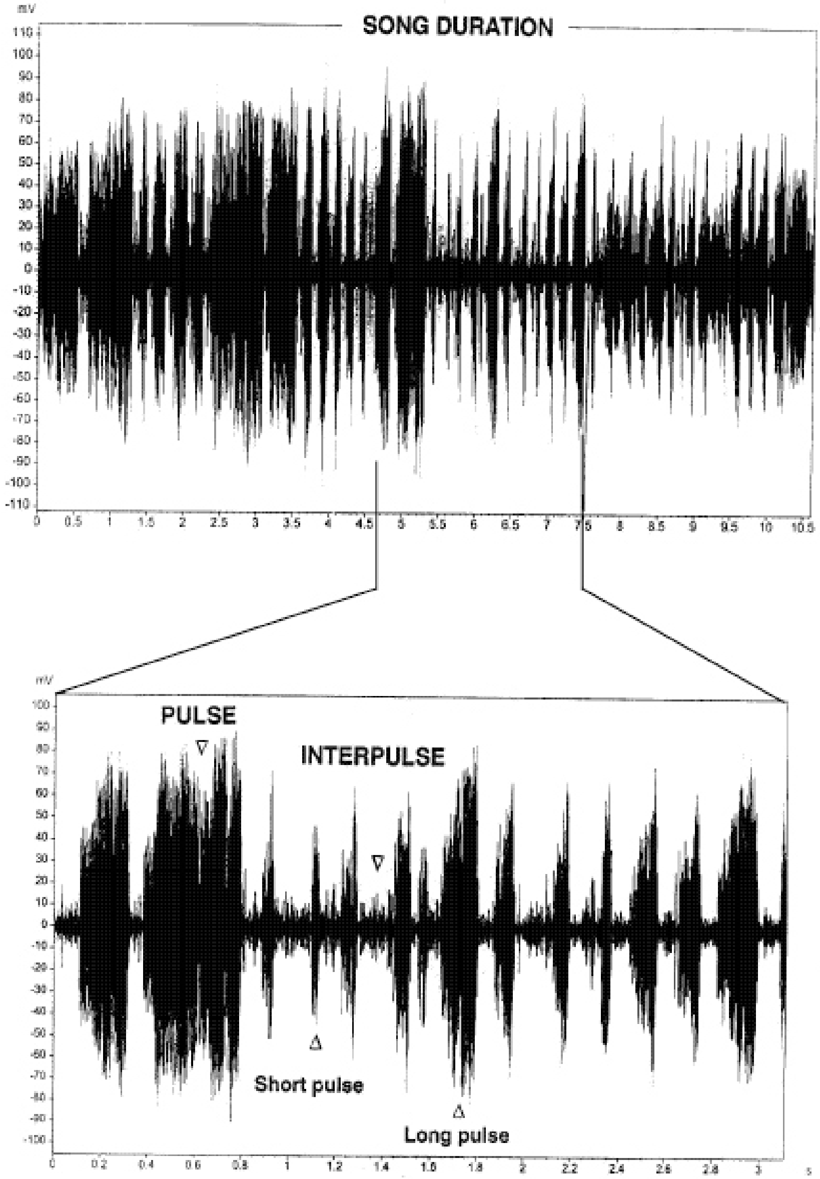

Figure 1B

Figure 1. A song consisting of pulsed sound produced inside the nest by the stingless bee *Melipona costaricensis*. **A**, frequency spectrum ranges from 429–588 Hz. **B**, the temporal structure of the song [amplitude (mV) vs. time (s)]. The extended part of above signal is showing single pulses.

3.3. Effect of the distance of the food source

We analyzed pulses when the food distances were 1 m (n = 37, *n* = 1229), 10 m (n = 30, n = 2046), 30 m (n = 19, n = 1882),50 m (n = 35, n = 1371), 55 m (n = 5, n = 291), 70 m (n = 29, n = 2557), 90 m (n = 21, n = 924), 100 m (n = 26, n = 1017), 130 m (n = 62, n = 2182) and 150 m (n = 32, n = 2099) from the hive. The duration of all sound pulses was significantly correlated with the distance of the food source ($P = 0.026$, $r = 0.18$) (Fig. 6). We analyzed *long pulses* for food distances 1 m ($n = 463$, 0.40 ± 0.7 s), 10 m ($n = 785$, 0.32 ± 0.32 s), 30 m ($n = 398$, 0.32 ± 0.58 s), 50 m ($n = 449$, 0.58 ± 0.68 s), 55 m ($n = 91$, 0.22 ± 0.17 s), 70 m ($n = 1035$, 0.34 ± 0.42 s), 90 m ($n = 395$, 0.75 ± 1.35 s), 100 m ($n = 346$, 0.30 ± 0.38 s), 130 m ($n = 760$, 0.34 ± 0.57 s) and 150 m ($n = 726$, 0.33 ± 0.43 s); and *short pulses* for food distances 1 m ($n = 766$, 0.038 ± 0.025 s), 10 m ($n = 1261$, 0.038 ± 0.25 s), 30 m ($n = 1484$, 0.034 ± 0.025 s), 50 m ($n = 922$, 0.044 ± 0.024 s), 55m ($n = 200$, 0.034 ± 0.026 s), 70 m ($n = 1522$, 0.040 ± 0.027 s), 90 m ($n = 529$, 0.040 ± 0.025 s), 100 m ($n = 671$, 0.05 ± 0.02 s), 130 m ($n = 1422$, 0.05 ± 0.02 s) and 150 m ($n = 1373$, 0.04 ± 0.02 s).

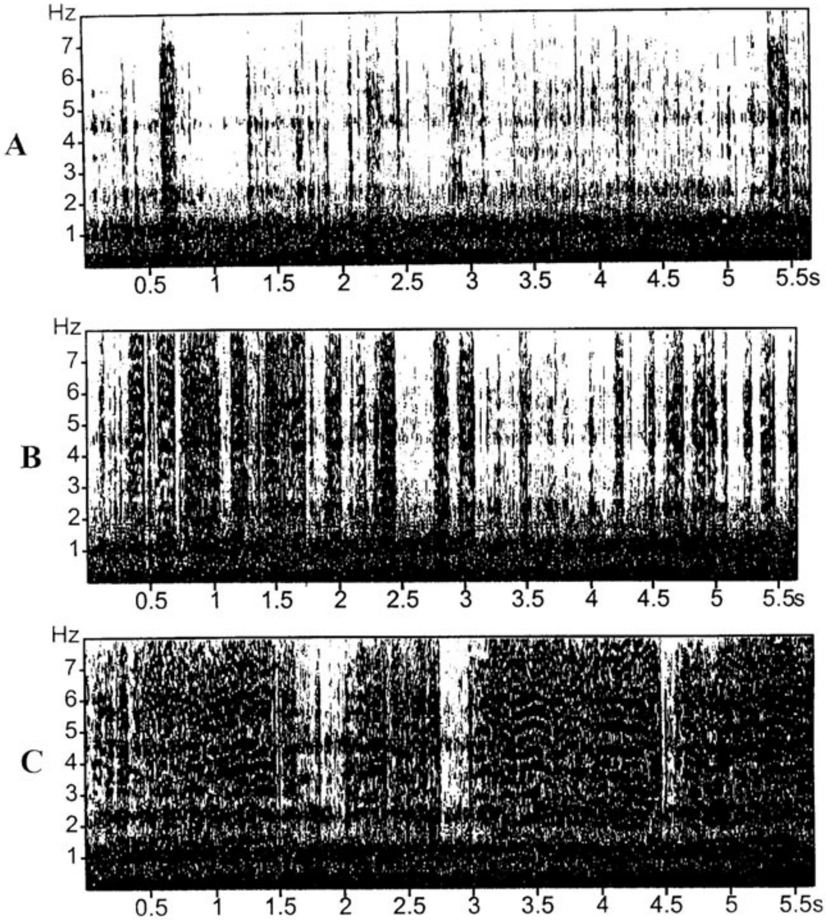

Figure 2. Examples of variation of spectogram (frequency vs. time) of the waveforms at different sugar concentrations of the stingless bee *Melipona costaricensis*: **A**, 0.5M; **B**, 1.0M and **C**, 2.0M.

Duration of long pulses was not correlated with distance of the food source (*P* > 0.01, *r* = 0.004) while the duration of the short pulses showed a significant relationship (*P* < 0.01, *r* = 0.094). The relation between short and long pulses did not increase with the increasing distance from hive (0.60, 0.62, 0.26, 0.48, 0.45, 0.68, 0.74, 0.51, 0.53, 0.52 respectively) (*P* > 0.0539, *r* = 0.114). Moreover, the percentage of long pulses neither increased with longer distances (37.67%, 38.37%, 21.15%, 32.75%, 31.27%, 40.48%, 42.75%, 34.02%, 34.83%, 34.59% respectively) nor with the percentage of short pulses (62.33%, 61.63%, 78.85%, 67.25%, 68.73%, 59.52%, 57.25%, 65.98%, 65.17% and 65.41% respectively).

We found a positive correlation between the duration of all interpulses and the food source distance (*P* = 0.0014, *r* = 0.025) (Fig. 7). On the other hand, the duration of a complete song (one performance inside the hive) was neither correlated with the food source distance (*P* < 0.086, *r* = – 0.1) nor the number of pulses per song (*P* > 0.3172, *r* = – 0.06). Number of pulses dropped as the distance to the feeding station increased (*P* < 0.00238, *r* = – 0.18). Thus, distance did significantly affect some of the acoustical variables.

4. DISCUSSION

It has been shown that acoustical signals are used among stingless bees for communication of distance and height of the food sources (Esch et al., 1965; Nieh and Roubik, 1998). However, different aspects of sounds are not correlated consistently with distance among the stingless bee species (Jarau et al., 2000).

As in *M. scutellaris*, *M. quadrifasciata* (Jarau et al., 2000) and *M. panamica* (Nieh, 1999), foragers of *M. costaricensis* produced long and short pulsed sounds. In *M. seminigra*, *M. quadrifasciata* (Esch et al., 1965) and *M. panamica* (Nieh and Roubik, 1998) foragers produced pulsed sounds, whose durations were positively correlated with the distance to the food source. However, *M. costaricensis* did not show the same behaviour. Nieh and Roubik (1998) made a more detailed analysis in

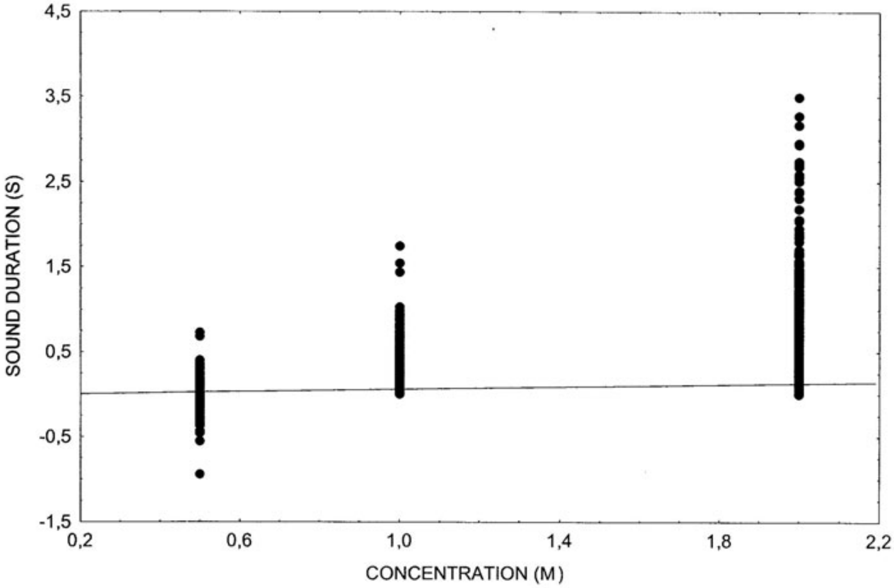

Figure 3. The relationship between the sound duration (total of all *soundpulses*) and the sugar concentration of the food source.

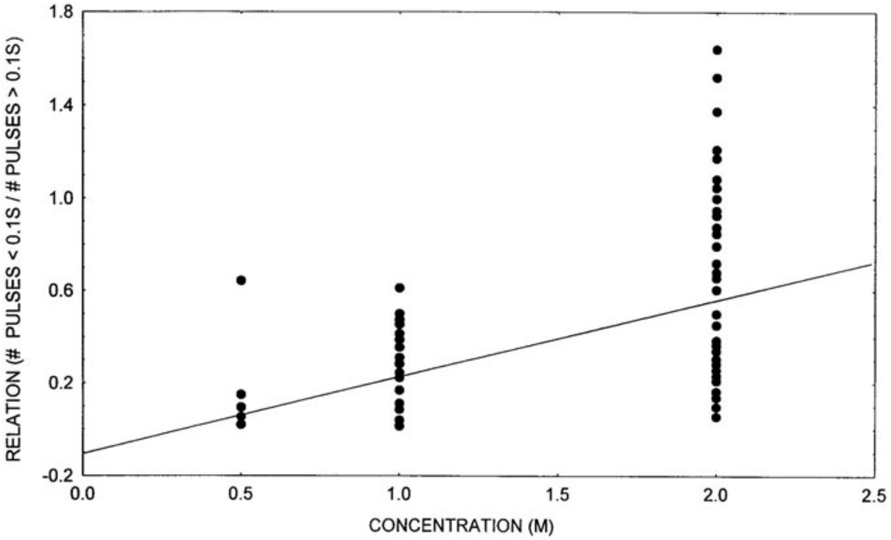

Figure 4. Relation between pulsed sounds < 0.1 s and pulsed sounds > 0.1 s with increasing sugar concentration of the food source.

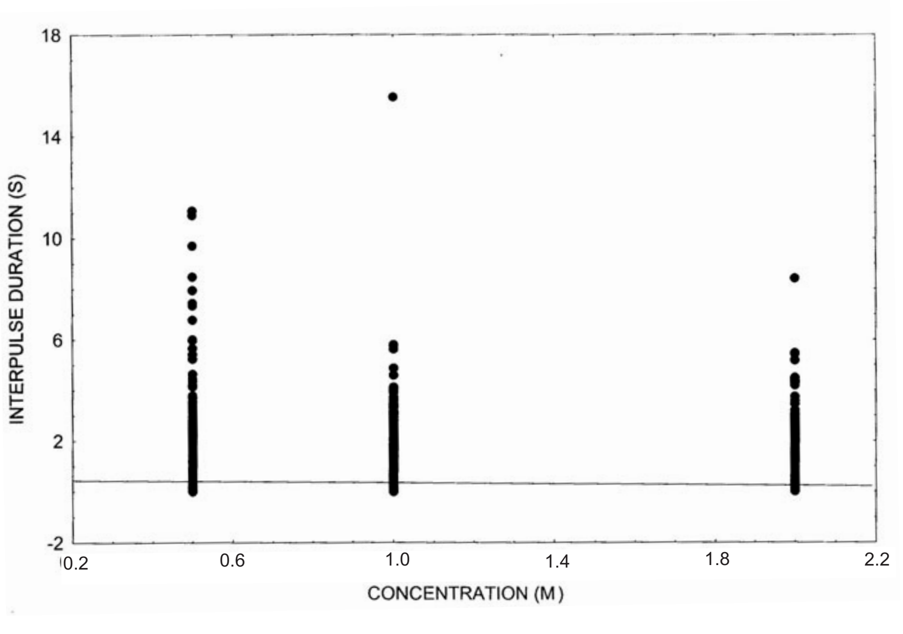

Figure 5. The relationship between the duration of all *interpulses* and the sugar concentration of the food source.

M. panamica and concluded that sound signals emitted during unloading of food give information about height, and that sounds emitted during a "dance" give information about distance. Jarau et al. (2000), by contrast did not observe in *M. quadrifasciata* and *M. scutellaris* the dance behaviour mentioned by Nieh (1998a) in *M. panamica*. Instead, they discovered that another behaviour of returning bees, called "jostling", was correlated with recruitment behaviour.

In the present study we found that trained bees of *Melipona costaricensis* produced sounds that varied significantly in relation to the variation of sugar concentration in the food source. When the quality of the food source was high, as in the experimental feeder filled with a 2.0M sucrose solution, all trained bees continued visiting the feeder, worked quickly, and produced strong sounds. When the quality was low (0.5M) most of the bees stopped visiting the feeder, and the ones that continued visiting the feeder foraged slowly, spent more time inside the hive between trips to the feeder, and performed fewer pulses. Such modifications of foraging behaviour in relation to the food source profitability have been characterized in honey bees (von Frisch, 1967; Núñez, 1966, 1970, 1982; Seeley, 1995) and recently have been observed in stingless bees (Jarau et al., 2000). Our findings confirm that workers of *Melipona* (Biesmeijer et al., 1999) are able to distinguish sugar solutions of different concentrations.

Spectrograms of the waveforms showed that returning foragers produced pulsed sounds that were very loud when they visited the feeder with the highest concentration (Fig. 2). The variation in this behaviour probably was caused by the higher frequency levels that the sound signals reached at greater sugar concentrations. The number of long pulses also increased with sugar concentration. Sugar concentration influences the body temperature of honey bees, and consequently their wingbeat frequency (Spangler, 1991; Waddington and Kirchner, 1992). In stingless bees more experiments are needed to confirm if sound production is related to changes in body temperature.

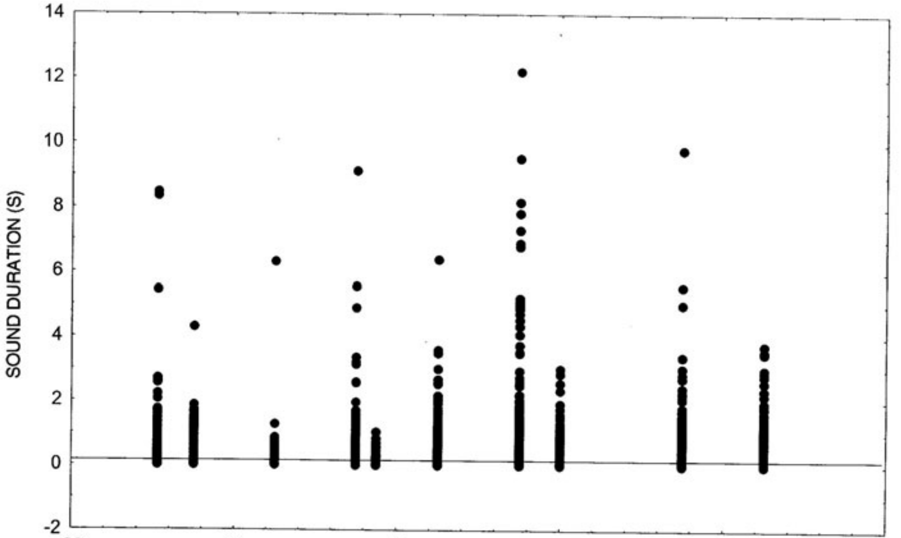

Figure 6. The relationship between the duration of all *sound pulses* and the distance between the colony and the food source.

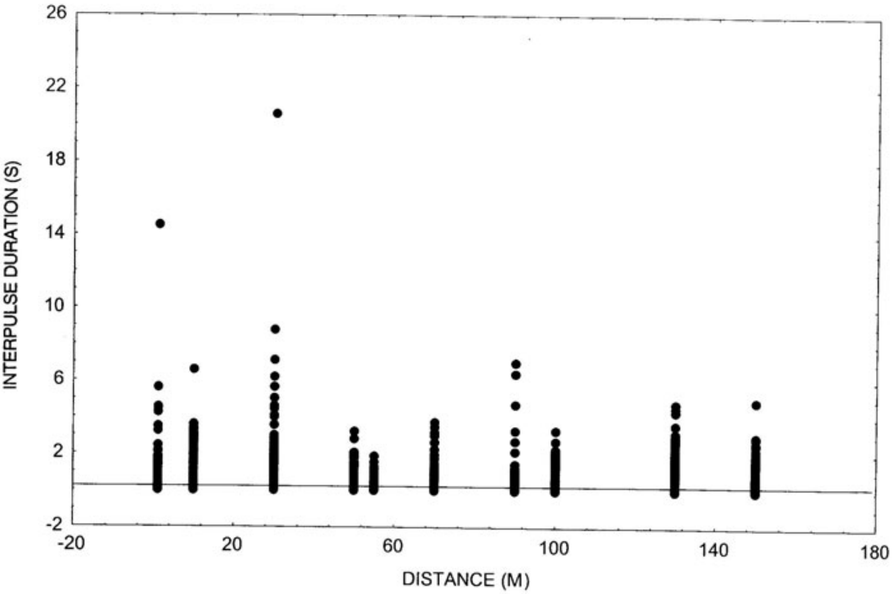

Figure 7. The relationship between the duration of all *interpulses* and the distance between the colony and the food source.

Our study shows that the variation in the probability of producing a song in *M. costaricensis* was explained by sugar concentration of the food source (97%, $r^2 = 0.970$). In *A. mellifera* and *A. dorsata* (Waddington and Kirchner, 1992; Kirchner and Dreller, 1993) this correlation suggests an alternative way by which profitable food sources are signaled.

According to our data, other aspects of sound signals, such as song duration and proportion of long pulses, are potential signals of richness of the food source in terms of sugar concentration for *M. costaricensis* and likely for others *Melipona* species. Firstly, this is supported by the finding (Nieh, 1998b) that nestmates of *M. panamica* preferably contact the abdominal region of a forager when a source offers food with sugar in high concentration. Hrncir et al. (2000) also found that recruits of *Melipona scutellaris* and *M. quadrifasciata* preferably contact a successful forager at the thoracic-abdominal region. That region is mentioned by Michelsen et al. (1987) as a region where air particle movements are more intensive in the waggle dance of *A. mellifera*. Secondly, Nieh (1998a) points out another interesting behaviour in *M. panamica*: at the feeder table, significantly more foragers produced sounds as the concentration of sucrose increased (from 0.50M to 2.50M), and the proportion of departures preceded by sounds increased linearly. Although Nieh did not record data on sounds inside the hive related with sugar concentration, he found that recruitment was higher at the feeder with the higher concentration of sugar. Increasing recruitment at higher concentrations also was found in *Trigona fulviventris* (Johnson, 1987). Thirdly, it appears that *Melipona* species prefer high concentrations (Roubik et al., 1995; Biesmeijer et al., 1999) and nectar of high sugar concentration becomes gradually more available through the day (Roubik, 1984). This finding parallels studies of daily patterns of nectar foraging, in *Melipona fasciata* (Biesmeijer, 1997).

In honey bees, a bee reports the profitability of a food source by adjusting the strength of her dance. This adjustment could involve modulation of signal duration (number of waggle runs per dance) or signal intensity (sounds) or both.

A colony of honey bees achieves high foraging success by allocating foragers simply in proportion to the amount of dancing for each source (Seeley, 1986, 1995). Why do stingless bees, using just sound signals, not make use of a similar method? Stingless bees do not have dances comparable with those of honey bees, but they do communicate direction or distance mainly outside of the hive by laying pheromones, a scent beacon, using the food odor, or by direct piloting. Inside the hive, it could be more important how fast new bees can be motivated and recruited to the available food source.

Stingless bee foragers returning to the hive from flower patches bring home information about multiple food sources. Only bees returning from highly profitable sources (e.g. 1.0M–2.0M) perform sounds. If we assume sound is a recruitment signal, foragers will intensify the rate of recruitment as the probability of song production increases with the availability of rich food sources, and as more foragers discover the rich food source more sounds signals will be emitted. The singers will share their information to bees standing near the entrance. Acoustical signals allow the nestmates of the stingless bees to perceive and distinguish the richer and poorer nectar collectors through the darkness of the hive (Kirchner, 1993). Recruitment, to pollen sources probably uses other strategies because pollen collectors of *M. costaricensis* and *M. favosa* never produced pulsed sounds inside the hive during our observations, but instead went straight to the pollen pots.

The relationships between decreasing sound pulses with distance to the food source confirm the relationship between the sound signals with recruitment to rich food sources. We found that with a constant food source, the number of sound pulses decreased significantly, as the distance to the food source increased. Food quality with a constant sugar concentration (2.0M) at the artificial food source, decreased as the distance to the food source increased. Thus, decline of food quality and thus in the number of pulses, may explain the decreased number of new bees at the food source.

In conclusion, sound signals should have an effect on recruitment to food sources. More research is needed to know the detailed functions of these sounds. The sound signals of the stingless bees can be also designed as a request for help to discharge the food brought into the nest as in honey bees (Seeley, 1995). Nevertheless, if the sound produced is only to inform nestmates of the need to be unloaded, then it takes much lesser effort to just produce a simple sound rather than vary the sound parameters depending on the quality of the source being brought in.

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Résumé – Les sons chez *Melipona costaricensis* (Apidae : Meliponini) : effet de la concentration en sucres et de la distance à la source de nourriture. Les abeilles sans aiguillon (Meliponini) utilisent divers signaux pour localiser une source de nourriture, mais on dispose de peu d’informations sur le comportement des butineuses et des recrues à l’intérieur du nid et il n’est pas certain que la qualité de la source alimentaire (la concentration en sucres) soit communiquée par des signaux sonores. Différentes concentrations en sucres ont été utilisées pour déterminer l’effet de la qualité d’une source alimentaire sur les sons produits par l’abeille sans aiguillon *Melipona costaricensis* dans la ruche. De nombreuses composantes des sons étaient positivement corrélées avec la concentration en sucres : la durée du chant, la durée de toutes les vibrations, la durée des vibrations longues et la relation entre le son vibré long et le son vibré court. La durée des vibrations courtes et de leurs intervalles était significativement modifiée par la distance à la source alimentaire. Nous avons trouvé en outre une relation inverse entre le nombre de vibrations et la distance à la source alimentaire ($P < 0{,}00238$, $r = 0{,}18$).

Les signaux sonores peuvent contribuer à recruter durant la journée des membres de la colonie pour des ressources alimentaires dont la richesse augmente. Avec une source alimentaire constante, le nombre de vibrations sonores diminuait significativement quand la distance à la source alimentaire augmentait. La qualité de la nourriture, avec une concentration en sucres constante de 2,0M à la source alimentaire artificielle, diminuait quand la distance à la source alimentaire augmentait. Ainsi, le déclin de la qualité de la nourriture, et donc le nombre de vibrations, peut expliquer le nombre réduit d'abeilles nouvelles à la source alimentaire.

Nos résultats confirment que les ouvrières de *M. costaricensis* sont capables de distinguer des solutions sucrées de diverses concentrations. Diverses espèces du genre *Melipona* produisent des sons vibrés dont les durées sont positivement corrélées avec la distance à la source alimentaire (Esch et al., 1965 ; Nieh et Roubik, 1998 ; Nieh, 1999 ; Jarau et al., 2000). Par contre notre étude montre que la variation de la probabilité d'émettre un chant chez *M. costaricensis* s'explique par la concentration en sucres de la source alimentaire (97 %, $r^2 = 0{,}970$). Cette corrélation suggère l'existence d'une autre voie par laquelle sont signalées des sources alimentaires fructueuses.

abeille sans aiguillon / communication sonore / concentration en sucres / source alimentaire / distance / Meliponini

Zusammenfassung – Schallerzeugung bei *Melipona costaricensis* (Apidae: Meliponini): Wirkung von Konzentrationen des Zuckers und Entfernungen der Nektarquellen. Die Wirkung der Qualität einer Futterquelle auf die Schallerzeugung im Volk wurde bei der stachellosen Biene *Melipona costaricensis* anhand von unterschiedlichen Konzentrationen von Zucker untersucht. Verschiedene Eigenschaften der erzeugten Töne waren positiv mit der Zuckerkonzentration korreliert: die Dauer der Schallerzeugung, die Dauer aller Vibrationspulse, die Dauer von langen Vibrationspulsen und das Verhältnis von kurzen zu langen Vibrationspulsen. Die Zeit zwischen den Schallproduktionen war mit der Zuckerkonzentration negativ korreliert. Die Dauer der kurzen Vibrationen und ihren Unterbrechungen wurde signifikant durch die Entfernung beeinflusst. Außerdem fanden wir ein inverses Verhältnis zwischen Zahl an Vibrationspulsen und der Entfernung der Futterquelle ($P < 0{,}00238$, $r = -0{,}18$). Schallsignale könnten zur Rekrutierung von Stockgenossinnen zu immer reichhaltigeren Futterstellen während des Tages beitragen. Wir fanden, dass bei konstanter Futterquelle die Anzahl der Schallzeichen signifikant abnahm, wenn die Entfernung zum Futter größer wurde. Die Qualität der Futterquelle nahm bei konstanter Zuckerkonzentration (2,0M) an der künstlichen Futterstelle mit zunehmender Entfernung des Futters ab. Demnach könnte die Erreichbarkeit des Futters und die entsprechende Änderung in der Anzahl der Vibrationen die abnehmende Zahl von neuen Bienen am Futter erklären.

Unsere Ergebnisse bestätigen, dass Arbeiterinnen von *M. costaricensis* Zuckerlösungen verschiedener Konzentration unterscheiden können. Mehrere Arten der Meliponinen erzeugen rhytmische Töne, deren Dauer positiv mit der Entfernung der Futterquellen korreliert sind (Esch et al., 1965; Nieh und Roubik, 1998; Nieh, 1999; Jarau et al., 2000). Andererseits zeigt unsere Studie, dass die Variation in der Wahrscheinlichkeit einer Schallerzeugung bei *M. costaricensis* durch die Zuckerkonzentration der Futterquelle (97 %, $r^2 = 0{,}970$) erklärt werden kann. Diese Korrelation legt einen alternativen Weg zur Anzeige einer profitablen Futterstellen nahe.

Schallerzeugung / Zuckerkonzentration / Entfernung / stachellose Bienen

REFERENCES

Biesmeijer J.C. (1997) Colony foraging activity of stingless bees in Costa Rica, with special reference to pollen, in: The organization of foraging in stingless bees of the genus *Melipona*, Thesis, Utrecht University.

Biesmeijer J.C., Richter J., Smeets M., Sommeijer J.M. (1999) Niche differentiation in nectar-collecting stingless bees: the influence of morphology, floral choice and interference competition, Ecol. Entomol. 24, 380–388.

Esch H. (1964) Beiträge zum Problem der Entfernungsweisung in den Schwänzeltänzen der Honigbiene, Z. Vgl. Physiol. 48, 534–546.

Esch H. (1967) Die Bedeutung der Lauterzeugung für die Verständigung der stachellosen Bienen, Z. Vgl. Physiol. 56, 199–220.

Esch H., Esch I., Kerr W.E. (1965) Sound: an element common to communication of stingless bees and to dances of the honeybee, Science 149, 320–321.

Frisch K. von (1967) The dance language and orientation of bees, Harvard University Press, Cambridge, MA, USA.

Hrncir M., Jarau S., Zucchi R., Barth F.G. (2000) Recruitment behavior in stingless bees, *Melipona scutellaris* and *M. quadrifasciata*. II. Possible mechanisms of communication, Apidologie 31, 93–113.

Jarau S., Hrncir M., Zucchi R., Barth F.G. (2000) Recruitment behavior in stingless bees, *Melipona scutellaris* and *M. quadrifasciata*. I. Foraging at food sources differing in direction and distance, Apidologie 31, 81–91.

Johnson L.K. (1987) Communication of food source location by the Stingless bee *Trigona fulviventris*, in: Eder J., Rembold H. (Eds.), Chemistry and Biology of Social Insects, Verlag J. Peperny, München, pp. 698–699.

Kerr W.E. (1959) Bionomy of Meliponids. VI. Aspects of food gathering and processing in some stingless bees, in: Cornell University (Ed.), Symposium on food Gathering Behavior of Hymenoptera, Ithaca, N.Y., pp. 2–4.

Kirchner W.H. (1993) Acoustical communication in honeybees, Apidologie 24, 297–307.

Kirchner W.H., Dreller C. (1993) Acoustical signals in the dance language of the giant honeybee, *Apis dorsata*, Behav. Ecol. Sociobiol. 33, 67–72.

Kirchner W.H., Sommer K. (1992) The dance language of the honeybee mutant diminutive wings, Behav. Ecol. Sociobiol. 30, 181–184.

Kirchner W.H., Dreller C., Grasser A., Baidya D. (1996) The silent dances of the Himalayan honeybee, *Apis laboriosa*, Apidologie 27, 331–339.

Kirchner W.H., Lindauer M., Michelsen A. (1988) Honeybee Dance Communication. Acoustical indication of Direction in round Dances, Naturwissenschaften 75, 629–630.

Lindauer M., Kerr W.E. (1958) Die gegenseitige Verständigung bei den stachellosen Bienen, Z. Vgl. Physiol. 41, 405–434.

Lindauer M., Kerr W.E. (1960) Communication between the workers of stingless bees, Bee World 41, 29–71.

Michelsen A., Towne W.F., Kirchner W.H., Kryger P. (1987) The acoustic near field of a dancing honeybee, J. Comp. Physiol. A 161, 633–643.

Michelsen A., Andersen B.B., Kirchner W.H., Lindauer M. (1989) Honeybees can be recruited by means of a mechanical model of a dancing bee, Naturwissenschaften 76, 277–280.

Michelsen A., Andersen B.B., Storm J., Kirchner W.H., Lindauer M. (1992) How honeybees perceive communication dances, studied by means of a mechanical model, Behav. Ecol. Sociobiol. 30, 43–150.

Nieh J.C. (1998a) The role of a scent beacon in the communication of food location by the stingless bees, *Melipona panamica*, Behav. Ecol. Sociobiol. 43, 47–58.

Nieh J.C. (1998b) The food recruitment dance of the stingless bee, *Melipona panamica*, Behav. Ecol. Sociobiol. 43, 133–145.

Nieh J.C. (1999) Stingless-Bee Communication, Am. Sci. 87, 428–435.

Nieh J.C., Roubik D.W. (1995) A stingless bee (*Melipona panamica*) indicates food location without using a scent trail, Behav. Ecol. Sociobiol. 37, 63–70.

Nieh J.C., Roubik D.W. (1998) Potential mechanisms for the communication of height and distance by a stingless bee, *Melipona panamica*, Behav. Ecol. Sociobiol. 43, 387–399.

Núñez J.A. (1966) Quantitative Beziehungen zwischen den Eigenschaften von Futterquellen und dem Verhalten von Sammelbienen, Z. Vgl. Physiol. 53, 142–164.

Núñez J.A. (1970) The relationship between sugar flow and foraging and recruiting behaviour of honey bees (*Apis mellifera* L.), Anim. Behav. 18, 527–538.

Núñez J.A. (1982) Honeybee foraging strategies at a food source in relation to its distance from the hive and the rate of sugar flow, J. Apic. Res. 21, 139–150.

Roubik D.W. (1984) Nectar selection by *Melipona* and *Apis mellifera* (Hymenoptera: Apidae) and the ecology of nectar intake by bee colonies in a tropical forest, Oecologia 61, 1–10.

Roubik D.W., Yanega D., Aluja M., Buchmann S.L., Inouye D.W. (1995) On optimal nectar foraging by some tropical bees (Hymenoptera: Apidae), Apidologie 26, 197–211.

Seeley T.D. (1986) Social foraging by honeybees: how colonies allocate foragers among patches of flowers, Behav. Ecol. Sociol. 19, 343–354.

Seeley T.D. (1995) The wisdom of the hive, Harvard University Press, Cambridge, MA, USA.

Spangler H.G. (1991) Do honey bees encode distance information into the wing vibrations of the waggle dance?, J. Insect Behav. 4, 15–20.

Waddington K.D., Kirchner W.H. (1992) Acoustical and Behavioral correlates of profitability of food sources in honey bee round dances, Ethology 92, 1–6.

Wilson E.O. (1971) The insect societies, Harvard University Press, Cambridge, MA, USA.