

# Current state and future directions of research on stingless bees in La Gamba

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Stingless bees are important pollinators of crops and wild plants in tropical regions. All species possess a highly eusocial lifestyle including division of labor, a complex communication system and diverse foraging strategies, ranging from solitary foraging to mass recruitment and chemically marking of rewarding feeding sites. In the area surrounding Gamba, which is a small community in the Golfo Dulce region, 26 species of stingless bees have been identified so far, comprising ca. 45 % of all Costa Rican species. Here, we summarize the research on these fascinating bees conducted at the 'La Gamba' field station during the past 12 years and discuss promising directions for future research.

**SPAETHE J., STREINZER M. & SOMMERLANDT F., 2019: Aktueller Stand der Forschung und zukünftige Forschungsthemen bei stachellosen Bienen in La Gamba.** Stachellose Bienen sind wichtige Bestäuber von Kultur- und Wildpflanzen in tropischen Regionen der Erde. Alle Arten zeigen einen hoch eusozialen Lebensstil, mit reproduktiver Arbeitsteilung und komplexer Kommunikation. Die verschiedenen Nahrungssammelstrategien reichen von solitärem Foragieren bis zur Massenrekrutierung mit chemischer Markierung der Futterstellen. In der Umgebung von Gamba, einer kleinen Gemeinde in der Golfo Dulce Region von Costa Rica, wurden bisher 26 Arten von stachellosen Bienen nachgewiesen, was einem Anteil von ca. 45 % aller aus Costa Rica bekannten Arten entspricht. In diesem Artikel fassen wir die bisherige Forschung zusammen, die in den letzten 12 Jahren in der Forschungsstation 'La Gamba' an dieser faszinierenden Bienengruppe durchgeführt wurde und zeigen Richtungen für zukünftige Projekte auf.

**Keywords:** Meliponini, Apidae, chemical communication, eusocial insects, pollination, social information, vision.

## Introduction

With over 500 described species, stingless bees (Meliponini, Apidae) are the largest group of eusocial bees and show a pantropical distribution with the highest diversity in Central and South America (MICHENER 2013, HRNCIR et al. 2016). They are important pollinators for native plants and also for many agriculturally important species. HEARD (1999) summarized that stingless bees visit flowers of about 90 crop species and significantly improve yield, for example, in macadamia, eggplant and coffee (HEARD 1987, VEDDELER et al. 2008, NUNES-SILVA et al. 2013). Furthermore, beekeeping with stingless bees has a long tradition, particularly in Meso- and South America, and the produced honey is used as a nutritional resource, for medication and for ancient ceremonial practices (WEAVER & WEAVER 1981, CRANE 1992, VIT et al. 2013).

All stingless bees are highly eusocial with a reproductive queen and functionally sterile workers, age-related division of labor among workers, and a complex communication system predominantly based on chemical cues and signals (WILLE 1983, LEONHARDT 2017). The number of colony members can range from a few hundred to more than one hundred thousand, thus exhibiting the largest colonies of eusocial bees (MICHENER 1974, ROUBIK 1983). To provision their brood, stingless bees forage for nectar and pollen from a large variety of plant species (ENGEL & DINGEMANS-BAKELS 1980, BIESMEIJER & SLAA

2006, ELTZ et al. 2001). They also utilize non-nutritive resources, such as resin, for nest building or defense against predators and pathogens (ROUBIK 2006, LEONHARDT 2017). Recruitment strategies vary considerably, from individual foraging to mass recruitment where hundreds of foragers can appear at a profitable food source within minutes (Fig. 1D; NIEH 2004). Species differ in size and level of aggression, and aggressive species sometimes push away heterospecific foragers at resources due to aggressive interactions or simply by outnumbering them (JOHNSON 1983, HOWARD 1985, BIESMEIJER & SLAA 2004, LICHTENBERG et al. 2010, KEPNER & JARAU 2016).

Nest constructions are extraordinarily diverse among species of stingless bees and are mainly built from propolis, which is a mixture of wax and resin collected from plants. Other materials used are mud, vertebrate feces, plant fibers, and chewed leaf material (WILLE & MICHENER 1973, ROUBIK 2006). Depending on species, nests can be found in termite and ant nests, tree cavities or in the ground, and the entrance is usually built as a tunnel made of propolis and other materials to protect against floods or predators such as ants (Fig. 1; ROUBIK 1983, COUVILLON et al. 2008).

Stingless bees are affected by the ‘global pollinator crisis’ (POTTS et al. 2010, LICHTENBERG et al. 2017), but due to the complex interaction of biotic and abiotic factors, we still have

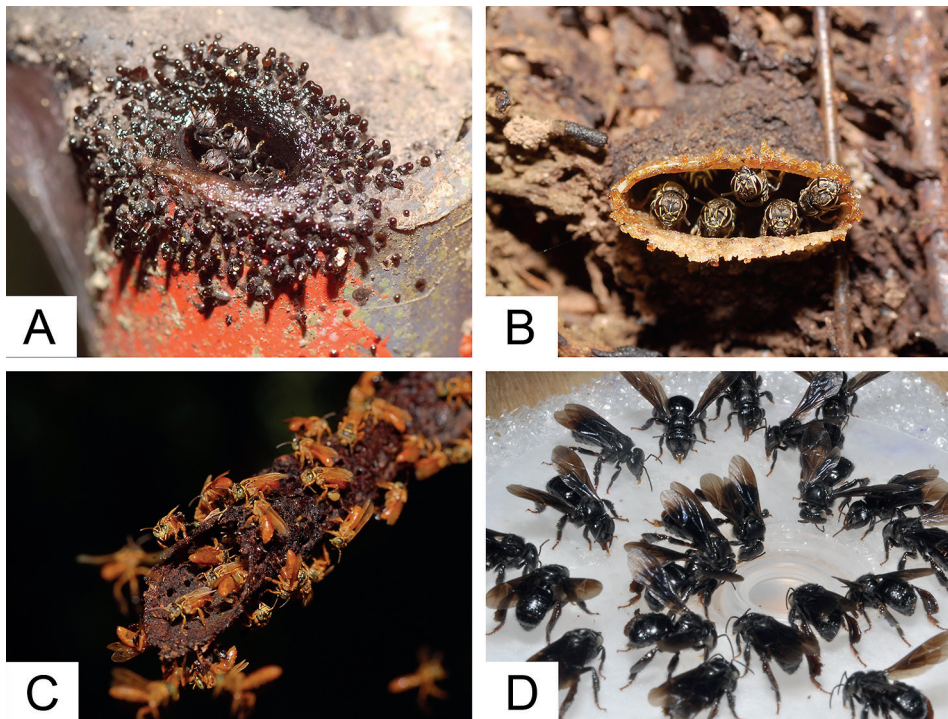


Fig. 1: Stingless bee species in La Gamba. Examples of nest entrance construction **A** *Trigonisca pipioli*, **B** *Paratrigona opaca*, and **C** *Tetragona zieglerei*. **D** Mass recruitment of *Trigona corvina* at an artificial feeder containing 1M sucrose solution. – Abb. 1: Stachellose Bienen aus La Gamba. Konstruktion der Nesteingänge von **A** *Trigonisca pipioli*, **B** *Paratrigona opaca*, und **C** *Tetragona zieglerei*. **D** Massenrekutierung von *Trigona corvina* an einer künstlichen Futterquelle mit 1M Zuckerlösung.

an incomplete understanding of how stingless bees respond to land-use transformation, agricultural intensification, pesticide use and climate change. BROSI (2009), for example, showed that species richness and abundance of stingless bees in Costa Rica were strongly correlated with forest cover and significantly decreased with increasing deforestation. Besides deforestation due to logging or land-use transformation, the intensive use of agrochemicals, in particular pesticides, may also impact stingless bee diversity and abundance (FREITAS et al. 2009). For example, the addition of imidacloprid, which is a neonicotinoid insecticide, to the diet of *Melipona quadrifasciata* worker larvae reduced their survival rate and negatively affected the development of the mushroom bodies, i.e. the neuronal integration centers of the bee's brain, which are important in learning and memory retention (TOMÉ et al. 2012). A variety of pesticides are used in intensified agriculture, almost all of which have a significant hazardous effect on stingless bees (VALDOVINOS-NÚÑEZ et al. 2009).

While the ecology and general behavior of stingless bees have been investigated in a large number of studies, research on (sensory) physiological and neurobiological aspects is relatively scarce compared to honey bees and bumble bees. In the Golfo Dulce region, 26 species of stingless bee have been recorded so far (JARAU & BARTH 2008), comprising almost half of all species described for Costa Rica (N=58; AGUILAR et al. 2013). During the past years, several projects on stingless bees have been initiated at the 'La Gamba' field station, addressing various aspects of visual and chemical ecology of stingless bees. Here we present a brief overview of the conducted studies, and discuss possible directions for future research.

### **Multimodal information use at a food sources**

Sympatric species of stingless bees often compete for the same limited food sources. Therefore, different strategies have evolved to exploit a feeding site. Such strategies include aggressive behavior or adaptation of the peak foraging activity to less favorable environmental conditions (such as dim light or rainy weather conditions; HUBBELL & JOHNSON 1978, KEPPNER & JARAU 2016). Moreover, an efficient recruitment system allows mass-recruiting species to monopolize a profitable food source. Providing olfactory information along the trail and at a food source allows for a rapid recruitment of nestmates and defense of the site against conspecific or heterospecific competitors. The chemical information used for communication and recruitment in bees is obtained from different sources, such as deliberately deposited anal droplets or gland secretions (reviewed in JARAU 2009). Moreover, foragers leave chemical footprints at food sources. These scent marks are produced by glandular epithelia of the claw retractor tendon and are likely left incidentally (JARAU et al. 2004). Both intentionally and unintentionally deposited scents can be exploited by nestmates and members of other bee species (reviewed in BARTH et al. 2008). The durability of the information transmitted by scent marks depends on its function. Repellent odor marks are usually rather short-lived and allow foragers, for example, to avoid visitation of flowers which were recently depleted. In contrast, attracting scents are often long-lasting and are used by foraging bees to advertise particularly rewarding food sources (STOUT & GOULSON 2001, JARAU 2009). Another source of chemical information is provided by the profile of cuticular hydrocarbons (CHC). With a rather short action range, CHCs provide species-, nest-, and task-specific information (JUNGNICKEL et al. 2004, LEONHARDT et al. 2009, FERREIRA-CALIMAN et al. 2010) and allows for recognition of nestmates. Nest-specific-

ity has also been demonstrated for the chemical composition as well as the behavioral attractiveness of food site marking pheromones secreted from a forager's labial glands (JARAU et al. 2010, 2011, JOHN et al. 2012). Besides the variety of olfactory cues and signals, foragers of stingless bees can also exploit visual information. The physical presence of other bees provides a visual stimulus which can affect decision making at the food site (BIESMEIJER & SLAA 2004). Particularly in group- and mass-recruiting bees, multimodal information might be used under natural conditions. The cues can be either attractive or repellent to a forager and can lead to local enhancement or inhibition. Major questions in research on information use at a food source are: which cues are used for decision-making and do cues of different modalities have redundant, hierarchical or additive functions?

*Trigona corvina* is a species of mass-recruiting stingless bee, which plays an important role in plant pollination in the neotropics. Its recruitment system includes field-based mechanisms, such as pheromone trails and deposition of scent marks (ROUBIK 1981, AGUILAR et al. 2005, JARAU et al. 2010). At a feeding site, newly arriving foragers prefer to land at food sources that are associated with conspecific cues and are attracted by both chemical and visual cues (Fig. 2; SOMMERLANDT et al. 2014). Freshly killed conspecific specimens, which provided their typical CHC profile, had the strongest attractive effect at a food source. Interestingly, the CHC profile, even though the range of its perceptibility is rather

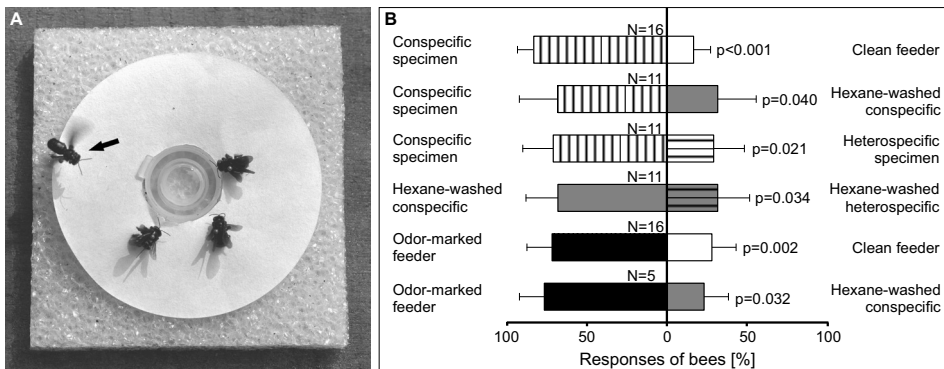


Fig. 2: Behavioral assay testing attractiveness of olfactory and visual cues at an artificial feeder. **A:** Experimental setup; a *Trigona corvina* forager (marked with an arrow) approaches a test feeder equipped with three freshly killed specimens of the same species. **B:** Responses of bees to cues presented in dual choice tests. The attractiveness of the following cues was tested in different combinations: three dead specimens of *T. corvina*, freshly killed by freezing; three dead heterospecific specimens of *T. zieglerei*; footprint-markings of 10–15 *T. corvina* foragers, which previously walked over the filter paper; three specimens of *T. corvina* that were hexane-washed to remove their CHC profile of the cuticle; three heterospecific specimens of hexane-washed *T. zieglerei*; and as control clean feeders without any cues (method and data adapted from SOMMERLANDT et al. 2014). – Abb. 2: Verhaltensversuch zum Test der Attraktivität olfaktorischer und visueller Reize an einer künstlichen Futterstelle. **A:** Versuchsaufbau; eine Arbeiterin von *Trigona corvina* (durch einem Pfeil markiert) nähert sich einer Futterstelle mit drei frisch getöteten Exemplare der eigenen Art. **B:** Wahlentscheidungen von Bienen auf unterschiedliche Reize. Die Attraktivität der folgenden Reize wurde in verschiedenen Kombinationen getestet: drei durch Einfrieren getötete Individuen der eigenen Art; drei getötete Individuen der Art *Tetragona zieglerei*; Fußspuren von 10–15 *T. corvina* Arbeiterinnen, die zuvor über Filterpapier gelaufen sind; drei Individuen von *T. corvina*, deren CHC-Profil durch Hexanwaschung entfernt wurden; drei in Hexan gewaschene Individuen der Art *T. zieglerei*; als Kontrolle dienten saubere Futtergefäße ohne zusätzliche Reize (Methode und Daten adaptiert aus SOMMERLANDT et al. 2014).

short, seemed to be an important cue. Foragers strongly preferred conspecifics possessing their typical CHCs over hexane-washed specimens (SOMMERLANDT et al. 2014). This indicates that stingless bees use the CHC profile to recognize nestmates not only at the nest (LEONHARDT 2017), but also in the field. Besides the chemical information obtained from the body surface, deposited odor marks also have a strong attracting effect (BOOGERT et al. 2006). Recruited *T. corvina* foragers land repeatedly on a novel food source and are likely to scent mark the site (AGUILAR & DEN HELD 2003).

Depositing attractive scent marks at the feeding site is a common but not the exclusive strategy in mass-recruiting bees. FLAIG et al. (2016), for example, showed mass recruitment in *Partamona orizabaensis*, but without deposition of any scent marks at the feeding site. In *T. corvina*, the strength of the scent is correlated with the number of visiting foragers. The attractive effect of the scent marks remains even when deposited by conspecifics of a different colony (BOOGERT et al. 2006). Even though scent marks are more important than visual cues at a feeding site (a fact which holds true for other stingless bees, such as *Tetragonisca angustula* and *Scaptotrigona mexicana*; VILLA & WEISS 1990; SÁNCHEZ et al. 2011), the visual stimulus of present conspecifics alone is sufficient to attract approaching bees. In the absence of chemical information, foragers of *T. corvina* can still discriminate conspecific individuals from heterospecifics of similar size but different color (*T. zieglerei*, Fig. 2; SOMMERLANDT et al. 2014). This indicates that color vision, which is used for flower recognition in stingless bees (VILLA & WEISS 1990, SPAETHE et al. 2014), may also play a role in species discrimination at feeding sites. However, when chemical and visual cues are simultaneously presented, the multimodal information has no additive effect (SÁNCHEZ et al. 2011). The bias towards olfaction, which is observed when chemical and visual information is available in competing situations, could be caused by differences in the sensitivity for olfactory and visual stimuli, or an innate preference of the bees for scent marks over visual stimuli. Except for CHCs, which are non-volatile, odor marks at food sources can transmit information over several meters (NIEH 1998; SCHMIDT et al. 2003). In contrast, due to the relatively low spatial resolution of the bee's apposition eyes, objects which are the same size as conspecifics (5–6 mm body length in *T. corvina*) are recognized only in the range of several centimeters (ZEIL & WITTMANN 1993). The pronounced local enhancement observed in *T. corvina* enables a rapid increase in the number of foraging nestmates at a profitable food source in order to monopolize it. The presence of a nestmate at a food site seems to be a general attractive cue in social bees (BIESMEIJER & SLAA 2004). However, in *Trigona amalthea* foragers, this preference depends on their previous experience. Naïve bees initially prefer to land on a flower next to nestmates, but with increasing experience they tend to completely avoid resources occupied by nestmates (BIESMEIJER & SLAA 2004). Thus, strategies to exploit profitable food sources differ not only among species but also among foragers of a single colony that have different past experiences.

## Visual ecology

Vision plays an important role in the ecology of stingless bees, e.g. for the detection and recognition of food plants, inter- and intraspecific communication, navigation and orientation between nest site and food sources and for mate detection (SRINIVASAN 2010, SOMMERLANDT et al. 2014). Bees use their compound eyes for (spatial) vision. The eyes are of the apposition type and consist of several thousand units, termed ommatidia. Each of these repetitive units can sample a small region of space through a tiny facet lens. The

quality of the images mostly depends on the number and angular separation of ommatidia and their light sampling capacity (LAND 1997). Individual ommatidia are usually equipped with two or three different photoreceptor types (KELBER et al. 2003). Perception of color, as a separate visual modality, may allow bees to detect flowers faster in cluttered visual environments and to reliably recognize rewarding food sources during foraging trips leading to an increase in foraging efficiency (SPAETHE et al. 2001, MORAWETZ & SPAETHE 2012). The basic requirement for perceiving color independently of object brightness is the existence of at least two photoreceptor types with different spectral sensitivities that sample the same region in space, and a color opponency mechanism to compare their outputs (KELBER et al. 2003). Electrophysiological recordings show a highly conserved set of three different receptor types among most bees, with maximum sensitivity in the ultraviolet, blue and green range of the light spectrum (PEITSCH et al. 1992). Most of our knowledge about color vision and visual ecology in bees stems from observations and experiments in honey bees and bumble bees (e.g. GIURFA et al. 1996, DYER et al. 2008), while our knowledge about stingless bees and other bee species is marginal.

Using a similar experimental approach as Nobel-laureate KARL VON FRISCH did in his pioneering study more than 100 years ago (VON FRISCH 1914), we tested for functional color vision in stingless bees (SPAETHE et al. 2014). Workers of *Trigona cf. fuscipennis* were trained to associate a sucrose reward with a colored stimulus. After training, bees were tested in an unrewarded test, where they had to recognize the previously learned color among a set of 12 different shades of grey. The proportion of bees that landed on the chromatic (colored) target was significantly higher than the landings on any achromatic (grey) card. The bees did not mistake any of the grey shades for the previously rewarded stimulus in experiments with four different colors (yellow, blue, purple and pink), which proves that true color vision is present in *Trigona cf. fuscipennis* (SPAETHE et al. 2014). In a follow-up experiment we tested the accuracy of their color discrimination abilities by using a simultaneous color discrimination paradigm, which was previously used to determine color discrimination in honey bees and bumble bees (DYER & NEUMEYER 2005, DYER et al. 2008). Bees were first trained to associate a saturated blue or yellow star on an achromatic grey background with a reward and then tested with colored stars of decreasing saturation to determine the threshold of color perception (SPAETHE et al. 2014). The workers were able to perceive the colored star down to ca. 0.07–0.08 hexagon units (a dimensionless value which describes the similarity of two different colors), which is significantly poorer than the 0.01–0.02 hexagon units found in honey bees and bumble bees (DYER & NEUMEYER 2005, DYER et al. 2008). However, the observed performance of *T. cf. fuscipennis* is comparable to the performance of another stingless bee species of similar size, the Australian *Tetragonula carbonaria* (SPAETHE et al. 2014).

Currently, the neural processing of color information is only superficially understood in stingless bees (GARCIA et al. 2017). Distinct differences exist even among closely related species, such as honey bees and bumble bees (DYER et al. 2008). At the current stage of research, we have not yet determined whether differences in the acuity of color vision are related to the phylogenetic background, physiological or morphological differences or other factors. It is entirely possible that the relatively poor visual abilities of the tested species are due to their small body size. Small eyes suffer from lower spatial acuity and capture less light, which likely affects signal-to-noise ratios (DYER et al. 2016). As a consequence of the lower light gathering abilities, small species may also be limited by the light conditions at

which they can forage. Apposition eyes are relatively insensitive and usually restrict flight activity to the bright daylight hours. Specific morphological and neuronal adaptations have been described in bees, which allow them to shift their temporal activity towards twilight and night-time (WARRANT & DACKE 2011), but in general smaller eyes are less sensitive (KAPUSTJANSKIJ et al. 2007). Vice versa, larger and thus more sensitive eyes may enable bees to forage in the relatively dark understory of tropical rain forests and to shift their activity to earlier and later times of the day, as was observed for *Partamona orizabaensis* at the La Gamba field station (KEPPNER & JARAU 2016). The latter is particularly important, since many flowering plants produce ample amounts of nectar and pollen in the early morning or late afternoon, which can be more efficiently exploited by species that are able to forage under low light conditions (WCISLO & TIERNEY 2009).

In a recent study, we investigated the scaling of compound eyes and sought to understand its functional consequences in a number of stingless bee species (STREINZER et al. 2016). Eye size, ommatidia number and size, and ocellar diameter were found to be positively correlated with body size. Based on theoretical considerations we anticipated that larger species would benefit from higher light sensitivity. To test this assumption, we quantified flight activity of several bee species in and around the La Gamba field station and measured the minimum light levels at which they commence foraging in the morning and cease flying in the evening. Smaller species were found to be more restricted and began flying about half an hour to an hour later in the morning and ended activity by the same period earlier in the evening (Fig. 3, STREINZER et al. 2016).

To summarize, all stingless bee species most likely possess color vision, which permits reliable detection and identification of rewarding flowers. However, due to the strong link between light sensitivity and spatial resolution on the one hand, and eye size on the other, smaller species are more restricted in their daily activity and need to deploy behavioral strategies to successfully compete with larger species.

## Future directions

The La Gamba field station is an excellent location for research on Meliponini due to the high diversity of stingless bee species, the available infrastructure including an extensive trail system and air-conditioned laboratory, and a multitude of different habitats in close vicinity. Based on these fortuitous conditions, we recommend two major directions of future research.

First, the combination of behavioral and physiological experiments in situ enables us to address questions regarding the chemical ecology of bees. As mentioned above, stingless bees use a multitude of chemical cues and signals in their daily life. Behavioral studies usually take place in the field in close vicinity to the colonies, since most species cannot easily be transferred into the lab. Thus, if one intends to analyze potentially relevant chemical cues, odors, or CHCs involved in a specific behavior, the potential (but still unidentified) substances must be sampled and transported to a suitable laboratory for subsequent analyses, which is time consuming and impedes the direct testing of substances (ETL et al. 2016). However, with the availability of an air-conditioned laboratory in La Gamba, sensitive equipment such as a gas-phase chromatograph (GC) can be operated in close proximity to the experimental field site. The currently available GC is combined with an electrophysiological setup for electroantennogram recordings (GC-EAD), which allows one

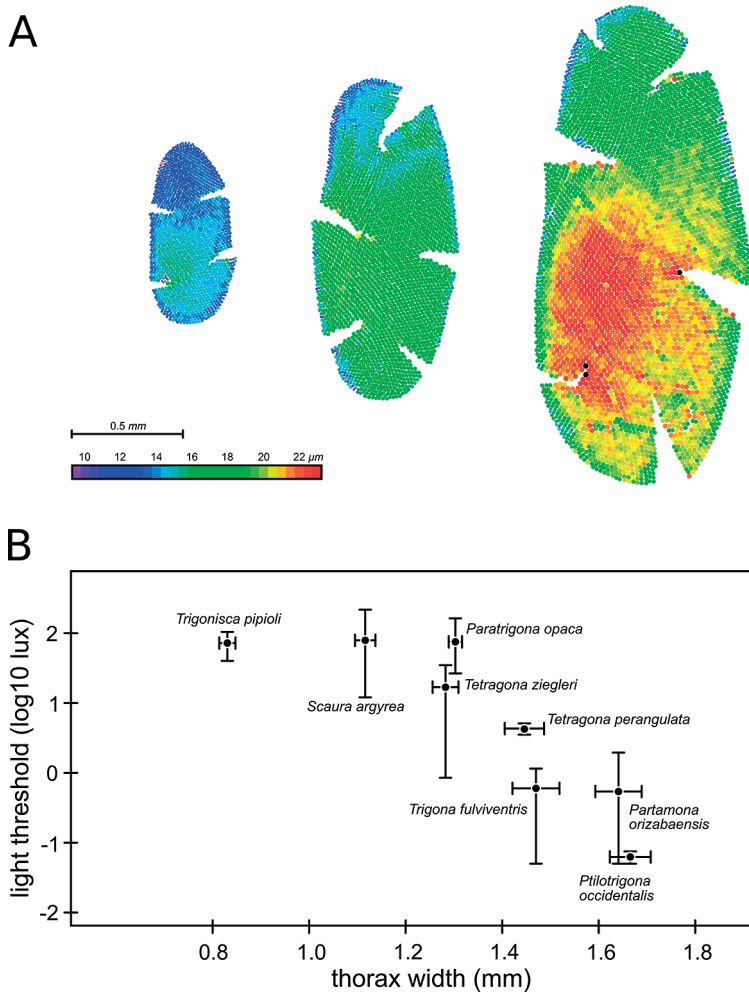


Fig. 3: Eye morphology and light intensity-dependent flight activity of stingless bees. **A:** Eye maps generated from replicas made of nail polish (for methods see STREINZER et al. 2016), showing facet diameter (color coded) of compound eyes of a small (*Trigonisca pipioli*), intermediate (*Paratrigona opaca*) and large (*Ptilotrigona occidentalis*) sized stingless bee species. **B:** Light thresholds at which bees are just able to fly, plotted against body size (measured as inter-tegulae span), in eight species of stingless bees from La Gamba, Costa Rica. Large species with larger eyes and facet lenses were able to start earlier in the morning and fly longer in the evening due to a higher light sensitivity. Colored scale bar in **A** indicates facet diameters. – Abb. 3: Augenmorphologie und Lichtintensität abhängige Flugaktivität stachelloser Bienen. **A:** Anhand von Nagellackabdrücken der Komplexaugen generierte Augenkarten, die die Verteilung der Facettendurchmesser (farbcodiert) von einer kleinen (*Trigonisca pipioli*), einer mittelgroßen (*Paratrigona opaca*) und einer großen (*Ptilotrigona occidentalis*) stachellosen Bienenart zeigen (Methode in STREINZER et al. 2016). **B:** Minimale Lichtintensität, bei der acht stachellose Bienenarten aus La Gamba fähig waren, zu fliegen, aufgetragen gegen ihre Körpergröße (gemessen als Distanz zwischen den Flügelschuppen des Thorax). Größere Arten mit größeren Augen und Facettendurchmessern und daraus resultierender höherer Lichtempfindlichkeit, konnten früher am Morgen und später am Abend fliegen. Der Farbbalken in **A** zeigt die jeweiligen Facettendurchmesser.



to measure antennal olfactory responses towards individual and identifiable compounds (STRUBLE & ARN 1984). The behavior of bees, in particular when they use chemical cues (SOMMERLANDT et al. 2014), can now be efficiently investigated by sampling the potential cue from the bees' bodies or other surfaces, separating it into its individual substances, and testing a bee's antennal response towards each substance by means of the GC-EAD. Subsequently, the identified substances that elicit a response can be tested directly in the field. This approach can also be used to investigate bee-flower relationships, e.g. to identify floral odors that are attractive to stingless bees (BURGER et al. 2012).

The second major direction of research is to quantify stingless bee diversity as a tool for evaluating the success of forest restoration. During the past 50 years, large areas of the primary tropical rainforest in the Golfo Dulce region have been deforested and transformed into agricultural land or urban areas, thus isolating the lowland Pacific rainforest area of the Piedras Blancas National Park from the eastern mountain range Fila Cal. The La Gamba field station has acquired several degraded plots in the area over the past years and has initiated reforestation efforts using local tree species (WEISSENHOFER et al. 2008). To evaluate the success of ecological restoration on wildlife and ecosystem function, it is necessary to design and implement suitable monitoring studies (BLOCK et al. 2001, RUIZ-JAEN et al. 2005). Stingless bees are very sensitive to forest degradation (BROSI 2009) and thus may be a suitable insect taxon to evaluate restoration progress, since they rely on both sufficient flowering plants to meet their nutritional requirements, and proper trees for nesting sites (ELTZ et al. 2002).

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## Literature

(\* indicates studies conducted at least partially in and around the field station of La Gamba)

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