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Vibrational signals of African stingless bees

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Abstract Many bee species produce thoracic vibrations in various contexts. Among the social stingless bees (Meliponini) pulsed thoracic vibrations are used to communicate with nestmates. To date all studies on stingless bee vibrational communication have been conducted in the Neotropics. We, therefore, focused on six African stingless bee species of five genera: *Meliponula, Hypotrigona, Liotrigona, Dactylurina, Plebeina*. We analysed the signals' temporal patterns. Vibrational signals appear to play a role in the recruitment of stingless bees. The degree of signal variation in the studied species was much lower than the variation in the signals of Neotropical stingless bees. Furthermore, the inter-signal variation of the temporal patterns exceeded intra-signal variation. This might reveal that the bees are able to modulate the temporal patterns and the signals potential communicative value. Furthermore, foraging activity correlates with pulse production in *H. gribodoi* and *M. bocandei*, supporting the hypothesis that the vibrational signals are used in the context of foraging and recruitment.

Keywords African stingless bees ·
Vibrational communication · Foraging ·
Thoracic vibrations · Temporal pattern

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Introduction

Vibrational communication is the most ancient form of non-chemical communication and widespread in arthropods and many vertebrates (for review see: Cocroft and Rodríguez 2005; Hill 2008). However, it is probably the least known and least understood of all the sensory modes (Endler 2014). Substrate vibrations are either used alone or in combination with other communication channels, such as chemical, tactile or visual (Hill 2009). Arthropods make use of vibrations in the context of mate location and identification, courtship and mating, maternal care, foraging, predation and predator avoidance (Hill 2009).

In social insects, the communication with nestmates is crucial for their success. Intra-colonial communication is primarily transmitted via chemical cues and signals (Richard and Hunt 2013). However, in some cases vibrational communication is used instead of chemical communication because it is more adequate and serves functions chemicals cannot (Hunt and Richard 2013). In drywood termites for example the resonance frequencies of a wood block are used to assess its size and attract nestmates (Evans et al. 2005, 2007). The fungus growing *Macrotermes* termites tend to drum with their heads against the substrate and create a pulsed vibration when attacked. Workers respond by a fast retreat into the nest while other soldiers start to drum and thereby amplify and propagate the signal (Hager and Kirchner 2013; Röhrig et al. 1999). In social wasps, vibrations, induced by antennal drumming guide caste development (Suryanarayanan et al. 2011). Within ants the presence and use of stridulatory organs to produce vibrational signals is highly variable and has probably evolved multiple times (Golden and Hill 2016). Ants stridulate to organise nest building (Pielström and Roces 2012), to appeal help when buried (Markl 1965) and to

recruit nestmates to food sources (Baroni-Urbani et al. 1988).

Among the eusocial bees of the Apidae family (Apini, Bombini and Meliponini), thoracic vibrations are employed to communicate with nestmates (for review see: Hrncir et al. 2006a). In honeybees (*Apis mellifera*), vibrational signals are very well studied. They are employed in the communication among young queens (Grooters 1987; Michelsen et al. 1986a; Simpson 1964), used as stop signal for foragers (Michelsen et al. 1986b; Nieh 1993, for review see: Michelsen 2014), might be employed in labour organization (Cao et al. 2007) and constitute an essential part of the famous waggle dance communication (Esch 1961; Hrncir et al. 2011). The honeybees waggle dance comprises more than one information component; the dances attract nestmates to the dancer, reactivate and provide information about the availability, location, profitability and olfactory characteristics of the food source (Grüter and Farina 2009). Acoustical signals of the waggle dance consist of several pulses with a duration of about 20 ms and a frequency of 250–300 Hz (Michelsen et al. 1987). It has been suggested that the acoustical components of the waggle dance encode the food source location. For example, the number of pulses increases with the distance of the food source (Wenner 1962). It was under discussion if the differences in the number of produced pulses are due to the increasing distance of the food source or due to its decreasing profitability that comes along with increasing distance. A more recent study focuses on the influence of food source profitability on the thoracic vibrations in honeybees. The authors do not find the number of pulses to vary with food profitability which indicates that pulse number could be a reliable indicator of the food source's location and thereby supports earlier studies (Hrncir et al. 2011).

The usage of vibrational signals is thought to be an early stage in the evolution of recruitment communication in Meliponini because solitarily foraging species, as well as species recruiting nestmates, make use of vibrational signals (Kerr 1969; Lindauer and Kerr 1958). Beside a simple alerting of nestmates, a precise communication of the food source location benefits efficient exploitation of food sources. For some stingless bee species, it is shown that they use visual odometry to measure height and distance of a food source (Eckles et al. 2012; Hrncir et al. 2003). Furthermore, some species can communicate three-dimensional location of a food source (Lindauer and Kerr 1958, 1960; Nieh and Roubik 1995, 1998; Nieh et al. 2003a; Nieh 2004). However, it has not yet been clarified in which way location information are shared with nestmates and to which extend vibrational signals are employed. In Meliponini, Lindauer and Kerr (1958, 1960) were the first to observe pulsed vibrational signals produced by foragers returning from a profitable food source. The signals have a pulsed structure

that has led to the idea that information about the food source might be encoded in the signals temporal patterns (Hrncir and Barth 2014). Early studies aimed to decode the message of the vibrational signals and suggested a relation of pulse duration and the distance to a food source (Esch et al. 1965; Esch 1967; Nieh and Roubik 1998; Nieh et al. 2003b) or its height above the ground (Nieh and Roubik 1998). However, more recent reinterpretations of the results suggest that the vibrations do not provide navigational information, but their occurrence and temporal patterns correlate with the net profitability during a foraging trip (Hrncir et al. 2004; Hrncir 2009), which is determined by sugar concentration, solution flow, handling time, and the presence of competitors (Hrncir and Barth 2014).

Barth et al. (2008) pointed out that the high variability found in vibrational signals produced by *Melipona* bees foraging at a certain food source raises doubts about their capacity to carry precise information and does, therefor, not support a hypothesised referential communication. The honeybees' referential communication system is very well studied (Schürch et al. 2015). Foragers encode food source information in the dances performed inside the hive (von Frisch 1965; Dyer 2002). Duration and angle of the dances are proportional to the distance and direction of the food source. In each dance, waggle runs and thereby location information are repeated. The waggle runs diverge in duration and angle from each other. To obtain accurate information, dance followers observe successive dances and take an average (Tanner and Visscher 2008; von Frisch and Jander 1957). Signal variability has been studied on different levels, ranging from variability between subspecies, the so-called dance dialects, to intra-individual and individual variability. It has also been discussed that some intra-dance variability in the indication of direction might be adaptive (for review see: Dyer 2002).

Stingless bees show a remarkable diversity of life style and ecology. The study of Meliponini is promising to give insights in the evolution of recruitment communication in Apidae. Particularities of the habitat, such as the spatial and temporal distribution of the food sources and competition among species, may have had widely differing effects on the evolution of communication systems in different species. Only a small fraction of the more than 500 stingless bee species has been studied in detail. Our knowledge on vibrational communication is so far limited to only 14 Neotropical stingless bee species (Hrncir and Barth 2014). We wanted to test whether old-world species of stingless bees produce pulsed vibrational signals in a foraging context, similar to Neotropical Meliponini, and whether their vibrational signals potentially provide information for nestmates. To include African stingless bee species into research efforts will contribute to a comprehensive understanding of stingless bees and the evolution of their

recruitment communication. Vibrational signals consist of repeated pulses with a specific pulse duration, pulse sequence duration and duty cycle. If these temporal patterns contain any reliable information, we would expect the intra-signal variation of the temporal pattern to be lower than variation between signals (inter-signal variation). A low intra-signal variation would suggest a high repetition rate and redundancy of a given information. At the same time a higher inter-signal variation indicates the bee's ability to modulate signals to communicate with nestmates.

Materials and methods

Study site and stingless bee species

This study was conducted from 2014 through 2016 in South Africa and Kenya and comprises six stingless bee species of five genera. *Hypotrigona gribodoi* and *Liotrigona bottegoi*, both nesting in rock crevices, were tested on-site in their natural nest cavities at the Goro Research Camp in South Africa (Soutpansberg Mountain Range, Limpopo Province). We studied *Plebeina hildebrandti, Dactylurina schmidti, H. gribodoi, Meliponula bocandei* and *Meliponula ferruginea* in Kenya (see Table 1 for details). In Voi, Kenya carpenter bees (*Xylocopa* spec.) drill nests in sisal stems used for roofing in the coastal region. These nests are subsequently occupied by *H. gribodoi* and have been used for study. *P. hildebrandti* builds underground nests situated in an average depth of 1.1 ± 0.4 m below the surface (Kiatoko 2012). Colonies of *P. hildebrandti* were excavated in a way that the bee nests remained surrounded by approximately 15 l of soil. These were brought from Taita Taveta to ICIPE

Duduville-Campus, Nairobi for experimentation. In Kenya's coastal rainforest Arabuke Sokoke, *Dactylurina schmidti* builds exposed nests on tree branches. Branches with nests of approx. 15–20 l volume were brought to ICIPE Duduville-Campus, Nairobi for study. In Kenya, both studied *Meliponula* species are commercially used in meliponiculture (Macharia et al. 2007, 2010). Beekeepers from Ivihiga and Isiekuti transferred *M. ferruginea* colonies from natural cavities into "UTOB-hives" (Utrecht University-Tobago, brood chamber: $12 \times 12 \times 25$ cm³, honey chamber: $42 \times 12 \times 7.5$ cm³, Sommeijer 1999; Kiatoko 2012). Two colonies of *M. bocandei* were transferred into compartmented "icipe 4M" hives (brood chamber: $12 \times 12 \times 14$ cm³ honey chamber: $12 \times 12 \times 25$ cm³) custom-designed by the International Centre for Insect Physiology and Ecology, Nairobi (Kiatoko 2012). The *Meliponula* spp. colonies were transferred into boxes at least 3 months before they were brought to Isecheno (Kakamega Forest Reserve) for experiments. Whenever the colonies were brought to another site, the bees quickly adapted to the new conditions and immediately started to forage.

Vibration recording

Vibrational signals produced by stingless bees and transmitted on the nest substrate were recorded using accelerometers mounted close to the nest entrance, charge amplifiers and a digital audio recorder (Tascam DR-40). Due to the small and fragile nest surface in *H. gribodoi*, *L. bottegoi* and *D. schmidti* we used light-weight IEPE accelerometers (Metra KS94B.100, preamplifier Metra M68D1). Recordings from *P. hildebrandti* were performed

Table 1 Study sites and stingless bee species

Species	Body length [mm][a]	Nesting habit/brood arrangement	Nests studied	Recordings on	Study days	Study site
M. ferruginea	5.1–5.9	Rocks, trees, walls, underground; hor. combs[b,c]	2	Wooden nest box	28 days in March–April 2014	I
M. bocandei	7.0	Trees; clustered[b,c]	2	Wooden nest box	28 days in March–April 2014	I
H. gribodoi	2.0–3.0	Rocks, trees, walls, sisal stems; clustered[b,c,d,e,f]	3	Natural nest surface, wax	3 days in June 2015	G
					10 days in October 2016	V
L. bottegoi	2.0–3.0	Rocks, trees, walls, clustered[f]	1	Natural nest surface, wax	3 days in June 2015	G
D. schmidti	5.0	External, vert. combs[a,b]	3	Natural nest surface, wax	7 days in March–April 2015–2016	N
P. hildebrandti	3.3–5.2	Termite mounds hor. combs[b,e]	2	Natural nest, clay	3 days in April 2016	N

G Goro Research Camp (South Africa), *I* Isecheno (Kenya), *N* Nairobi (Kenya), *V* Voi (Kenya)

[a] Eardley (2004), [b] Kiatoko (2012), [c] Kajobe (2007), [d] Darchen (1972), [e] Namu and Wittmann (2016), [f] Krausa (2012)

using Metra measuring equipment (KD37, M68D1). Wet clay was used to mount the accelerometers next to the nest entrance. The clay dried within minutes and ensured tight coupling to the soil surrounding the nest. In all other species wax was used to mount the accelerometers on the surfaces of the nests. Accelerometers were attached outside of the nest 5 cm from the nest entrance. This was done without destroying the outer nest structure. Whenever possible, we used two accelerometers to identify and localise the source of vibration and control the detection of all signals produced inside the hive. Bees' movements away from the accelerometer would lead to an amplitude decrease, rather than a complete stop of the recorded signal. However, this was not the case and, therefore, all analysed signals had a stable amplitude. The signal recordings were done during the dry season at constant weather conditions.

Signal analysis

Stingless bees produce vibrational signals by contracting their indirect flight muscles (Hrncir et al. 2008). The vibrations are transmitted through the substrate the bees stand on. Signal amplitudes are known to be attenuated strongly when transmitted through the substrate, whereas temporal patterns hardly change between the vibrating bee and the substrate (Hrncir et al. 2006b). Frequencies are filtered depending on the substrate the vibrational waves travel in (Michelsen et al. 1982). Therefore, amplitude and frequency features appear unlikely to contain any reliable information for nestmates. Hence, we focused the analysis on the temporal patterns of signals.

At least three consecutive pulses of the same amplitude produced by one individual are regarded as a signal. Measurements were performed continuously, which enabled us to record the complete duration of a signal. Solely vibrations clearly produced by a single bee were analysed. Signals were filtered using digital 10 Hz–10 kHz band-pass filter or 1 kHz low-pass filter when necessary. We analysed the temporal patterns of the vibrational signals using RavenPro 64.1.4. Pulse duration (PD), inter-pulse duration (IPD), pulse sequence duration (PSD) and duty cycle (DC = PD/PSD) were analysed following Hrncir et al. (2004). In addition, we measured the duration of the complete vibrational signal (SD) (Fig. 1), the number of pulses per signal (PN) and calculated its pulse repetition rate (PRR). For the pulse repetition rate we measured the duration from the first pulse to the start of the last pulse. The inverse of this duration divided by the respective number of pulses included equals pulse repetition rate [Hz].

The frequency content of vibrational signals was analysed using Hanning Fast Fourier Transformation (256 pts) in Raven Pro 64.1.4. The highest amount of energy in the FFT was used as a measure for the main frequency component. Sound ruler was used to visualise the signals.
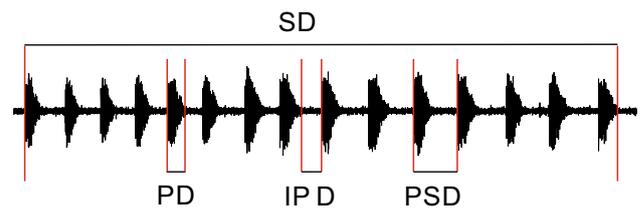
Fig. 1 Typical recording of a vibrational signal of *M. ferruginea*. Parameters examined: signal duration (SD), pulse duration (PD), inter-pulse duration (IPD), pulse sequence duration (PSD) and duty cycle (DC = PD/PSD)

To analyze the variability of PD, PSD, IPD and DC, we calculated the coefficient of variation. The coefficient measured the variation independent from mean value (CV = SD × 100/mean). Variation was calculated between signals (inter-signal) as well as for every signal (intra-signal). To compare inter-signal variation with intra-signal variation, a one-sample *t* test was performed for each temporal pattern in each species.

Foraging activity and production of vibrational signals in *H. gribodoi* and *M. bocandei*

We wanted to test whether the vibrational signals are produced in a foraging context. Two nests of *H. gribodoi* located in sisal stems used for roofing in Voi, Kenya, were used for experiments. We used wax to attach an accelerometer (Metra KS94B.100, IEPE adapter AVM MP48) alongside of the nest, 5 cm next to the nest entrance. A digital audio recorder (Tascam DR40) was used to record the vibrational signals produced inside the hive. Simultaneously to the recording we counted the number of foragers entering the hive. Afterwards the recordings were analysed and the number of the produced pulses were counted. The same procedure was carried out for *M. bocandei*. The accelerometer (B&K 4381, charge amplifier B&K 2635) was attached 5 cm next to the entrance tube of a colony situated in a compartmental "icipe 4M" hive. Pearson's *r* was used to correlate foraging activity and pulse production.

Results

Temporal structure of the vibrational signals

In this study, we included 13 stingless bee nests of six species belonging to five genera of stingless bees. In every nest that was wire-tapped using accelerometers, vibrational signals were recorded. All measured signals had a pulsed structure in common (Fig. 2). However, the PRR of the six stingless bee species differed considerably. The mean PRR

Fig. 2 a–f Temporal structure and sonagram of typical vibrational signals of African stingless bees. **a** *M. ferruginea*: the signal contains 15 pulses. Band-pass filter 10 Hz–10 kHz, FFT, 256. **b** *M. bocandei*: the signal contains 8 pulses. Band-pass filter 10 Hz–10 kHz, FFT, 256. **c** *H. gribodoi:* th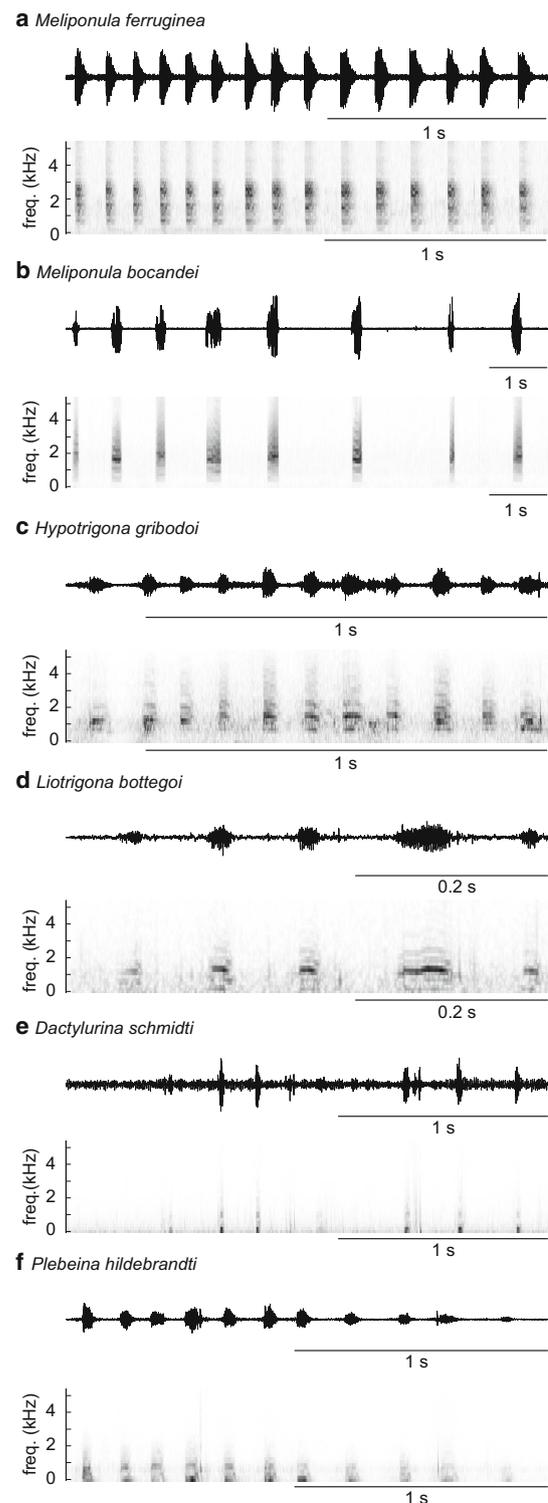e signal contains 11 pulses. Low-pass filter 1 kHz, FFT, 256. **d** *L. bottegoi*: the signal contains 5 pulses. Low-pass filter 1 kHz, FFT, 256. **e** *D. schmidti:* the signal contains 6 pulses. Band-pass filter 10 Hz–10 kHz, FFT, 256. **f** *P. hildebrandti*: the signal contains 11 pulses. Low-pass filter 1 kHz, FFT, 256

of *H. gribodoi* and *L. bottegoi* were 8.4 and 9.8 Hz, respectively. The lowest mean PRR was found in *M. bocandei* (1.2 Hz). Details on inter-pulse duration, pulse-sequence duration and duty cycle in all six species are given in Table 2. Vibrational signals of all species were broadband and rich in harmonics. Main frequency components ranged from 290 Hz in *P. hildebrandti* to 1100 Hz in *M. ferruginea*. Typical temporal structure and sonograms of vibrational signals are shown in Fig. 2.

Variation of the vibrational signals

We analysed the inter- and intra-signal variation of PD, IPD, PSD and DC by calculating the coefficient of variation (Fig. 3). In both *Meliponula* species and in *H. gribodoi*, the inter-signal PD variation was low, with values of less than 30% (Table 3). Inter-signal PD variation in *D. schmidti*, by contrast, was high, showing a value of 64.5%. In all species, intra-signal PD variation was significantly lower compared to inter-signal PD variation (Fig. 3a, one-sample *t* tests: $P < 0.05$). This shows that the PD variation occurred between signals rather than within signals. Inter-signal variation in PSD was between 26% in *M. ferruginea* and 76% in *H. gribodoi*. Intra-signal PSD variation was considerably smaller than inter-signal variation (Fig. 3b, one-sample *t* test: $P < 0.05$). Also, inter-signal DC variation exceeded intra-signals variation in all species (Fig. 3d, one-sample *t* test: $P < 0.05$). The highest inter- and intra-signal variation could be observed in IPD. In *H. gribodoi* inter-signal IPD varied up to 103% and in all species, except for *L. bottegoi* (one-sample *t* test: $P = 0.249$), intra-signal duration was significantly lower compared to the variation between signals (Fig. 3c, one-sample *t* test: $P < 0.001$).

Foraging activity and production of vibrational signals in *H. gribodoi* and *M. bocandei*

Foraging activity and vibrational signals were recorded on 4 days in *H. gribodoi* and 2 days in *M. bocandei*. Observations were made between 10 a.m. and 14 a.m. One continuous recording of around 30 min/day was partitioned in time intervals of 1 min length. For *H. gribodoi* a total of 111 time intervals and for *M. bocandei* 68 time intervals have been analysed. Flight activity was measured by counting the number of foragers entering the hive. We found a strong positive correlation between the number of pulses produced inside the nest and flight activity in both species (Fig. 4: a Pearson's $r = 0.663$, $P < 0.001$, $n = 111$; b Pearson's $r = 0.809$, $P < 0.001$, $n = 68$).

Table 2 Temporal patterns of the vibrational signals of African stingless bees

Species	SD [s]		PN		PD [ms]		IPD [ms]		PSD [ms]		DC		PRR [Hz]	
	Mean ± sd	n	Mean ± sd	n	Mean ± sd	n	Mean ± sd	n	Mean ± sd	n	Mean ± sd	n	Mean ± sd	n
M. ferruginea	2.68 ± 1.0	91	15 ± 5	91	51 ± 13	1018	114 ± 41	1018	165 ± 43	1018	0.32 ± 0.09	1018	6.3 ± 1.6	91
M. bocandei	8.78 ± 4.8	22	8 ± 4	22	168 ± 42	169	833 ± 623	169	1003 ± 630	169	0.22 ± 0.11	169	1.2 ± 0.5	22
H. gribodoi	1.15 ± 0.6	20	7 ± 6	20	35 ± 9	143	99 ± 102	143	134 ± 102	143	0.31 ± 0.13	143	8.4 ± 1.7	20
L. bottegoi	1.22 ± 0.9	16	7 ± 5	16	28 ± 20	109	74 ± 29	109	104 ± 35	116	0.3 ± 0.23	109	9.8 ± 2.3	16
D. schmidti	1.05 ± 0.5	11	4 ± 1	11	56 ± 36	45	234 ± 142	45	292 ± 137	45	0.23 ± 0.17	45	3.9 ± 1.8	11
P. hildebrandti	2.60 ± 1.4	16	8 ± 5	16	70 ± 24	130	204 ± 156	130	275 ± 165	130	0.32 ± 0.26	130	4.4 ± 2.2	16

SD signal duration, *PN* pulse number, *PD* pulse duration, *IPD* inter-pulse duration, *PSD* pulse sequence duration, *DC* duty cycle, *PRR* pulse repetition rate, *sd* standard deviation
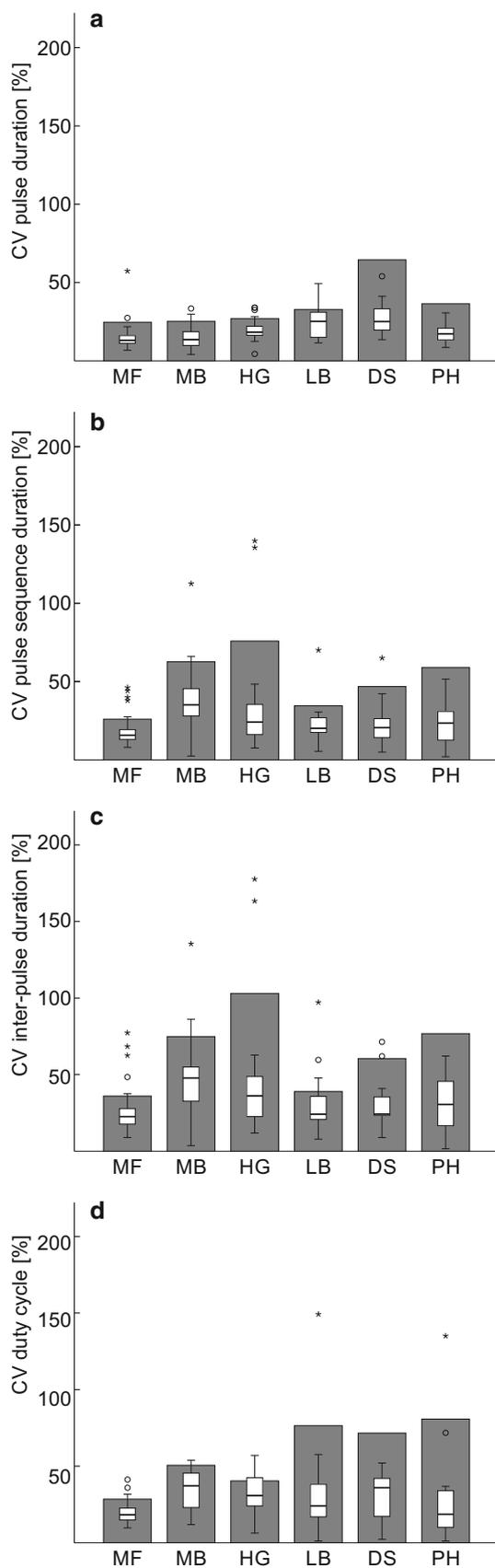
Discussion

The study of vibrational communication is a rapidly growing field. More and more studies show that vibrations are used to communicate in many insect taxa and various behavioural contexts (Cocroft et al. 2014). So far, the usage of vibrational signals in African Meliponini finds only one record in literature (Esch et al. 1965). Here we examine for the first time six different species belonging to five African stingless bee genera. All species investigated here produce vibrational signals consisting of a sequence of pulses. Mean PD ranged from 28 ms in *L. bottegoi* to 168 ms in *M. bocandei*. This is much shorter compared to PD in Neotropical species ranging from 0.1 s to more than 1 s (Hrncir et al. 2000) The pulse repetition rates of the 6 stingless bee species differed considerably, ranging from 1.2 Hz in *M. bocandei* to 9.8 Hz in *L. bottegoi*. The fact that all investigated species produce vibrational signals highlights once again the broad usage of vibrational signals in Meliponini.

The pulse duration of stingless bees' vibrations is the most obvious feature of the signals and has been studied regarding its possible information content. The fact that some studies found the pulse duration to correlate with the distance and height to a food source (Esch et al. 1965; Esch 1967; Nieh and Roubik 1998; Nieh et al. 2003b) led to the conclusion that bees modulate pulse duration to communicate distance and height. Assuming the vibrational signals deliver redundant information by a repetition of pulses, a low intra-signal variability of this temporal pattern is a prerequisite for the extraction of reliable information (Hrncir and Barth 2014). However, variation of temporal patterns in *Melipona* species foraging at a certain distance has been found to be quite high (Nieh and Roubik 1998; Hrncir et al. 2004). Therefore, in Neotropical *Melipona*, it appears to be unlikely that bees can extract any reliable information from the examined temporal patterns (Hrncir and Barth 2014). As stated by Barth et al. (2008) the diversity of lifestyle found among the many species makes generalisations difficult and risky.

In our experiments, we tested the intra- and inter-signal variability of the temporal patterns in six African stingless bee species. Since we did not control which food sources the stingless bees used we assumed foragers to use various resources with different qualities and at different locations. In case the bees communicate the food source location or quality by modulating temporal patterns of the vibrations, we would expect the intra-signal variation to be lower than the inter-signal variation. This is exactly what we found. Temporal patterns (PD, PSD, IPD, DC) in all six species have been found to have a smaller intra-signal variation than inter-signal variation. Intra-signal pulse duration varied from 14% in *M. ferruginea* to 28% in *D. schmidti* whereas inter-signal variation was 24.7 and 64.5% in the same species. Since the intra-signal variation of temporal patterns is low, the pulsed signals may provide repeated information on food source characteristics to nestmates. Thus, information would be provided redundantly so that nestmates would receive the same information no matter when they contact the forager, i.e., perceive the vibrations through the substrate.

In honeybees (*A. mellifera*), foragers perform dances that consist of waggle runs. The number of waggle runs depends on food profitability (Seeley et al. 2000) and their angle and duration gives information about the food source's distance and direction (von Frisch 1965). Each waggle run is the repetition of the same information. However, angle and duration vary in between one dance. To obtain reliable information about the distance and direction of the advertised food source, dance followers level variations in angle and duration of successive waggle runs by taking an average (Tanner and Visscher 2008; von Frisch and Jander 1957). The same could be true for stingless bees that perceive several successive repetitions of the same temporal pattern. The differences between intra- and inter-signal variations could, therefore, be due to a modulation of signals to transmit specific information to nestmates. Vibrational signals in Neotropical stingless bees are found most likely to depend on food source profitability rather than its location (Hrncir 2009). There is much evidence that stingless bees

use a multimodal communication system employing numerous chemical and mechanical signals and cues when communicating about food sources (Barth et al. 2008). Further studies should be conducted to further reveal the communication value of the temporal patterns and examine individual variability of signal production.

Signal transmission in stingless bee nests

Stingless bee vibrational signals might be transmitted in three ways, via substrate vibrations, air particle movement, or direct physical contact between sender and receiver. The range of signal transmission appears to differ considerably between these three pathways (Hrncir et al. 2006b, 2008). Air particle oscillations and direct vibrations can only be detected by bees very close to the vibrating forager, whereas, substrate-borne vibrations have medium-range transmission (Hrncir and Barth 2014). In the 14 Neotropical stingless bee species surveyed so far, the main frequency components of the vibrational signals lie between 200 and 600 Hz (Hrncir and Barth 2014). Vibrational signals of all studied African stingless bee species were broadband and rich in harmonics. Spectra of the substrate vibrations are highly influenced by frequency dependent attenuation on different substrates (White 1965). The physical properties of *A. mellifera* combs have been studied to some extent, revealing that honeybee combs are very complicated structures. The attenuation of lower frequencies, for example, is relatively low and depending on the size of the comb, as well as whether they are empty or filled with brood or honey (Michelsen et al. 1986b; Sandmann et al. 1996). Stingless bees use a variety of different types of cavities and substrates, and different materials to build their nests (Table 1), which, owing to different physical properties, affect signal transmission. Some species seem to be opportunistic, while others are more specialised. For example, *H. gribodoi* nests in various cavities like trees, rocks, houses/walls, poles and even free (Darchen 1972; Eardley 2004; Kajobe 2007; Kiatoko 2012; Krausa 2012; Namu and Wittmann 2016; pers. observation). *M. ferruginea* naturally occupies cavities in trees, houses/walls, rocks or underground (Kajobe 2007; Kiatoko 2012).

Table 3 Coefficient of variation

Species	CV pulse duration			CV pulse sequence duration			CV inter-pulse duration			CV duty cycle			n
	Inter-signal	Intra-signal	P	Inter-signal	Intra-signal	P	Inter-signal	Intra-signal	P	Inter-signal	Intra-signal	P	
M. ferruginea	24.7	14.4	**	26.1	17.5	**	36.0	24.7	***	28.5	19.4	***	67
M. bocandei	25.3	15.7	***	62.8	38.5	***	74.9	47.2	***	50.6	34.4	***	22
H. gribodoi	27.0	19.9	**	75.9	36.5	***	103.0	48.6	***	40.4	32.1	*	19
L. bottegoi	32.8	25.1	*	34.6	23.9	*	39.0	32.0	ns	76.4	34.0	***	15
D. schmidti	64.5	28.0	***	46.9	24.2	**	60.5	32.0	**	71.6	30.3	***	11
P. hildebrandti	36.5	17.6	***	59.0	23.5	***	76.8	31.1	***	80.8	29.4	***	16

CV coefficient of variation

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, one-sample t test
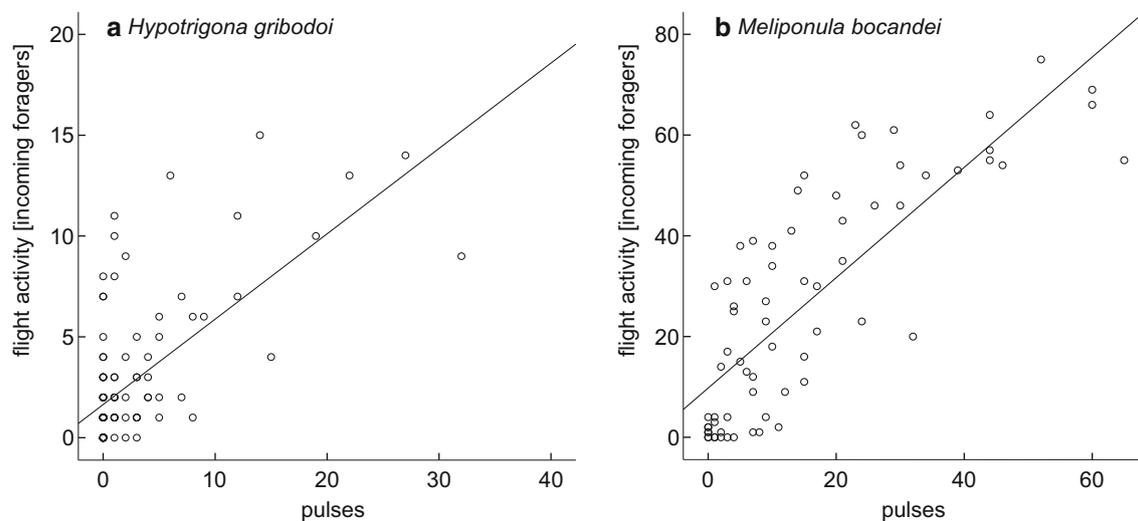
Fig. 4 Flight activity (incoming foragers) correlates positively with the with the number of pulses produced inside the hive per minute (**a** *H. gribodoi*, Pearson's $r = 0.663$, $P < 0.001$, $n = 111$; **b** *M. bocandei*, Pearson's $r = 0.809$, $P < 0.001$, $n = 68$)

Nests of *M. bocandei* are reported to be in trees and underground cavities (Kajobe 2007; Kiatoko 2012). *P. hildebrandti* has a rather special nesting habit, using termite mounds as nesting substrate. Their nest entrance passes up to 1.2 m inside the mound in cavities formed by the termites (Namu and Wittmann 2016). *Dactylurina* is the only African stingless bee genus that builds exposed nests. While vibrational communication in the other species may also take place on soil or wood, signals of *Dactylurina* are mainly produced on nest material made from wax and resin. The physical properties of the different nest materials should be studied in respect to frequency filtering and attenuation to examine whether signals are tuned in this respect.

Context and potential meaning of the vibrational signals

As we know from Neotropical stingless bees, the vibrational signals of foragers are mainly produced during trophallaxis

with their nestmates (Esch 1967; Hrncir et al. 2004; Lindauer and Kerr 1958). During trophallaxis, receivers obtain multimodal information about the food source, including sugar content and scent. McCabe et al. (2015) studied thoracic vibrations in the context of odour learning in *Melipona quadrifasciata*. Foragers modulate the thoracic vibrations during trophallaxis depending on whether the experienced food source is scented or not, which suggests, that indirect odour learning via trophallaxis might influence the receiver's ability to learn food odours. The same might be true for *M. ferruginea* recruits, which are able to learn odours (Henske et al. 2015) and experience trophallaxis before reaching the advertised food source (Krausa et al. in prep.).

In several Neotropical species, it has been shown that the vibrational signals activate nestmates to collect food (Aguilar and Briceño 2002; Esch et al. 1965; Esch 1967; Hrncir et al. 2000; Nieh and Roubik 1998; Nieh et al. 2003a; Schmidt et al. 2006, 2008). In *H. gribodoi* and *M. bocandei*, we found flight activity to correlate positively with the

number of pulses produced inside the nest. Which suggests that foragers produce vibrations to activate the foraging force and exploit food sources. This corresponds with a brief report by Esch et al. (1965), mentioning that African *M. ferruginea* (syn. *Trigona tescorum*) foragers activate their nestmates acoustically.

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