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COMPARATIVE BIOACOUSTICAL STUDIES ON FLIGHT AND BUZZING OF NEOTROPICAL BEES

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Abstract—The presence of bees is typically accompanied by the humming sound of their flight. Bees of several tribes are also capable of pollen collecting by vibration, known as buzzing behaviour, which produces a buzzing sound, different from the flight sound. An open question is whether bee species have species-specific buzzing patterns or frequencies dependent of the bees' morphology or are capable to adjust their individual buzzing sound to optimize pollen return. The investigations to approach this issue were performed in northeastern Brazil near Recife in the state of Pernambuco. We present a new field method using a commercially available portable system able to record the sound of bees during flight and buzzing at flowers. Further, we describe computer linguistical algorithms to analyse the frequency of the recorded sound sequences. With this method, we recorded the flight and buzzing sequences of 59 individual bees out of 12 species visiting the flowers of *Solanum stramoniifolium* and *S. paniculatum*. Our findings demonstrate a typical frequency range for the sounds produced by the bees of a species. Our statistical analysis shows a strong correlation of bee size and flight frequency and demonstrates that bee species use different frequency patterns.

Keywords: *pollen,* Solanum, Xylocopa, *buzz pollination, poricidal anthers, bioacoustic*

INTRODUCTION

Flowers of numerous species in 72 plant families hide pollen in poricidal anthers, like, for example, those of Melastomataceae, Leguminosae-Cassiinae and Solanaceae including the huge genus *Solanum* (Buchmann & Hurley 1978; Buchmann 1983). This pollen is easily accessible only to bees that are capable of shaking the pollen grains out of the apical pores of the anthers by vibrations (King *et al.* 1996). This phenomenon, described as buzz pollination, is widespread among bees, but restricted to certain clades. Females of carpenter bees (*Xylocopa* – Xylocopini), bumble bees (Bombini), and neotropical orchid bees (Euglossini), Centridini and Augochlorini, among others, are able to vibrate flowers to collect pollen, but not the majority of the common tropical stingless honeybees (Meliponini) or the honeybees (Apini) (Hurd & Linsley 1976; Buchmann 1983; Houston & Thorp 1984; Neff & Simpson 1988; Thorp 2000; Harter et al. 2002; Teppner 2005). Among the fraction of the bee fauna that is capable of buzzing, flowers with poricidal anthers are an abundant pollen source (Harter et al. 2002). Vibrating the flowers, the females produce an audible buzzing sound using the flight musculatur with decoupled wings (Michener 1962; Wille 1963; King et al. 1996). Because of the changing resonance properties of the thorax with decoupled wings, the sound of buzzing usually has an about two times higher frequency than the sound of flight (King & Buchmann 2003). In other insect taxa, body size and wingbeat frequency is correlated in a manner that smaller insects beat their wings faster than larger ones, when flying (Byrne et al. 1988). It is not known, if this is also true for flower vibrating bees, whose flight musculature is decoupled from the wings when collecting pollen. According to the results of King & Buchmann (1996) on flowers of *Solanum laciniatum* the optimal frequency of pollen dispensing is not in the range bees are able to achieve by buzzing. Despite this fact, pollen collecting bee females might be able to adjust buzzing frequency in the given range to the kind of flower or to change their buzzing according to pollen release during buzzing behaviour. Earlier studies by Harter et al. (2002), performed with several plant species including *Solanum,* showed no significant relationship in bee size related to flower diameter, raising the question whether buzz pollination is independent of the bee size.

For our buzzing study we chose two shrubby species of *Solanum* Subgenus *Leptostemonum,* common weeds in northeastern Brazil: *S. stramoniifolium* Jacq. and *S. paniculatum* L. (Levin et al. 2006). The pollination of both species had been already investigated earlier (Forni-Martins et al. 1998; Bezerra & Machado 2003; Silva et al. 2004). These studies have shown that their flowers are mainly pollinated by several buzz pollinating medium to large sized bees of the genera *Xylocopa, Centris, Bombus* and *Melipona*.

Using a sensitive microphone to record the sound of buzzing or flying of flower vibrating bees in the field and software for computer linguistic analysis, we asked: What are the characteristics of the buzzing sounds of bees collecting pollen in flowers of the two species of *Solanum*? Do females

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adjust buzzing patterns at the flowers of these species? Is there a specific frequency for individual bee species during flight or buzzing and are these buzzing frequencies correlated to the body size of the bee females?

METHODS

Study site and plant species

The observations and recordings were performed in the municipality of Camaragibe, near Recife, Pernambuco, northeastern Brazil (S 07°58.230' W 035°00.179'). The temperature during the observation period from November 2010 to January 2011 was almost constant with an average maximum temperature of 29.6 ± 0.7 °C and an average minimum night temperature of 25.2 ± 1.1 °C. The relative humidity was on average 69 ± 5 % but increased to 85 % due to heavy rainfalls during the last weeks in January. The study sites are characterized by the presence of houses and small farms with numerous ornamental plants and tropical fruit crops, surrounded by diverse secondary Atlantic Rainforest.

Solanum paniculatum and *S. stramoniifolium* are ruderal plants or weeds and grew in open areas in the vicinity of tropical rainforest and within an orchard of soursop (*Annona muricata* L., Annonaceae). *Solanum paniculatum* is an up to 2 m tall shrub with spiny stems (Knapp & Jarvis 1990). The main stem is usually unbranched and carries an apical inflorescence with light purple to whitish pentamerous flowers. The plants were very common and grew as dominant weeds in large groups with high density in several open areas. *Solanum stramoniifolium* is an overall spiny shrub with a circumference of up to 2 m and up to 2 m height (Silva et al. 2004). Different to *S. paniculatum*, the inflorescences were axillary over the whole plant and usually carried only one or two white flowers at the same time. The plants of *S. stramoniifolium* were also common but occurred less aggregated than the other species.

Flower visitors and sound recordings

At the beginning of the study we collected the flower visitors and determined the pollinator spectrum of both plant species. Bees were caught at the flowers with entomological nets and killed by ethyl acetate. All bees were pinned, dried, labelled and then identified in the laboratory. The specimens were included in the Entomological Collection of the Universidade Federal de Minas Gerais, Belo Horizonte, Brazil.

Sounds of the flower visiting bees were recorded in the field during the flower visits. The microphone was carefully placed as near as possible to the buzzing bees at the flowers. While buzzing, most of the bees did not react to disturbances in the surroundings. This allowed us to place the microphone as close as 1 cm to the bees. Generally, the microphone recordings were done in a distance of 1 to 5 cm. When recording small and silent bees, we tried to move the microphone as close as possible. When departing from the flower we recorded the flight sound of the bee during takeoff. Every bee was followed as long as possible to ensure the recording of at least one evaluable sequence of flight and buzzing. As microphone and recording device an Android smartphone (Legend, HTC, Taoyuan, Taiwan) was used running the application Hertz 1.1.1 producing *.wav data at a sample rate of 16 000 Hz or 22 050 Hz. By Soundforkes and computer generated tones of a given frequency the range of the microphone was tested from 50 Hz up to 1 kHz with positive results and therefore stated as sensitive in the range of bee sounds. After recording the bees were collected for identification. From the bee individuals the intertegular distance as a standard measure for bee size was determined (Cane 1987).

Sound analyses

For analysis the soundfiles were divided in flight samples and single buzzings at flowers, which contained solely the sound of a single buzzing. All soundfiles were processed using Audacity 1.2.6 (Audacity, GNU General Public License). Every file was then labeled to assign it to the specific bee which produced the sound to build up a database of bee sounds. This database was analysed using the toolset of the computer phonetics programm Praat 5.2.15 (Boersma 2002). The pitch (ac) function searched in every sound sample for the basic frequency (Boersma 1993). The parameters of the function were adapted using the earlier results of other authors (King & Buchmann 2003; Nunes-Silva et al. 2010) to output the basic frequency of the bees wingbeat and buzzings. For further analysis the toolset of Praat was used to output average, maximum, minimum and standard deviation of the basic frequency and the length of each sound sample. Samples which contained too much disturbing noise were filtered out by a threshold for unregular high standard deviation of the basic frequency. (The script used with Praat is provided in Appendix 1)

All data processing and statistical tests were performed using Microsoft Excel 2002 (Microsoft Corp., Redmond, USA) and Graphpad Prism 4.0 (GraphPad Software Inc., La Jolla, USA). Statistical analysis was done with the Students t-test. Differences between data sets were regarded as significant with $P < 0.05$.

RESULTS

During the study period we observed bees of 11 species buzzing the flowers of *S. stramoniifolium* and of 12 species those of *S. paniculatum*. Only the large carpenter bees *Xylocopa (Neoxylocopa) frontalis* and *X. (N.) suspecta* visited the flowers of both *Solanum* species (Tab. 1).

During the field work several hundred sound recordings were performed. Here, we evaluated 59 recordings for which the associated bee was caught. The pitch analysis performed in Praat and further processed (Tab. 2), shows buzzing and flight frequencies and buzzing durations for several observed species. Within tribes similarity can be found, as seen in *Centris* and *Euglossa* which have high buzzing frequencies, while *Xylocopa, Eulaema* and *Augochloropsis* buzz with lower frequencies (Tab. 2).

The frequency of wingbeat is negatively correlated (Slope = -17.72 ± 1.73, r^2 = 0.66) with the intertegular distance of the bees (Fig. 1), whereas the buzzing frequency has also a

TAB. 1. Bee species found buzzing on both *Solanum* species. *Solanum stramoniifolium* (*S. s.*), *S. paniculatum* (*S. p.*). Nomenclature of bees after Moure et al. (2007).

bee species	family, tribe	visited species S. s.	S. p.
Xylocopa frontalis	Apidae, Xylocopini	X	X
Xylocopa suspecta	Apidae, Xylocopini	X	X
Xylocopa muscaria	Apidae, Xylocopini		X
Bombus brevivillus	Apidae, Bombini	X	
Centris aenea	Apidae, Centridini		X
Centris flavifrons	Apidae, Centridini		X
Centris tarsata	Apidae, Centridini		X
Centris sponsa	Apidae, Centridini		X
Centris spilopoda	Apidae, Centridini		X
Euglossa cordata	Apidae, Euglossini	X	
Eulaema cingulata	Apidae, Euglossini	X	
Eufriesea surinamensis	Apidae, Euglossini	X	
Eulaema nigrita	Apidae, Euglossini	X	
Melipona scutellaris	Apidae, Meliponini	X	
Pseudaugochlora graminea	Halictidae, Augochlorini	X	
Augochloropsis sp. 1	Halictidae, Augochlorini		X
Augochloropsis sp. 2	Halictidae, Augochlorini	X	
Exomalopsis sp. 1	Apidae, Exomalopsini		X
Exomalopsis sp. 2	Apidae, Exomalopsini		X
Thygater sp.	Apidae, Eucerini	X	
Centris sp.	Apidae, Centridini		X

negative trend (Slope = -5.66 ± 1.86, r^2 = 0.14). Large bees were found to fly and buzz with a lower frequency than smaller bees. This correlation was not observed in individuals of *Augochloropsis* which buzz at about the same frequency as their flight frequency (Fig. 2).

In a further analysis, the buzzing frequency of females of *X. frontalis* and *X. suspecta* on the flowers of the *Solanum* species were compared (Fig. 3). A significant difference was found for those of *X. frontalis*, buzzing flowers of *S. stramoniifolium* with a slightly higher frequency (224.2 ± 3.9 Hz) than those of *S. paniculatum* (211.0 ± 2.9 Hz). The buzzing frequencies of individuals of *X. suspecta* were not significantly different between the two *Solanum* species. Measurements of the size of the flowers of *S. paniculatum* and *S. stramoniifolium* showed similar average size in diameter (S.s. 23.7 mm; S.p. 25.5 mm) and stamen length (*S.s.* 7.0 mm; *S.p.* 6.7 mm).

The frequency pattern of buzzings of different species revealed that the buzzing frequency is reducing during each buzzing of the investigated bee species, with exception of those of *Pseudaugochlora graminea* that showed no clear pattern (Fig 4).

DISCUSSION

In this study, a method of sound recording and analysing was tested with two *Solanum* species and several occuring bee species to answer different questions about the buzzing frequency. The pollen removal from poricidal anthers by buzzing is a mechanical phenomenon which consists of several parameters on the bee side including force, acceleration or frequency and other parameters on the plant side such as the mass of the flower or the size of the pores (Buchmann & Hurley 1978; King & Lengoc 1993). In this work, the parameter of the frequency of female bee´s vibration was chosen as it is probably the only parameter that is modifiable by the bee itself and differs from species to species (King & Buchmann 2003; Nunes-Silva et al. 2010).

TAB. 2. Mean frequency of buzzing, duration of single buzzings, flight frequency, and intertegular span of recorded bee species sorted by the latter parameter. In total, 59 samples of individuals from different species on flowers of *S. stramoniifolium* and *S. paniculatum* are tabulated. All data shown in mean ± SD, n is given in brackets.

bee species	buzzing frequency [Hz]	buzzing duration [s]	flight frequency [Hz]	intertegular span [mm]
Xylocopa frontalis (18)	218.3 ± 12.4 (103)	0.59 ± 0.23	106.5 ± 3.5 (69)	8.81 ± 0.41
Xylocopa suspecta (21)	251.0 ± 10.7 (141)	0.51 ± 0.22	116.0 ± 5.4 (55)	6.67 ± 0.46
Centris flavifrons (2)	294.5 ± 18.6 (4)	0.53 ± 0.13	151.2 ± 12.3 (3)	6.12 ± 0.28
Eulaema nigrita (2)	220.9 ± 5.6 (11)	0.97 ± 0.29	126.9 ± 2.5 (7)	5.68 ± 0.11
Eulaema cingulata (1)	206.9 ± 13.8 (4)	1.04 ± 0.32	124.3 ± 3.6 (1)	5.68
Eufriesea surinamensis (1)	239.0 ± 10.1 (3)	0.44 ± 0.26	no data	5.20
Centris aenea (2)	324.1 ± 12.1 (5)	0.68 ± 0.19	221.4 ± 10.0 (4)	5.08 ± 0.17
Bombus brevivillus (1)	267.7 ± 8.9 (3)	0.55 ± 0.22	125.1 ± 2.3 (1)	4.00
Euglossa cordata (2)	294.2 ± 10.3 (7)	0.65 ± 0.08	251.8 ± 3.8 (2)	3.64 ± 0.06
Centris tarsata (2)	311.4 ± 7.0 (4)	0.76 ± 0.16	249.6 ± 3.3 (5)	3.24 ± 0.06
Melipona scutellaris (2)	282.2 ± 27.4 (2)	1.05 ± 0.63	229.0 ± 11.5 (4)	3.00 ± 0.06
Pseudaugochlora graminea (3)	221.9 ± 22.8 (20)	0.84 ± 0.55	190.2 ± 6.8 (3)	2.19 ± 0.37
Augochloropsis sp.2 (1)	172.7 ± 6.8 (10)	0.50 ± 0.26	170.2 ± 4.9 (1)	2.08
Augochloropsis sp.1 (1)	210.0 ± 6.0 (8)	0.83 ± 0.61	191.3 ± 13.4 (1)	1.76

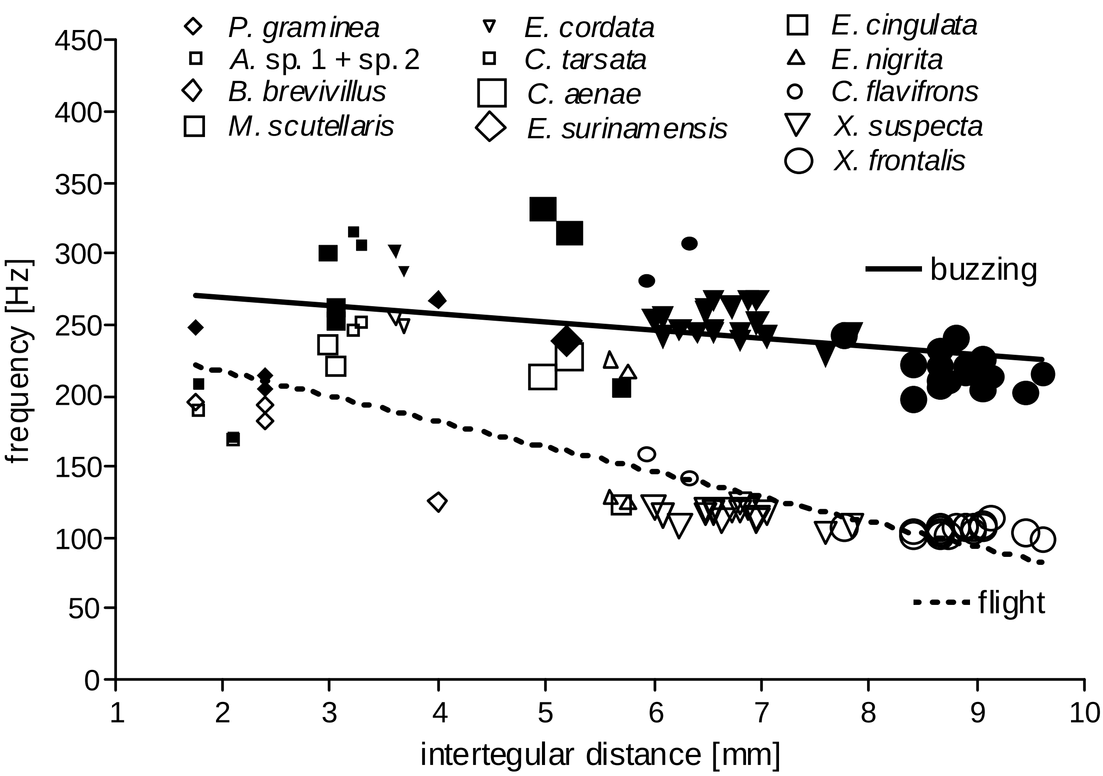

FIG. 1. Correlation of intertegular distance as a standard for bee size and the frequency of buzzing (solid symbols) and the frequency of flight (open symbols). Each symbol stands for a collected individual. All individuals of a species were assigned the same symbol. Linear regression is indicated by the lines, solid for buzzing frequency and dotted for flight frequency.

Earlier measurements of vibratory effects in buzzing and flight were often done using an accelerometer or a contact free laser accelerometer (King & Ferguson 1994; King & Buchmann 2003; Hrncir et al. 2004). Both systems face problems due to their limited in-field capability. A sensitive microphone is able to record the sound field, produced by a flying or buzzing bee (Hrncir et al. 2004), which can be used to analyse the length of a flower visit (Ehrlich & Lunau 2009). In addition, data about the frequency of the flight musculature movement can be made accessible by the sound of the bee. The buzzing sound is of complex structure and composed of harmonics and other noises, generated by different oscillations of parts of the bee body (King & Buchmann 2003). To overcome this, we used computer linguistical analysis after the recording to determine the basic frequency of the sound (Boersma 1993; 2002).

The described system delivered good results as an in field setup. This is an advantage over other methods which need to fix the bee to a laser accelerometer or measure the frequency with stroboscobic methods inside a laboratory. Supporting the observations by King & Buchmann (2003) and Hrncir et al. (2004) we found different frequency ranges in different bee species. The flight frequency seems to be in a range which is anatomically fixed and correlated to the intertegular distance and thus to the size of the bee. These findings follow the measurements of Byrne et al. (1988) who showed that smaller insects have higher wingbeat frequencies. However, the buzzing frequency seems to be linked to the wingbeat frequency (Fig. 1) and is – mainly for large bees – about two times higher, as stated earlier by King & Buchmann (2003). A possible explanation was seen in the second harmonics, which allow a system like the flight apparatus to oscillate at twice the natural frequency, using little energy. In this view, the two-times higher buzzing frequency is an adaptation to save energy costs for collecting pollen at high vibration frequency.

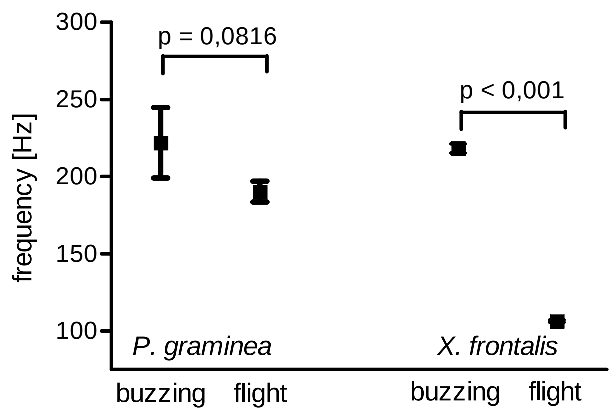

FIG. 2. Comparison of the buzzing and flight frequencies of the small *Pseudaugochlora graminea* (Halictidae) (n = 3) and the big *Xylocopa frontalis* (Apidae) (n = 18) (mean ± SD).

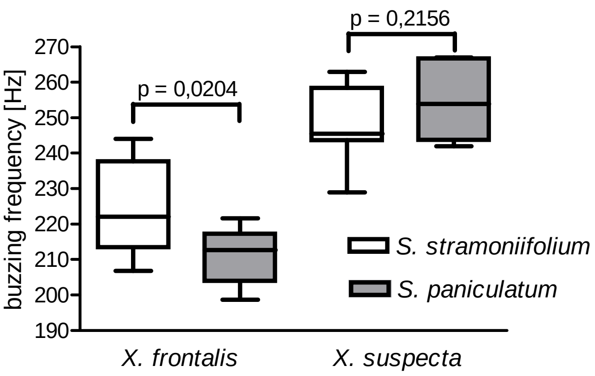

FIG. 3. Box wisker plot showing buzzing frequency of indivudals of *Xylocopa frontalis* on the flowers of *Solanum stramoniifolium* (n = 10) and *S. paniculatum* (n = 8) and of individuals of *X. suspecta* on the flowers of *S. stramoniifolium* (n = 12) and *S. paniculatum* (n = 8).

This correlation did not apply to medium to small sized bees which have an intertegular distance of less than 4 mm. These smaller bees, especially *Euglossa cordata, Centris tarsata* and *Melipona scutellaris*, have a high flight frequency, ranging from 229 to 252 Hz. Other than in larger bees, their buzzing frequency, ranging from 282 to 311 Hz, is far less than the double of the flight frequency. Furthermore in several recorded small *Augochlorini* individuals, belonging to the family of Halictidae, an atypical buzzing frequency close to the wingbeat frequency was found. When comparing the ratio of buzzing to flight frequency (Fig. 5) we found a close to linear relationship ranging from 2, as found in big bees, to 1 in the smallest ones. As the anatomical reason for these findings is largely unknown we could assume a general difference in the buzzing system of small bees as compared to larger ones. On the other hand, an adapation of small bees to a potentially optimal buzzing frequency could cause this deviant behaviour. This range of the buzzing frequency was found to be between 200 and 300 Hz for most bees. Despite these observations all bees collected during the study have obviously collected pollen, thus the ability of shaking pollen out of poricidal anthers of *S. stramoniifolium* and *S. paniculatum* via buzzing is independent of the size of the bee.

Because sound recording is very sensitive, frequency analysis permitted to resolve the frequency pattern performed during a single buzzing. While the wingbeat frequency during flight is almost constant, which is necessary for flight control, the buzzing frequency has no comparable limitation. However, we found a dynamic pattern ranging for more than 50 Hz during one buzzing which lasts for less than one second. When examining recordings of single buzzings no obvious tendency in frequency shift was seen. To overcome this, we performed trend analysis including all buzzings of single species (Fig. 4.). Observed species were found in average to start with a high and end with a low

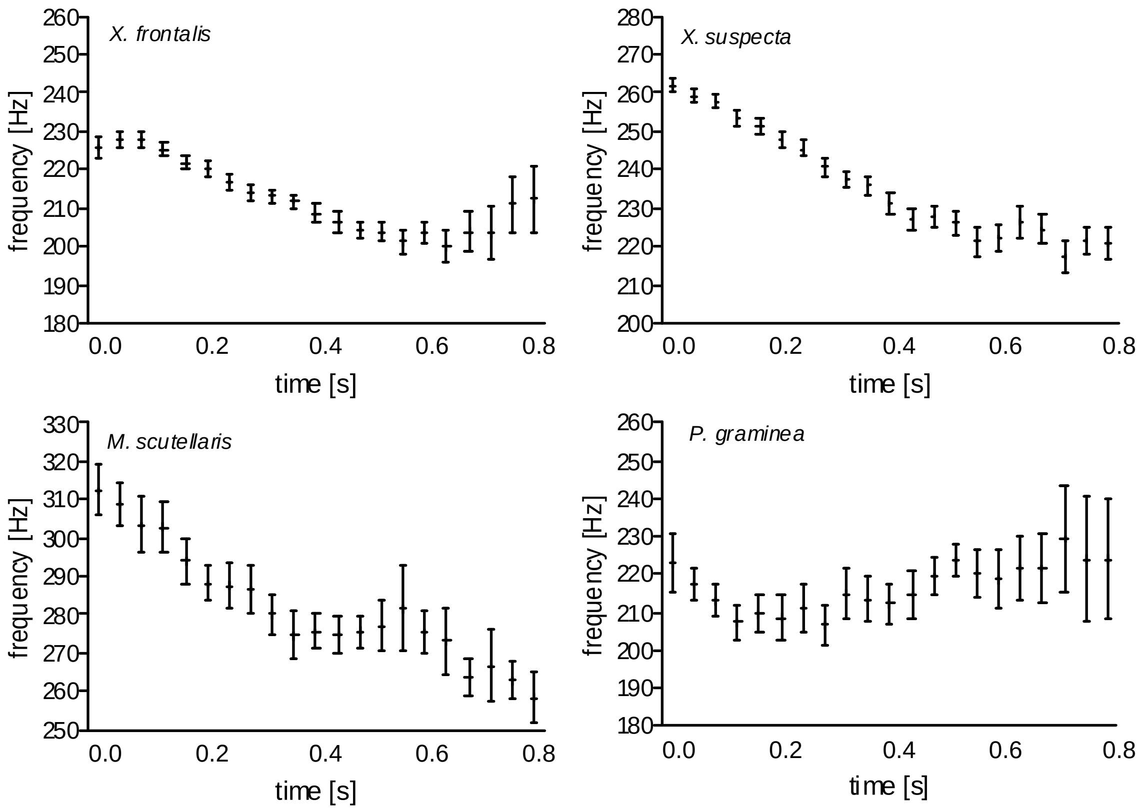

FIG. 4. Buzzing pattern of *Xylocopa frontalis* (n = 103), *X. suspecta* (n = 141), *Melipona scutellaris* (n = 12) and *Pseudaugochlora graminea* (n = 20); average pattern plotted in 0.04 s steps (mean ± SEM).

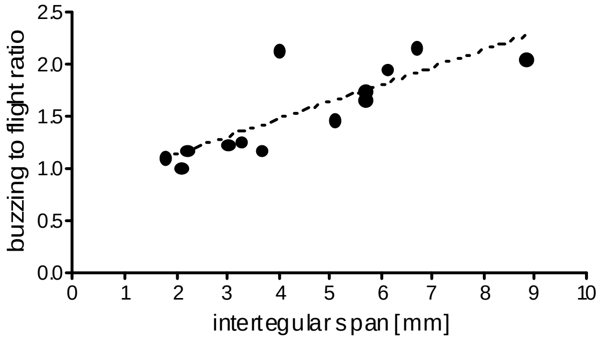

FIG. 5. Buzzing to flight ratio of the average frequencies as found in the bee species listed in Tab.2. The dotted line indicates linear regression ($r^2 = 0.672$).

frequency during a single buzzing, except for *Pseudaugochlora graminea* which showed no clear trend in its buzzing frequency. The buzzing frequency, thus, is not an absolutely fixed parameter, but changes during single buzzings. The possible reasons for frequency shifts are diverse and range from a better pollen removal by applying changing frequencies to fatigue of the flight musculatur due to the energy intensive buzzing behaviour.

We also tested whether there is a difference in the same species of bee buzzing on flowers *of S. stramoniifolium* and *S. paniculatum*. We found a significant difference in the used frequencies of *X. frontalis* but not in *X. suspecta*. This could be caused by behavioural differences or by other unknown reasons. As the flowers of both *Solanum* species in this study were morphologically similar, we encourage further frequency and resonance measurements on flowers with less morphological and size similarities. This could provide an answer to the question whether bees adapt their buzzing frequency to the given flower type.

Taken together, our study demonstrated the successful introduction and evaluation of a novel field and computer linguistical method to investigate aspects of the buzzing behaviour of neotropical bees.

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APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix I. Praat script for analysing bee sounds

REFERENCES

Bezerra ELS, Machado IC (2003) Biologia floral e sistema de polinização de *Solanum stramonifolium* Jacq.(Solanaceae) em remanescente de Mata Atlântica, Pernambuco. Acta Botanica Brasilica 17:247-257.

Boersma PPG (1993) Accurate short-term analysis of the fundamental frequency and the harmonics-to-noise ratio of a sampled sound. IFA Proceedings 17:97-110.

Boersma PPG (2002) Praat, a system for doing phonetics by computer. Glot International 5:341-345.

Buchmann SC (1983) Buzz pollination in angiosperms. In: Eugene CE, Little RJ (eds) Handbook of experimental pollination biology. Van Nostrand Reinhold Company Inc., New York, pp 73-114.

Buchmann SL, Hurley JP (1978) Biophysical model for buzz pollination in angiosperms. Journal of Theoretical Biology 72:639-657.

Byrne DN, Buchmann SL, Spangler HG (1988) Relationship between wing loading, wingbeat frequency and body mass in homopterous insects. Journal of Experimental Biology 135:9-23.

Cane JH (1987) Estimation of bee size using intertegular span (Apoidea). Journal of the Kansas Entomological Society 60:145-147.

Ehrlich I, Lunau K (2009) Untersuchungen zur Pollendetektion von Hummeln. Enomologie heute 21:141-149.

Forni-Martins ER, Marques MCM, Lemes MR (1998) Biologia floral e reprodução de *Solanum paniculatum* L.(Solanaceae) no estado de São Paulo, Brasil. Revista Brasileira de Botanica 21:117-124.

Harter B, Leistikow C, Wilms W, Truylio B, Engels W (2002): Bees collecting pollen from flowers with poricidal anthers in a south Brazilian Araucaria forest: a community study. Journal of Apicultural Research 41:9-16.

Houston TF, Thorp RW (1984) Bionomics of the bee *Stenotritus greavesi* and ethological characteristics of Stenotritidae (Hymenoptera). Records of the Western Australian Museum 11:375-385.

Hrncir M, Jarau S, Zucchi R, Barth FG (2004) Thorax vibrations of a stingless bee (*Melipona seminigra*). I. No influence of visual flow. Journal of Comparative Physiology A 190:539-548.

Hurd PD, Linsley EG (1976) The bee family Oxaeidae with a revision of the North American species (Hymenoptera, Apoidea). Smithsonian Institution Press, Washington.

King MJ, Buchmann SL (2003) Floral sonication by bees: mesosomal vibration by *Bombus* and *Xylocopa*, but not *Apis* (Hymenoptera: Apidae), ejects pollen from poricidal anthers. Journal of the Kansas Entomological Society 76:295-305.

King MJ, Buchmann SL, Spangler H (1996) Activity of asynchronous flight muscle from two bee families during sonication (buzzing). Journal of Experimental Biology 199:2317-2321.

King MJ, Buchmann S (1996) Sonication dispensing of pollen from *Solanum laciniatum* flowers. Functional Ecology 10:449-456.

King MJ, Ferguson AM (1994) Vibratory collection of *Actinidia deliciosa* (kiwifruit) pollen. Annals of Botany 74:479-482.

King MJ, Lengoc L (1993) Vibratory pollen collection dynamics. Transactions-America Society of Agricultural Engineers 36:135-140.

Knapp S, Jarvis CE (1990) The typification of the names of New World *Solatium* species described by Linnaeus. Botanical Journal of the Linnean Society 104:325-367.

Levin RA, Myers NR, Bohs L (2006) Phylogenetic relationships among the "spiny *Solanums*" (*Solanum* subgenus

Leptostemonum, Solanaceae). American Journal of Botany 93:157-169.

Michener CD (1962) An interesting method of pollen collecting by bees from flowers with tubular anthers. Un método interesante de colectar polen en flores con anteras tubulares por parte de las abejas. Revista de Biologia Tropical 10:167-175.

Moure JM, Urban D, Melo GAR (2007) Catalogue of bees (Hymenoptera, Apoidea) in the Neotropical Region, Curitiba. Sociedade Brasilieira de Entomologia 1:272-578.

Neff JL, Simpson BB (1988) Vibratile pollen-harvesting by *Megachile mendica* Cresson (Hymenoptera, Megachilidae). Journal of the Kansas Entomological Society 61:242-244.

Nunes-Silva P, Hrncir M, Imperatriz-Fonseca VL (2010) A Polinização por Vibração. Oecologia Australis 14:140-151.

Nunes-Silva P, Hrncir M, Venturieri GC, Imperatriz-Fonseca VL (2010) O potencial das abelhas *Melipona* na polinização por vibração, considerando as características físicas da vibração. Anais do IV Encontro sobre Abelhas 43:76-84.

Silva AC, Kinupp VF, Absy ML, Kerr WE (2004) Pollen morphology and study of the visitors (Hymenoptera, Apidae) of *Solanum stramoniifolium* Jacq. (Solanaceae) in Central Amazon. Acta Botanica Brasilica 18:653-657.

Teppner H (2005) Pollinators of Tomato, *Solanum lycopersicum* (Solanaceae), in Central Europe. Phyton 45:217-235.

Thorp RW (2000) The collection of pollen by bees. Plant Systematics and Evolution 222:211-223.

Wille A (1963) Behavioral adaptations of bees for pollen collecting from *Cassia* flowers. Revista de Biologia Tropical 11:205-206.