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ASPECTS OF MELIPONICULTURE WITH EMPHASIS ON THE GENUS *Scaptotrigona*

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ABSTRACT - Meliponiculture is the rational exploitation of stingless bees, in which different species of bees are exploited. This diversity ensures differences in morphological and biological aspects, nesting habits, resource gathering behaviors, defense and productivity. Knowledge of the aspects of this diversity of bees makes it possible to understand and disseminate technical-scientific information. However, the difficulty of obtaining knowledge in this area that is on the rise is something that hinders the dissemination of scientific knowledge. This review aims to disclose the importance of meliponiculture, its main aspects and emphasize the productive potential of the genus *Scaptotrigona*. This genus has productive potential and can be exploited commercially or as a research objective to increase production rates. Given the above, studies of the bionomic characteristics of meliponines are relevant for the economy, pollination services, conservation of plant and animal species, standardization of materials and equipment, in addition to enabling the establishment of adequate management, contributing to increased productivity.
Keywords: stingless bees, behavior, meliponines.

ASPECTOS DA MELIPONICULTURA COM ÊNFASE NO GÊNERO Scaptotrigona

RESUMO - A meliponicultura é a exploração racional das abelhas sem ferrão, na qual são exploradas diferentes espécies de abelhas. Essa diversidade garante diferenças em aspectos morfológicos e biológicos, hábitos de nidificação, comportamentos de coleta de recursos, defesa e produtividade. O conhecimento dos aspectos dessa diversidade de abelhas possibilita a compreensão e divulgação de informações técnico-científicas. No entanto, a dificuldade de obtenção de conhecimento nessa área que está em ascensão é algo que dificulta a divulgação do conhecimento científico. Esta revisão visa divulgar a importância da meliponicultura, seus principais aspectos e enfatizar o potencial produtivo do gênero *Scaptotrigona*. Este gênero apresenta potencial produtivo e pode ser explorado comercialmente ou como objetivo de pesquisa para aumentar os índices de produção. Diante do exposto, os estudos das características bionômicas dos meliponíneos são relevantes para a economia, serviços de polinização, conservação de espécies vegetais e animais, padronização de materiais e equipamentos, além de possibilitar o estabelecimento de manejo adequado, contribuindo para o aumento da produtividade.
Palavras-chave: abelhas sem ferrão, comportamento, meliponíneos.

INTRODUCTION

Bee breeding is divided into two modalities: apiculture and meliponiculture (SILVA et al., 2019; ZULHENDRI et al., 2022). Unlike beekeeping, which is more widespread and works with a bee species, in meliponiculture there are numerous species, and thus present greater complexity to understand the best techniques to be applied in handling (BASARI et al., 2018). The diversity of stingless bee species, or also known as indigenous or meliponines bees, are distributed in tropical and subtropical regions (QUEIROZ et al., 2019).

Approximately 550 species belonging to 58 genera have been described (MICHENER, 2013; GRÜTER, 2020). These have different behaviors, productive, morphological and biological aspects vary between species, which makes it difficult to deepen and spread knowledge (VENTURIERI et al., 2012; PEDRO, 2014; REYES GONZÁLEZ et al., 2020). Stingless bees (Meliponini) and the ones from *Apis* (Apini) genus are groups of eusocial bees, live in colonies and new ones can be established by the process of swarming and colony division (MICHENER, 2013; SILVA et al., 2014).

Different from what is observed in *bees of the Apis* genus, in which the defense mechanism is sting, and the bee ends up sacrificing itself for the colony (BREED et al., 2004), the meliponines have different behaviors as their defense mechanism. They can bite, enter the nose, curling up in the eyebrows, hair, body hair, clothing, production of characteristic odors, and the use of sticky materials for immobilization of enemies and even a social reorganization for nest defense (GRECO et al., 2010; HALCROFT et al., 2011; LEONHARDT, 2017; BAUDIER et al., 2019;

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AMEER et al., 2021; ZULHENDRI et al., 2022). An example of a defense mechanism is the *bee Oxytrigona tataira*, which can mummify the enemy or use secretions that can cause burns (SOUZA et al., 2007). It is necessary to use personal protective equipment (PPE) when handling the colonies of certain species.

The creation of meliponines is observed as an important economic activity and not merely *a hobby* (SILVA and PAZ, 2012; FAQUINELLO et al., 2013; ZULHENDRI et al., 2022). Its activities go beyond the rational breeding of bees, such as pollination (LAVINAS et al., 2019) and collection of food resources, which help in the conservation of species of both bees and vegetables, meeting economic, social and ecological requirements, through the generation of income and use of family labor (JAFFÉ et al., 2015; BASARI et al., 2018).

Among the stingless bees that present rusticity, and with breeding potential stands out the bees of the *genus Scaptotrigona*, due to honey production, adaptability and use in crop pollination. With the advances of meliponiculture and the diversification of the obtained products, it is necessary to understand about several factors that influence stingless bees, and their interactions with the environment. However, little knowledge is generated, which hinders the work and dissemination of information (BARBOSA et al., 2017). Based on this, this review aimed to explore the main aspects of meliponiculture, bionomic characteristics and emphasize the productive potential of bees of the *genus Scaptotrigona*.

DEVELOPMENT

Meliponiculture in Brazil

Meliponiculture is the fusion between the knowledge of indigenous peoples about natural resources and the inclination of Europeans to domesticate animals, in this process, initially the stingless bees were used as a source of honey and cerumen (JONES, 2013; NEOV et al., 2019). Before the production of sugarcane and the introduction of *Apis mellifera* honeybees in Brazil, honey from "indigenous bees" was used as a natural sweetener and energy source (ZULHENDRI et al., 2022).

Initially, stingless bees were taxonomically separated into two main tribes: Trigonini and Meliponini, however reclassification of the meliponines (family Apidae, subfamily, Apinae) constituting only one tribe, the Meliponini, which has been used to date. The lack of knowledge of the species and places of occurrence hinder the dissemination of knowledge, even with the advance of Meliponicultural activity in Brazil. Thus, it is necessary to use better management techniques, study of species (VENTURIERI et al., 2012; BASARI et al., 2018) and development of research in the area of meliponiculture.

The use of stingless bees is widespread for millennia through the practice of meliponiculture (REYES-GONZÁLEZ et al., 2020; ZULHENDRI et al., 2022) worldwide. Its use ranges from pollination services (LAVINAS et al., 2019), beehive products and commercialization of colonies, used as pets (JAFFÉ et al., 2015; LI et al., 2021).

Meliponines are fundamental for the maintenance of wild species and increased productivity of crops (FREITAS and NUNES-SILVA, 2012; BALLANTYNE et al., 2017; NEOV et al., 2019; GRÜTER, 2020). Due to the great diversity of stingless bees, the pollination process can be facilitated by selecting the most efficient species in pollinating certain crops (SILVA et al., 2014; KLEIN et al., 2020).

With the popularization of meliponiculture, technical events and courses are held, and the Ministry of Agriculture, Cattle and Supplying began to recognize the meliponiculture activity as a viable agricultural activity (VENTURIERI et al., 2012). And the Ministry of Environment recognized the importance of these bees and created the resolution that guide the breeding of these bees in the country (CONAMA, 2020). Some Brazilian states have regulated the creation and commercialization of stingless bees, such as Law No. 17,896 of January 11, 2022 (Ceará), Normative 6 of 2019 of the Environmental Institute of Paraná, provides for the management, rearing, trade and transportation of native social bees (IAP, 2019; CEARÁ, 2022), meeting scientific, sociocultural, conservation, reproduction and preservation requirements of species.

Currently, interest in meliponiculture activity is increasing, however it is not yet considered as the main activity within the property, being intercropped with other agricultural and livestock activities. Most of the people linked to the activity in Brazil are people from the agricultural sector, civil servants or pensioners, who learned the activity with grandparents or parents (REYES-GONZÁLEZ et al., 2020), with an average age of 47 years, with an average uptime of 27 years, in their meliponary have from 1 to 3,500 colonies, but on average less than 100 colonies are maintained (JAFFÉ et al., 2015).

The market is receptive to the different products of stingless bees, including honey, pollen (saburá), propolis or geopropolis (SEREIA et al., 2018; VOLLET-NETO et al., 2018; ZULHENDRI et al., 2022). Products from meliponiculture have added value and an opportunity to generate income, due to their sensory and therapeutic characteristics (SILVA et al., 2014; SEREIA et al., 2018; ZULHENDRI et al., 2022). Because they are differentiated products, they are in ascendancy in the market (VENTURIERI et al., 2012; SEBRAE, 2015; FREITAS et al., 2020b).

In view of the fact that it does not require large tracts of land for creation, daily care, and does not require high investments for the beginning of the activity, it aroused the interest of people of different ages and social classes even in the urban area (SEBRAE, 2015; CORTOPASSI-LAURINO and NOGUEIRA-NETO, 2016). Thus, the development of meliponiculture occurs, generating knowledge of the species and their behaviors and, on the other hand, the conservation of species (OLIVEIRA et al., 2013). However, for the creation of stingless bees in the states it is necessary to comply with Ordinance No. 665 of November 3, 2021 of the Ministry of Environment which determines which species and their respective habitats (BRASIL, 2021).

General biology of stingless bees

Stingless bees are considered eusocial due to the complex organization and relationship between adults, they are groups called matrilinies (mothers and daughters) with two generations interacting (MICHENER, 1969). The differentiation of varieties occurs due to the amount of food received by the larva, except for bees of the genus *Melipona* in which the differentiation occurs by genetics added to a minimum amount of food (SANTOS and CRUZ-LANDIM, 2002).

The genus *Melipona* consists of robust bees, of medium to large size (7 to 15 mm), on the other hand the other bees are thin, small to medium size (from 2 to 11 mm), the main difference besides morphology is in the process of formation of the queen (OLIVEIRA et al., 2013) comprises bees of the genus *Trigona*, *Tetragonisca*, *Tetragona*, *Scaptotrigona* among others. This diversity of size and body characteristics influence activities such as pollination services, colony organization (CHOLE et al., 2019) and production potential.

In meliponines, the female workers construct the offspring cell, deposit larval food (Figure 1a) at approximately 2/3 of the cell capacity (GRÜTER, 2020). Later, the queen performs the posture and the cell is closed by the workers, which remains sealed until the emergence of the individual (OLIVEIRA et al., 2013; KOEDAM, 2017).

The development time of a stingless bee from the egg phase to adulthood depends according to the species, *Melipona quadrifasciata bees* from 30 to 37 days (KERR, 1950), *Melipona rufiventris* 39 to 45 for other species this information is scarce. The variation in the development period occurs due to several factors, difference within the species, between species, sex and caste of individuals (AIDAR, 2010).

After the emergence of workers, the average life time is 50 to 55 days, queens, after being fertilized, become laying queens, and live on average from one to three years. The colony of stingless bees presents individuals of two sexes, the male represented by the bumblebees and the female composed of two varieties, the queen and the workers, the latter has the function of performing the works and the others by reproduction (CRUZ-LANDIM, 2009).

In most species of stingless bee queens are produced in differentiated cells, these are larger than the cells of worker and male, and these cells (Figure 1b) are located at the ends of the brood discs (OLIVEIRA et al., 2013; BARBOSA-COSTA and CARVALHO-ZILSE, 2013; CORTOPASSI-LAURINO and NOGUEIRA-NETO, 2016; KOEDAM, 2017). Due to the size of the cell, the larva receives a greater amount of food that gives rise to the queen, except in the *Melipona* in which the cells are undifferentiated (MICHENER, 1969; OLIVEIRA et al., 2013; SILVA et al., 2014). The queen is morphologically different from the others and is responsible for the production of fertile eggs of the colony, the workers when laying, the eggs are sterile, called trophic eggs, these are used for the queen's feeding (MICHENER, 1969; OLIVEIRA et al., 2013; SILVA et al., 2014).

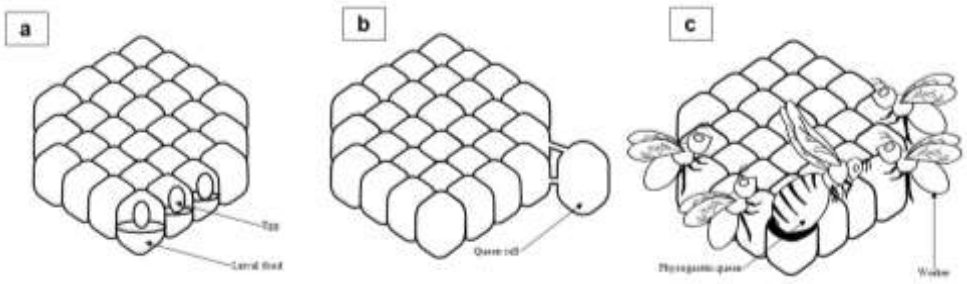

FIGURE 1 - Offspring disc characteristics of the genus *Scaptotrigona*. a. offspring disc, with larval food and egg, b. offspring disk with queen cell, c. offspring disc with physogastric queen and workers. Source: author.

Following fertilization, the abdomen dilates due to the increase of the ovaries, they are practically unable to fly (SILVA et al, 2014; KOEDAM, 2017). This phenomenon is called physogastric being the laying queen known as physogastric queen (Figure 1.c), it is possible to verify the difference of the queen between the other bees with the naked eye (OLIVEIRA et al., 2013; CORTOPASSI-LAURINO and NOGUEIRA-NETO, 2016).

Males differ from other female employees due to the absence of pollen basket, smaller jaws and longer antennae these sporadically perform tasks such as honey dehydration and wax manipulation (SILVA et al, 2014; CORTOPASSI-LAURINO and NOGUEIRA-NETO, 2016). The best way to observe a male is when they are in a zone called the drone congregation, usually near the colony waiting for the queen's departure to mate (OLIVEIRA et al., 2013).

The workers are the most abundant individuals in the colony, in the third pair of legs the pollen basket is present, a structure that is used to transport resources to the colony (OLIVEIRA et al., 2013). These bees perform all activities in the colony, being divided by age, young workers perform work within the nest as nurseries, or cleaning, and older activities, external activities such as those related to foraging (MATEUS et al., 2019; GRÜTER, 2020; LAYEK et al., 2021). Despite being different both in functions and morphologically, all members of the colony

seek a common good, and work altruistically and cooperatively (RODRIGUES and GARDNER, 2021).

Bionomic characteristics

Bionomic characteristics are the relationship between biotic (living beings) and abiotic (non-living), in relation to the way they interact in the environment in which they are inserted, such as construction habits, behaviors, habitat, foraging strategies and eating habits. Through the bionomic characteristics it is possible to differentiate and compare the species, or the variation within the same genus or species thus providing the development of better management techniques, conservation and productivity increase (SOUZA et al., 2008).

Meliponini bees have the atrophied stinger (LAVINAS et al., 2019), and differ from other bees not only by morphological characteristics, but also by the characteristics of the nest and colony development (CORTOPASSI-LAURINO and NOGUEIRA-NETO, 2016; AMEER et al., 2021). The study of the bionomic characteristics is necessary for a better understanding of the behavior of the species of interest and the relationship with the environment in which they are inserted.

Stingless bees build elaborate nests and store their young and food. Nesting and nesting are objects of study interest due to the complexity and diversity among species (GRÜTER, 2020). Nesting habits and nest construction are varied (LAYEK et al., 2018), depending on the species, and can be nested in a branch, or in a pre-existing cavity (CORTOPASSI-LAURINO and NOGUEIRA-NETO, 2016; SHANAHAN and SPIVAK, 2021).

Different sites are used for nesting, we have natural ones, such as tree hollows, cracks in rocks, holes made by other animal species, termite nests, ant nests, subterranean in the soil, or anthropic environment, such as cracks in walls, lampposts, roofs, telephone boxes cavities or holes in walls (MICHENER, 2013; LAYEK et al, 2018). Despite the variation of nesting and nest construction sites, for almost all stingless bees, it is performed with resins, which are collected and used at some point in the nest (BASARI et al., 2018; ROLDÃO-SBORDONI et al., 2018; GRÜTER, 2020).

The main material used for the construction of nests is cerumen, which is a material composed of secreted wax and collected resin (GRÜTER, 2020; SHANAHAN and SPIVAK, 2021). Cerumen is compared to propolis of the bee *Apis mellifera* (MASSARO et al., 2011). It has light brown coloration, malleable containing higher proportion of wax and less resin, or dark brown and more rigid color containing more resin and less wax (ROLDÃO-SBORDONI et al., 2018). Resin and propolis are used for the architecture of food pots and discs of offspring (ZULHENDRI et al., 2022).

Unlike the vertical combs composed of alveoli used as rearing cells and storage of food in bees *Apis mellifera*, meliponines usually build discs horizontally and the cells of offspring are spherical to ovoidal (SILVA et al., 2014). Mature offspring discs are easily distinguished from recent graduates, because they do not have the cerumen layer, they are lighter in color (CORTOPASSI-LAURINO and NOGUEIRA-NETO, 2016).

Pollen and honey food pots are ovoid or cylindrical spheres that vary in size by species (SILVA et al., 2014; CORTOPASSI-LAURINO and NOGUEIRA-NETO, 2016) allocated separately from the rearing discs, above or below the enclosure (SÁNCHEZ and VANDAME, 2013). In the nest there are other components besides food pots and offspring discs, such as the wrapper which is composed of layers of soft cerumen (LI et al., 2021) and limits the space within the colony and has the function of maintaining homeostasis (CORTOPASSI-LAURINO and NOGUEIRA-NETO, 2016) and nest protection.

Other components of the nest are the support pillars, which have the function of separating one disc from the other, and are present or absent varying the bee species (GRÜTER, 2020). The inlet tube is a component located at the entrance of the nest externally, and is characteristic of each species, and may be used as a means of identifying species in the field the tube goes from the nest to the outside, and the length, shape and material used varies according to the species (RASMUSSEN, 2013).

Behavior

The different behaviors are fundamental for the social organization of the colony. As an example, the way meliponines respond to threats, they have peculiar defense mechanisms, which are related to the architecture of the nest or even its morphology (CORTOPASSI-LAURINO and NOGUEIRA-NETO, 2016; WANG et al., 2018). Stingless bees are less defensive than *Apis* honey bees, due to the atrophied stinger (LAVINAS et al., 2019), they do not sting, however they use other defense mechanisms (OLIVEIRA et al., 2013; LEONHARDT, 2017; TUKISITHA et al., 2018; AMEER et al., 2021).

In addition to the characteristic behavior of defense, the behavior of resource collection is fundamental for the colony, as they exploit a maximum foraging range, which alternates with the species of each bee, of 500 m for small bees and 1000 to 2000 m for large bees (LAYEK et al., 2021). However, this behavior may be influenced by the external conditions of the colony (BARBOSA et al., 2020; MOURA et al., 2022).

According to the bee species the percentage of foragers can vary from 30 to 90%. In the foraging behavior the collected resources are diverse such as resin, nectar, pollen, water, soil or animal feces (FREITAS et al., 2020b).

Among the collected resources, pollen and nectar are used as a source of proteins and carbohydrates (MOHAMMAD et al., 2020; TRINKL et al., 2020), and the other resources collected are used for construction and protection of the colony (WANG et al., 2018). When bees find a place with availability of resources, they communicate and recruit the other ones, indicating the location and distance, thus increasing the efficiency of the collection. Some bees potentiate foraging by collecting nearby sites to optimize energy and time, such as *Heterotrigona itama* stingless bees (BASARI et al., 2018).

In established colonies with food stock and high population, stingless bees present the reproductive behavior of swarming, in which the workers of the primary colony seek a new place for nesting (MICHENER, 2013). The workers carry building materials (wax, propolis, cerumen) of the colony maintaining a bond with the primary colony until it is independent (SILVA et al., 2014; CORTOPASSI-LAURINO and NOGUEIRA-NETO, 2016; KOEDAM, 2017; AMEER et al., 2021).

Corbiculated bees collect and use resins (MARTINS, 2014; HARANO et al., 2020). In particular, stingless bees collect large amounts of resin that are collected from plants, which may be present in fruits, flowers, vegetative and reproductive buds and wounds (LEONHARDT et al., 2014). Of sticky consistency, bees use it for various purposes, such as the construction of nests, food pots or structures for colony protection (SHANAHAN and SPIVAK, 2021). The resin is also used to defend the colony, including since the trapping of possible predators the construction of barriers in the nest (DRESCHER et al., 2014; NUNES et al., 2014; ZULHENDRI et al., 2022).

Construction of nest structures

In the construction of the nest of stingless bees some components are fundamental to ensure the defense of the colony and its development. Among the components, the wax that is produced in the dorsal region of the abdomen by the wax glands (between the III and the VI segment) is mixed with plant resins forming the cerumen, used in the construction of the nest, and the development of these glands is related to the need for wax within the colony (CAVALCANTE et al., 2000; HARANO et al., 2020).

The term propolis is used to name the mixture composed of resins and balms (50%), responsible for the physical, chemical and biological characteristics of propolis, wax (30%), essential and aromatic oils (10%), pollen (5%) and other components (5%) (ZULHENDRI et al., 2022). The term propolis means pro (defense) and polis (city), that is, defense of the colony. Propolis has a function of maintaining temperature, covering holes in the colony, but also as a means of protection against enemies (HUANG et al., 2014; POPOVA et al., 2021).

The term propolis, geopropolis is used by some researchers as a synonym for cerumen (MASSARO et al., 2011), or similar to batumen and for LAVINAS et al. (2019) geopropolis is the mixture of propolis with soil, which is characteristic in the genus *Melipona*. These terms are used to describe the material used in the construction of the nest structures. GRÜTER (2020) avoids the use of the term propolis when it comes to stingless bees, and uses the terms cerumen, resins, or depending on batumen composition.

The cerumen is used in the construction of internal and external structures of the nest and to close cracks, smooth walls and structures present in the hive (ZULHENDRI et al., 2022). Batumen is the cerumen with the addition of other materials, such as seeds, stone, soil and in some species animal feces. Layers of batumen eat are used to cover cavity walls to protect the nesting site (GRÜTER, 2020), limit space and avoid overheating.

Food sources

Nectar is the main source of carbohydrate and energy for bees, through dehydration honey is produced, being stored later in pots (OLIVEIRA et al., 2013). The bees go to the nectar source, collect with their specialized oral apparatus and transport them in the melliferous vesicle to the colony (CORTOPASSI-LAURINO and NOGUEIRA-NETO, 2016). The process of collecting the food resource can suffer action from the environment hindering or facilitating the procurement process (MOURA et al., 2022).

The main protein, lipid and vitamin source for bees is pollen, which is collected from floral sources, mixed with nectar and secretions (OLIVEIRA et al., 2013). Pollen after being collected from the flowers is transported in the corbicula to the colony (CORTOPASSI-LAURINO and NOGUEIRA-NETO, 2016) being pre-stored in the pots, with microbial fermentation occurring, which is fundamental for its correct storage. Then occurs the change of the odor, flavor and texture of pollen, this after fermented is called saburá and results of the mixture of pollen grains with nectar and honey (MENEZES et al., 2013; OLIVEIRA et al., 2013). The honey and pollen produced are stored in oval pots within the colony, and the amount of pots varies with the density of bees present in the colony (FAQUINELLO et al., 2013).

Genus *Scaptotrigona*

Among the species of stingless bees those belonging to the *genus Scaptotrigona* are popularly known as Tubuna, Tubi, Mandaguari, Canudo and Tubiba bees, because they present as a characteristic the entrance of the colony in the form of a funnel. Among the various species of this genus, *Scaptotrigona bipunctata* (Lepeletier, 1836), has a characteristic of greater defensiveness (JUNGNICKEL et al., 2004), produces a characteristic odor of the species similar to coconut smell and has as common names: canudo, tubuna, tapesuá (WANG et al., 2018).

Stingless bees of the genus *Scaptotrigona*, with emphasis on *S. bipunctata*, are resistant bees with productive potential, can be explored commercially, or as a research objective to increase productive rates. In relation to common bionomic characteristics within the genus, the breeding discs in *Scaptotrigona* are constructed horizontally or helically, these supported by wax pillars (SOUZA et al., 2009). Both species have similar characteristics of behavior and productivity, as they are characteristics of the genus and this fact is related to the difficulty in identifying them (CAMARGO and PEDRO, 2013).

The variation in the number of breeding discs is due to the development of the colony, time of year and food supply (PEREIRA et al., 2019) and the amount corroborates the quantification of the population and development of the colony. The number of bees present in the colony is fundamental, because the more bees, the greater the number of field forages collecting resources, the better thermoregulation, and the greater the protection against invaders (BRITO et al., 2013; FREITAS et al., 2020a). Considering the animal science aspect, the better or more

controlled the factors mentioned above, the better the productive indices.

The behavior of stingless bees varies according to their population, which can be tens to thousands of individuals. Depending on age the workers perform different activities inside and outside the colony the so-called temporal polyethism (VEIRA et al., 2013; MATEUS et al., 2019).

CONCLUSION

In conclusion, meliponiculture plays an important role for economics, through pollination and conservation, and the information addressed in the review can be used to establish appropriate management, increase in productivity, deepening and understanding about bionomy and behavior of the species of zootechnical interest.

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REFERENCES

AIDAR, S.S. **A mandaçaia.** Riberião Preto: FUNCEP. 2a. ed. 2010. 162p.

AMEER, M.; SHWETHA, B.V.; ARUNKUMARA, C.G. Study on foraging behaviour of stingless bee, *Tetragonula iridipennis* Smith (Hymenoptera) at natural nesting site. **Insect Environment**, v.24, n.3, p.430-436, 2021.

BALLANTYNE, G.; BALDOCK, K.C.R.; RENDELL, L.; WILLMER, P.G. Pollinator importance networks illustrate the crucial value of bees in a highly speciose plant community. **Scientific Reports**, v.7, n.1, p.1-13, 2017.

BARBOSA-COSTA, K.; CARVALHO-ZILSE, G.A. **Processo de oviposição da abelha da Amazônia *Scaptotrigona xanthotricha* Moure, 1950.** In: CASTELLÓN BERMÚDEZ, E.G.; TELES, B.R.; KEPPLER, R.L.F. (Eds.). Entomologia na Amazônia Brasileira. Manaus: Instituto Nacional de Pesquisas da Amazônia, v.2, [s.n.], p.91-105, 2013.

BARBOSA, D.B.; CRUPINSKI, E.F.; SILVEIRA, R.N.; LIMBERGER, D.C.H. As abelhas e seu serviço ecossistêmico de polinização. **Revista Eletrônica Científica da UERGS**, v.3, n.4, p.694-703, 2017.

BARBOSA, A.B.S.; MENESES, H.M.; ROSA, F.L.; FREITAS, B.M. Flight activity of the stingless bee *Plebeia aff. flavocincta* in tropical conditions as indicator of the general health of the colony. **Sociobiology**, v.67, n.4, p.545-553, 2020.

BASARI, N.; RAMLI, S.N.; KHAIRI, N.A.S.M. Food reward and distance influence the foraging pattern of stingless bee, *Heterotrigona itama*. **Insects**, v.9, n.138, p.1-10, 2018.

BAUDIER, K.M.; OSTWALD, M.M.; GRÜTER, C.; SEGERS, F.H.I.D.; ROUBIK, D.W.; PAVLIC, T.P.; PRATT, S.C.; FEWELL, J.H. Changing of the guard: mixed specialization and flexibility in nest defense (*Tetragonisca angustula*). **Behavioral Ecology**, v.30, n.4, p.1041-1049, 2019.

BRASIL. Instituto Chico Mendes de Conservação da Biodiversidade. **Portaria Nº. 665, de 3 de novembro de 2021**. Available at: <https://in.gov.br/en/web/dou/-/portaria-n-665-de-3-de-novembro-de-2021-357715380>. Access in: 25 apr. 2022.

BREED, M.D.; GUZMÁN-NOVOA, E.; HUNT, G.J. Defensive behavior of *honeybees*: organization, genetics, and comparisons with other bees. **Annual Reviews of Entomology**, v.49, n.1, p.271-298, 2004.

BRITO, B.B.P.; FAQUINELLO, P.; PAULA-LEITE, M.C.; CARVALHO, C.A.L. Parâmetros biométricos e produtivos de colônias em gerações de *Melipona quadrifasciata anthidioides*. **Archivos de Zootecnia**, v.62, n.238, p.265-273, 2013.

CEARÁ. Lei Nº. 17.896, de 11 de janeiro de 2022. **Dispõe sobre a criação, o manejo, o comércio e o transporte de abelhas sem ferrão (meliponíneos) no estado do Ceará.** Diário Oficial do Estado. Série 3, Fortaleza, Ceará, ano 14, n.7, p.1-3, 2022.

CAMARGO, J.M.F.; PEDRO, S.R.M. **Meliponini Lepeletier, 1836.** 2013. In: MOURE, J.S.; URBAN, D.; MELO, G.A.R. (Eds.). Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region. Available at: <http://www.moure.cria.org.br/catalogue>. Access in: 25 nov. 2021.

CAVALCANTE, V.M.; OLIVEIRA, V.T.P.; CRUZ-LANDIM, C. Comparative study of wax glands in four Meliponini bees (Hymenoptera, Apidae) producing different quantities of wax. **Iheringia.** Série Zoologia, v.89, p.193-198, 2000.

CHOLE, H.; WOODARD, S.H.; BLOCH, G. Body size variation in bees: regulation, mechanisms, and relationship to social organization. **Current Opinion in Insect Science**, v.35, [s.n.], p.77-87, 2019.

CONAMA. CONSELHO NACIONAL DO MEIO AMBIENTE. **Resolução nº 496, de 19 de agosto de 2020.** Disciplina o uso e o manejo sustentáveis das abelhas-nativas-sem-ferrão em meliponicultura. Diário Oficial da União, 20 de agosto de 2020. Available at: <https://www.in.gov.br/en/web/dou/-/resolucao-n-496-de-19-de-agosto-de-2020-273217120>. Access in: 23 jan. 2022.

CORTOPASSI-LAURINO, M.; NOGUEIRA-NETO, P. **Abelhas sem ferrão do Brasil.** São Paulo: Edusp, 2016. 124p.

CRUZ-LANDIM, C. **Abelhas:** morfologia e função de sistemas. São Paulo: Ed. UNESP. 2009. 408p.

DRESCHER, N.; WALLACE, H.M.; KATOULI, M.; MASSARO, C.F.; LEONHARDT, S.D. Diversity matters: how bees benefit from different resin sources. **Oecologia**, v.176, n.4, p.943-953, 2014.

FAQUINELLO, P.; BRITO, B.B.P.; CARVALHO, C.A.L.; PAULA-LEITE, M.C.; ALVES, R.M.O. Correlação entre parâmetros biométricos e produtivos em colônias de *Melipona quadrifasciata anthidioides* Lepeletier (Hymenoptera: Apidae). **Ciência Animal Brasileira**, v.14, n.3, p.312-317, 2013.

FREITAS, B.M.; NUNES-SILVA, P. **Polinização Agrícola e sua Importância no Brasil.** In: IMPERARIZ-FONSECA, V.L.; CANHOS, D.A.L.; ALVES, D.A.; SARAIVA, A.M. (Eds.). Polinizadores no Brasil. São Paulo: Edusp. 2012, p.103-118.

FREITAS, P.V.D.X.; ZANATA, R.A.; SILVA, I.E..; FAQUINELLO, P.; SILVA-NETO, C.M. Feed supplementation in the diet of *Melipona rufiventris*. **Journal of Apicultural Research**, v.62, n.2, p.1-5, 2020a.

FREITAS, P.V.D.X.; SILVA, I.E.; FAQUINELLO, P.; ZANATA, R.A.; ARNHOLD, E.; E SILVA-NETO, C. M. External activity of the stingless bee *Melipona fasciculata* (Smith) kept in the Brazilian Cerrado. **Journal of Apicultural Research**, v.61, n.3, p.1-6, 2020b.

GRECO, M.K.; HOFFMANN, D.; DOLLIN, A.; DUNCAN, M.; SPOONER-HART, R.; NEUMANN, P. The alternative pharaoh approach: stingless bees mummify beetle parasites alive. **Naturwissenschaften**, v.97, n.3, p.319-323, 2010.

GRÜTER, C. **Stingless Bees:** their behavior, ecology and evolution. Bristol: Fascinating Life Sciences, 2020. 385p.

HALCROFT, M.; SPOONER-HART, R.; NEUMANN, P. Behavioral defense strategies of the stingless bee, *Austroplebeia australi*s, against the small hive beetle, *Aethina tumida*. **Insectes Sociaux**, v.58, [s.n.], p.245-253, 2011.

HARANO, K.; MAIA-SILVA, C.; HRNCIR, M. Why do stingless bees (*Melipona subnitida*) leave their nest with resin loads? **Insectes Sociaux**, v.67, n.1, p.195-200, 2020.

HUANG, S.; ZHANG, C.P.; WANG, K.; LI, G.Q.; HU, F.L. Recent advances in the chemical composition of propolis. **Molecules**, v.19, n.12, p.19610-19632, 2014.

IAP. INSTITUO AMBIENTAL DO PARANÁ. 2019. **Portaria IAP Nº 006, de 17 de janeiro de 2019.** Available at: <http://celepar7.pr.gov.br/sia/atosnormativos/form_cons_ato1.asp?Codigo=4083> Access in: 10 jan. 2022.

JAFFÉ, R.; POPE, N.; CARVALHO, A.T.; MAIA, U.M.; BLOCHTEIN, B.; CARVALHO, C.A.L.; CARVALHO-ZILSE, G.A.; FREITAS, B.M.; MENEZES, C.; RIBEIRO, M.F.; VENTURIERI, G.C.; IMPERATRIZ-FONSECA, V.L. Bees for development: Brazilian survey reveals how to optimize stingless beekeeping. **PloS One**, v.10, n.3, p.1-21, 2015.

JONES, R. **Stingless bees:** a historical perspective. In: VIT, P.; PEDRO, S.R.M.; ROUBIK, D.W. (Eds.). Pot-honey: a legacy of stingless bees. New York: Springer Science & Business Media, 2013, p.219-227.

JUNGNICKEL, H.; COSTA, A.J.S.; TENTSCHERT, J.; PATRICIO, E.F.L.R.A.; IMPERATRIZ-FONSECA, V.L.; DRIJFHOUT, F.; MORGAN, E.D. Chemical basis for inter-colonial aggression in the stingless bee *Scaptotrigona bipunctata* (Hymenoptera: Apidae). **Journal of Insect Physiology**, v.50, n.8, p.761-766, 2004.

KERR, W.E. Genetic determination of castes in the genus Melipona. **Genetics**, v.35, n.2, p.143-152, 1950.

KLEIN, A.M.; FREITAS, B.M.; BOMFIM, I.G.A.; BOREUX, V.; FORNOFF, F.; OLIVEIRA, M.O. **Insect pollination of crops in Brazil:** a guide for farmers, gardeners, politicians and conservationists. Nature Conservation and Landscape Ecology. Freiburg: Albert-Ludwigs University Freiburg. 2020.

KOEDAM, D. **Ninhos e a biologia geral:** comparando as abelhas africanizadas e as abelhas sem ferrão. In: FONSECA, V.L.I.; KOEDAM, D; HRNCIR, M. (Eds.). A abelha Jandaíra: no passado, presente e no futuro. Mossoró: EduFERSA, p.27-39, 2017.

LAVINAS, F.C.; MACEDO, E.H.B.C.; SÁ, G.B.L.; AMARAL, A.C.F.; SILVA, J.R.A.; AZEVEDO, M.M.B.; VIEIRA, B.A.; DOMINGOS, T.F.S.; VERMELHO, A.B.; CARNEIRO, C.S.; RODRIGUES, I.A. Brazilian stingless bee propolis and geopropolis: promising sources of biologically active compounds. **Revista Brasileira de Farmacognosia**, v.29, [s.n.], p.389-399, 2019.

LAYEK, U.; KARMAKAR, P. Nesting characteristics, floral resources, and foraging activity of *Trigona iridipennis Smith* in Bankura district of west Bengal, India. **Insectes Sociaux**, v.65, [s.n.], p.117-132, 2018.

LAYEK, U.; BISUI, S.; KARMAKAR, P. Flight range and resource loading-unloading behavior of stingless bee *Tetragonula iridipennis* (Smith). **Journal of Apicultural Research**, [s.v.], [s.n.], p.1-12, 2021.

LEONHARDT, S.D.; BAUMANN, A.M.; WALLACE, H.M.; BROOKS, P.; SCHMITT, T. The chemistry of an unusual seed dispersal mutualism: bees use a complex set of olfactory cues to find their partner. **Animal Behaviour**, v.98, [s.n.], p.41-51, 2014.

LEONHARDT, S. Chemical ecology of stingless bees. **Journal of Chemical Ecology**, v.43, [s.n.], p.385-402, 2017.

LI, Y.R.; WANG, Z.W.; YU, Z.R.; CORLETT, R.T. Species diversity, morphometrics, and nesting biology of Chinese stingless bees (Hymenoptera, Apidae, Meliponini). **Apidologie**, v.52, [s.n.], p.1239-1255, 2021.

MARTINS, A.C.; MELO, G.A.R.; RENNER, S.S. The corbiculate bees arose from new world oil-collecting bees: Implications for the origin of pollen baskets. **Molecular Phylogenetics and Evolution**, v.80, [s.n.], p.88-94, 2014.

MASSARO, F.C.; BROOKS, P.R.; WALLACE, H.M.; RUSSELL, F.D. Cerumen of Australian stingless bees *(Tetragonula carbonaria)*: gas chromatography-mass spectrometry fingerprints and potential anti-inflammatory properties. **Naturwissenschaften**, v.98, [s.n.], p.329-337, 2011.

MATEUS, S.; FERREIRA-CALIMAN, M.J.; MENEZES, C.; GRÜTER, C. Beyond temporal-polyethism: division of labor in the eusocial bee *Melipona marginata*. **Insectes Sociaux**, v.66, [s.n.], p.317-328, 2019.

MENEZES, C.; VOLLET-NETO, A.; FONSECA, V.L.I. An advance in the in vitro rearing of stingless bee queens. **Apidologie**, v.44, [s.n.], p.491-500, 2013.

MICHENER, C.D. Comparative social behavior of bees. **Annual Review of Entomology**, v.14, n.1, p.299-342, 1969.

MICHENER, C.D. **The meliponini.** In: VIT, P.; PEDRO, S.R.M.; ROUBIK, D.W. (Eds.). Pot-honey: a legacy of stingless bees. New York: Springer Science & Business Media, 2013, p.3-17.

MOHAMMAD, S.M.; MAHMUD-AB-RASHID, N.K.; ZAWAWI, N. Botanical origin and nutritional values of bee bread of stingless bee *(Heterotrigona itama)* from Malaysia. **Journal of Food Quality**, v.2020, [s.n.], p.1-12, 2020.

MOURA, M.E.K.; FAITA, M.R.; AMANDIO, D.T.T.; BERTOLDO, J.G.; LIMA, V.P.; POLTRONIERI, A.S. Influence of some abiotic factors on the flight activity of stingless bees (Hymenoptera: Meliponini) in Southern Brazil. **Journal of Apicultural Research**, [s.v.], [s.n.], p.1-7, 2022.

NEOV, B.; GEORGIEVA, A.; SHUMKOVA, R.; RADOSLAVOV, G.; HRISTOV, P. Biotic and abiotic factors associated with colonies mortalities of managed honey bee (*Apis mellifera*). **Diversity**, v.11, n.237, p.1-16, 2019.

NUNES, T.M.; VON ZUBEN, L.G.; COSTA, L.; VENTURIERI, G.C. Defensive repertoire of the stingless bee *Melipona flavolineata Friese* (Hymenoptera: Apidae). **Sociobiology**, v.61, n.4, p.541-546, 2014.

OLIVEIRA, F.F.; RICHERS, B.T.T.; SILVA, J.R.D.; FARIAS, R.C.; MATOS, T.A.D.L. **Guia ilustrado das abelhas "sem ferrão" das Reservas Amanã e Mamirauá, Amazonas, Brasil (Hymenoptera, Apidae, Meliponini)**. 2013. IDSM. 267p.

PARANÁ. Lei N° 19.152, de 3 de outubro de 2017. **Dispõe sobre a criação, o manejo, o comércio e o transporte de abelhas sociais nativas (meliponíneos).** Assembleia Legislativa do Estado do Paraná, n.10041, p.1-5, 2017.

PEDRO, S.R. The stingless bee fauna in Brazil (Hymenoptera: Apidae). **Sociobiology**, v.61, n.4, p.348-354, 2014.

PEREIRA, F.M.; MEIRELLES, R.N.; MORAES, J.I.S.; PEREIRA, L.A.; SOUZA, B.A.; LOPES, M.T.R. Contribuição ao conhecimento da bionomia de abelha tiúba, *Melipona fasciculata*. **Sociedade Brasileira de Recursos Genéticos**, v.5, n.1, p.23-28, 2019.

POPOVA, M.; TRUSHEVA, B.; BANKOVA, V. Propolis of stingless bees: A phytochemist's guide through the jungle of tropical biodiversity. **Phytomedicine**, v.86, [s.n.], p.1-52, 2021.

QUEIROZ, A.C.M.; LEÃO, K.L.; CONTRERA, F.A.L.; TEIXEIRA J.C.; MENEZES, C. Stingless bees fed on fermented soybean-extract-based diet had reduced lifespan than pollen-fed workers. **Sociobiology**, v.66, n.1, p.107-112, 2019.

RASMUSSEN, C. Stingless bees (Hymenoptera: Apidae: Meliponini) of the Indian subcontinent: Diversity, taxonomy and current status of knowledge. **Zootaxa**, v.3647, n.3, p.401-428, 2013.

REYES-GONZÁLEZ, A.; CAMOU-GUERRERO, A.; DEL-VAL, E.; RAMÍREZ, M.I.; PORTER-BOLLAND, L. Biocultural diversity loss: the decline of native stingless bees (Apidae: Meliponini) and local ecological knowledge in Michoacán, Western México. **Human Ecology**, v.48, [s.n.], p.411-422, 2020.

RODRIGUES, A.M.M.; GARDNER, A. Reproductive value and the evolution of altruism. **Trends in Ecology & Evolution** v.37, n.4, p.1-13, 2021.

ROLDÃO-SBORDONI, Y.S.; NASCIMENTO, F.S.; MATEUS, S. Estimating colonies of *Plebeia droryana* (Friese, 1900) (Hymenoptera, Apidae, Meliponini): adults, brood and nest structure. **Sociobiology**, v.65, n.2, p.280-284, 2018.

SÁNCHEZ, D.; VANDAME, R. **Stingless bee food location communication:** from the flowers to the honey pots. In: VIT, P.; PEDRO, S.R.M.; ROUBIK, D.W. (Eds.). Pot-honey: a legacy of stingless bees. New York: Springer Science & Business Media, 2013, p.187-199.

SANTOS, T.C.A.; CRUZ-LANDIM, C. Determinação das castas em *Scaptotrigona postica* (Latreille) (Hymenoptera, Apidae, Meliponini): diferenciação do ovário. **Revista Brasileira de Zoologia**, v.19, n.3, p.703-714, 2002.

SEBRAE. **Potencialidades da meliponicultura:** criação de abelhas nativas. 2015. Available at: <https://www.sebrae.com.br/sites/PortalSebrae/artigos/potencialidades-da-meliponicultura-criacao-de-abelhas-nativas,36267383f9cbe410VgnVCM1000003b74010aRCRD>. Access in: 20 oct. 2021.

SEREIA, M.J.; SEREIA, A.L.; PARPINELLI, R.S.; LIMA, E.G.; SANTOS, A.R.; ANJO, F.A.; SILVA JÚNIOR, C.G.; TOLEDO, V.A.A. Freeze and spray drying of *Scaptotrigona bipunctata* (Lepeletier, 1836) pollen-development and physicochemical characterization. **African Journal of Food Science**, v.12, n.12, p.367-373, 2018.

SHANAHAN, M.; SPIVAK, M. Resin use by stingless bees: a review. **Insects**, v.12, n.8, p.1-20, 2021.

SILVA, G.R.; PEREIRA, F.M.; SOUZA, B.A.; LOPES, M.T.R.; CAMPELO, J.E.G.; DINIZ, F.M. Aspectos bioecológicos e genético-comportamentais envolvidos na conservação da abelha Jandaíra, *Melipona subnitida* Ducke (Apidae, Meliponini) e o uso de ferramentas moleculares nos estudos de diversidade. **Agricultural Entomology**, v.81, n.3, p.299-308, 2014.

SILVA, M.G.; DANTAS, M.C.A.M.; MOREIRA, J.N.; PEREIRA JUNIOR, E.B.; OLIVEIRA NETO, J.N.; MEDEIROS, A.C.; GADELHA, H.S. Criação racional de abelhas Jandaíra e sua importância ambiental. **Revista Brasileira de Gestão Ambiental**, v.13, n.1, p.13-18, 2019.

SILVA, W.P.; PAZ, J.R.L. Abelhas sem ferrão: muito mais do que uma importância econômica. **Natureza on line**, v.10, n.3, p.146-152, 2012.

SOUZA, B.A.; ALVES, R.M.O.; CARVALHO, C.A.L. Nest architecture diagnosis of *Oxytrigona tataira* (Smith, 1863) (Hymenoptera: Meliponinae). **Biota Neotropica**, v.7, n.2, p.83-86, 2007.

SOUZA, B.A.; CARVALHO, C.A.L.; ALVES, R.M.O. Notas sobre a bionomia de *Melipona asilvai* (Apidae: Meliponini) como subsídio à sua criação racional. **Archivos de Zootecnia**, v.57, n.217, p.53-62, 2008.

SOUZA, B.A.; CARVALHO, C.A.L.; ALVES, R.M.O.; DIAS, C.S.; CLARTON, L. Munduri (*Melipona asilvai*): a abelha sestrosa. **Embrapa Meio-Norte-Livro técnico (INFOTECA-E)**, v.1, [s.n.], p.1-46, 2009.

TRINKL, M.; KALUZA, B.F.; WALLACE, H.; HEARD, T.A.; KELLER, A.; LEONHARDT, S.D. Floral species richness correlates with changes in the nutritional quality of larval diets in a stingless bee. **Insects**, v.11, n.2, p.1-19, 2020.

TUKSITHA, L.; CHEN, Y.L.S.; CHEN, Y.L.; WONG, K.Y.; PENG, C.C. Antioxidant and antibacterial capacity of stingless bee honey from Borneo (Sarawak). **Journal of Asia-Pacific Entomology**, v.21, n.2, p.563-570, 2018.

VENTURIERI, G.C.; VOLLET-NETO, A.; VILLAS-BÔAS, J.K.; CARVALHO, C.A.L.; MENEZES, C.; IMPERATRIZ-FONSECA, V.L. **Meliponicultura no Brasil:** situação atual e perspectivas futuras para o uso na polinização agrícola. In: IMPERATRIZ-FONSECA, V.L.; CANHOS, D.A.L.; ALVES, D.A.; SARAIVA, A.M. (Eds.). Polinizadores no Brasil. São Paulo: Edusp. 2012, p.213-236.

VOLLET-NETO, A.; KOFFLER, S.; SANTOS, C.F.; MENEZES, C.; NUNES, F.M.F.; HARTFELDER, K.; IMPERATRIZ-FONSECA, V.L.; ALVES, D.A. Recent advances in reproductive biology of stingless bees. **Insectes Sociaux**, v.65, n.2, p.201-212, 2018.

WANG, S.; WITTWER, B.; HEARD, T.A.; GOODGER, J.Q.; ELGAR, M.A. Nonvolatile chemicals provide a nest defense mechanism for stingless bees *Tetragonula carbonaria* (Apidae, Meliponini). **Ethology**, v.124, n.9, p.633-640, 2018.

ZULHENDRI, F.; PERERA, C.O.; CHANDRASEKARAN, K.; GHOSH, A.; TANDEAN, S.; ABDULAH, R.; LESMANA, R. Propolis of stingless bees for the development of novel functional food and nutraceutical ingredients: A systematic scoping review of the experimental evidence. **Journal of Functional Foods**, v.88, [s.n.], p.1-20, 2022.