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NAME OF SUPERVISOR/*NOM DU DIRECTEUR DE THÈSE* Dr. J.H. Borden

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THE BIONOMICS, ECONOMICS AND PEST MANAGEMENT OF NEOTROPICAL STINGLESS BEES (APIDAE, MELIPONINI)

by

John Frank Henigman

B.Sc. Simon Fraser University, 1971

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Name: John Frank Henigman

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Examining Committee:

Chairman:

Dr. J. H. Borden
Senior Supervisor

Professor T. Finlayson

Dr. P. Belton

Dr. J. S. Barlow
External Examiner

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Author:

(signature)

John Frank Henigman

(name)

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(date)

ABSTRACT

The literature and the author's research on stingless bees, tribe Meliponini (Hymenoptera: Apidae: Meliponinae) is reviewed. Included are aspects of the bionomics: morphology and taxonomy, nest architecture and social life; the economic importance: economic benefits and economic damage to tropical crops including banana, citrus, eucalyptus and macadamia nut trees; and practical pest control methods: locating nests and destroying them, treating affected crops with insecticides, attractants and repellents, biological controls and physical controls. A summary is presented of a successful project to control 2 meliponinid species, *Trigona (Trigona) corvina* Cockerell and *T. (Trigona) silvestriana* Vachal damaging *Macadamia* tree species in Costa Rica.

Stingless bees are both important pollinators and pests. Thus, pest control must be species-specific. Spraying insecticides on affected crops, the commonly used method, is not recommended because of the lack of specificity and resulting insecticide residue pollution. Two methods: finding and destroying all offending nests, or attracting foraging bees with a pheromone or attractive forage material and then killing them or allowing them to poison their colony with sublethal doses of insecticide are preferred. The author recommends that before tropical jungle areas are cleared for agriculture or large pest control projects are undertaken against bee pests, a host plant survey of the bees be made to appraise their significance as pollinators or pests to crops and wild plants. In addition, the population dynamics of the bees should be studied to determine the probable effect of manipulating their populations.

ACKNOWLEDGEMENTS

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INTRODUCTION

Stingless bees of the tribe Meliponini are a little studied group of social insects. They exist only in the tropics, especially in South and Central America. In the past, some species of stingless bees have been kept as domestic honey and wax producers. This practice has generally disappeared. As tropical agriculture has been intensified in recent years, these bees have increased in importance as pollinators and as pests. The bees damage crops such as banana, citrus, eucalyptus and macadamia, which only within the last 20 years have become of economic interest to many tropical countries.

Throughout most of Central America (excluding Mexico), agriculture is the major economic industry (Lombardo 1969, Ruddle and Odermann 1971). Coffee and bananas constitute 66% of the total exports. Over the last 20 years most of the countries involved have tried to diversify their export crops to provide a broader economic base. Some of the crops introduced have been cotton, citrus, macadamia, and eucalyptus. Productivity is increasing yearly (Ruddle and Odermann 1971). In 1971, Latin America produced 24% of the world's oranges and tangerines and 66% of the bananas. Planting techniques, fertilizing or lack of storage facilities have been common problems for these crops. Many of these introduced crops have failed because of insect infestation or disease, e.g. cotton in Guatemala (Lombardo 1969). As crops such as banana, citrus, macadamia and eucalyptus become more important to tropical areas like Central America, stingless bee pests will become more of a problem, particularly since there is little information on their control.

This paper is a review of published literature on the bionomics, economics, pest damage and control of stingless bees in Latin America. Included are my own observations on the bionomics and economics. A summary of my work to develop practical methods of control for bees damaging macadamia and citrus trees in Costa Rica is presented. A glossary of terms specific to stingless bees and pest management is given in Appendix 1.

BIONOMICS OF STINGLESS BEES

Morphology and Taxonomy

The Family Apidae includes several subfamilies, 2 of which are the Meliponinae including the Tribe Meliponini, and the Apininae which contains the Tribe Apini. All species of Apidae are highly evolved social insects, which store honey, and produce and build with wax, and have a complex social order including a reproductive and a worker caste. The Meliponini, have many unique morphological adaptations, the most striking of which is their vestigial sting. They are in a practical sense, stingless.

The Meliponini are easily differentiated from other bees by the transverse cubital veins of the wings which are vestigial. Schwarz (1948) and Michener (1944) list other characteristics: jugal lobe of the posterior wing present; marginal cell open (or its vein weak) distally, tapering from the base; pterostigma of moderate to large size, extending well beyond base of radial vein; posterior hind tibiae without apical spur; tarsal claws of female simple; labrum 3 to 4 times as broad as long; eyes sparsely hairy in some queens; sting reduced. Wax is secreted by males as well as workers (Moure, Nogeira-Neto and Kerr 1958).

The two major genera of the Meliponini are *Trigona* and *Melipona;* a third recently included genus, *Meliponula,* is of some importance in determining the evolutionary relationships between *Melipona* and *Trigona* but is unimportant economically. Other genera, such as *Lestrimelitta* and *Dactylurina* are occasionally also included. These genera can be considered closely related to *Trigona* (Wille 1963), and will not be considered in detail in this project.

The morphological differences between worker *Trigona* and *Melipona* are presented in Table 1. For ease in recognition, *Trigona* are small with wings extending past the abdominal apex whereas *Melipona* are large with wings not extending past the abdominal apex. *Meliponula* possess characteristics of both *Trigona* and *Melipona* (Wille 1963). They are large and robust, with wings extending past the abdominal apex. In comparison with the Meliponini, *Apis mellifera* L., is large, (length: 12 mm), and robust with wings not extending past the abdominal apex.

There are approximately 200 species of Meliponini, 11 of which are of significant economic importance: *Trigona (Trigona) corvina* Cockerell, *T. (Partamona) cupria* Smith, *T. (Trigona) ferricauda* Cockerell, *T. (Trigona) fuscipennis* Guerin, *T. (Trigona) hyalinata* (Lepeletier), *T. (Trigona) nigerrima* Cresson, *T. (Partamona) testacea* Cockerell, *T. (Trigona) ruficrus* (Latreille), *T. (Trigona) silvestriana* Vachal, *T. (Trigona) trinidadensis* (Provander), *Melipona beecheii* Bennett. Some species of the subgenus *Oxytrigona* may be economically important in some cases.

Nests

The hives or nests of many social insects can often be used to identify the species that built them. Such structures as the brood combs, the entrance tube or the food storage area commonly are unique for each species. Nest structure often follows an evolutionary trend. Such a trend is evident in Meliponini despite enormous variation in nest construction.

Table 1. Morphological characteristics differentiating the genera *Trigona* and *Melipona* (from Schwarz 1948, Wille 1963).

Character	*Trigona*	*Melipona*
Size	2 to 8 mm in length and slender	8 to 15 mm in length and robust
Pubescence	usually short and sparse	upper half of head and thorax densely hairy, hairs long
Basal area of Propodeum	usually glabrous, but sometimes tessellate and pubescent	tessellate and entirely pubescent
Length of Wings	usually long and extending well beyond apex of abdomen	relatively short and not or slightly surpassing tip of abdomen
Submarginal angle of first r cell	variable	distinctly acute
Hamuli	usually from 5 to 8	usually from 9 to 16
Shape of Hind Tibia	variable	normal without any type of depression
Nervous System	abdominal ganglion 3 located in metathoracic segment	abdominal ganglion 3 located in thorax
Dorsal Circulatory System	thoracic portion straight	thoracic portion making an arch between longitudinal muscles of thorax

Nesting sites

Some meliponinid subterranean nests have truly primitive brood combs. However, other more advanced species have apparently readopted a ground nesting habit retaining a more sophisticated brood comb structure (Fig. 1). None of the soil-nesting species actually excavate their own nesting sites. Therefore associations are common between some meliponinid species and other ground nesting insects such as ants. Usually, the ants are leaf cutters of the genus *Atta*. The bees may often occupy deserted ant nests. However *T. (Paratrigona) lineata* var. *nuda* (Lepeletier) has been found nesting in coexistence with *Atta sexdens* Buckley (Schwarz 1948). This relationship is not well understood, but is of interest because leaf cutter ants are usually predators of stingless bees.

Since none of the ground-nesting stingless bees are economically important, no detailed description of their nests will be given. Descriptions can be found in Schwarz (1948), Wille (1966b) and Moure *et al.* (1958). Much of the general description on nest architecture is applicable to all species of ground nesting meliponinids.

The vast majority of meliponinid species nest in hollows of trees, logs or in rock or wall cavities, these nests are described by Schwarz (1948), Moure *et al.* (1958), and Wilson (1971) (Fig. 2). There is great variation between these nests, even within the same species, because each cavity is differently shaped. Unlike the subterranean species these bees usually build more sophisticated nest walls, or batumens, to protect their brood combs. Generally, bees nesting in tree trunks are physiologically more capable of resisting temperature extremes.

Fig. 1 A subterranean stingless bee nest (redrawn from Wille 1966b).

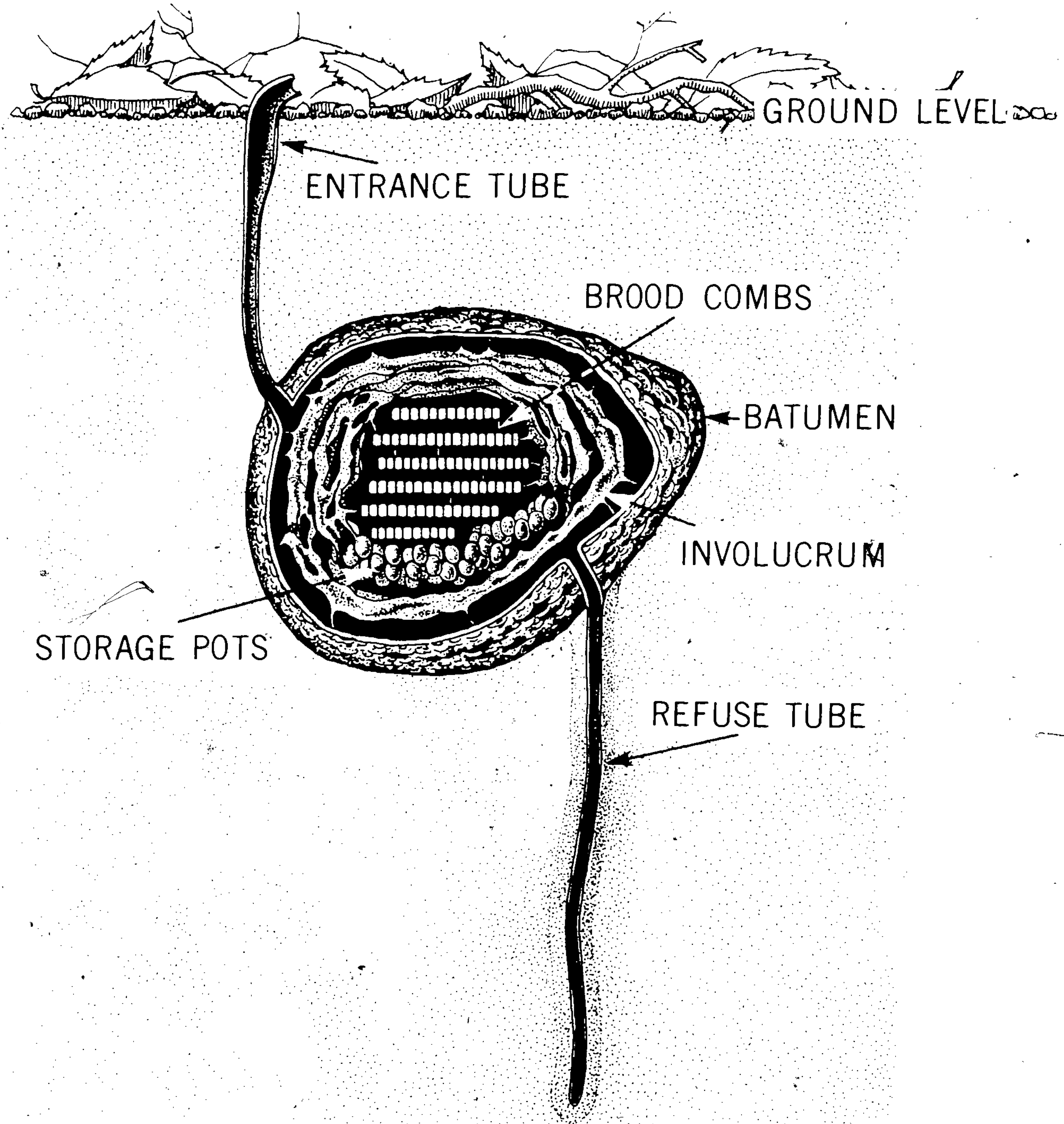
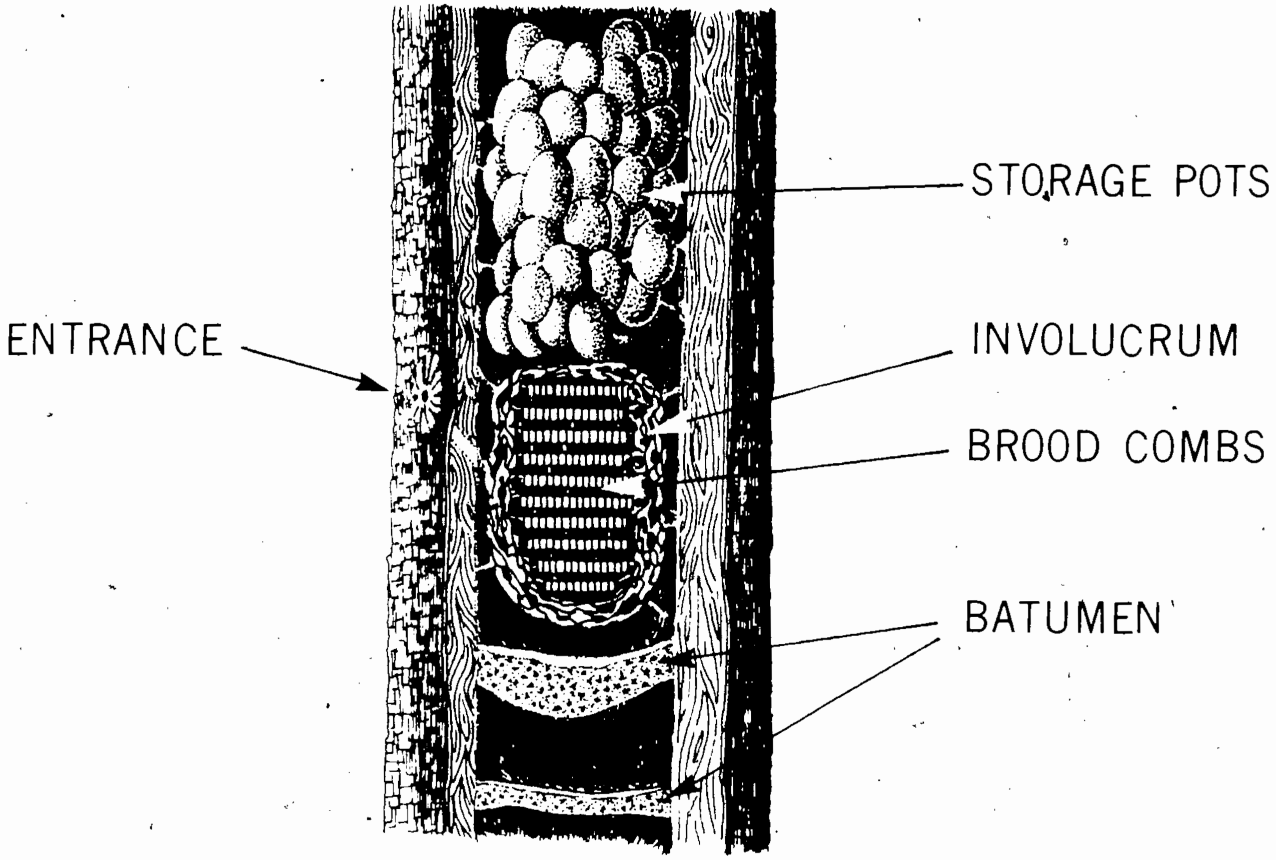

GROUND LEVEL
ENTRANCE TUBE
BROOD COMBS
BATUMEN
INVOLUCRUM
STORAGE POTS
REFUSE TUBE

Fig. 2 A stingless bee nest found in a hollow tree (redrawn from Wilson 1971).


STORAGE POTS
ENTRANCE
INVOLUCRUM
BROOD COMBS
BATUMEN

Though there are differences in construction, the basic arrangement is the same. Batumen walls section off the nest from above and below. There are brood combs centered within the cavity. Storage containers or pots for honey and pollen normally are placed above the brood combs. There is one entrance, usually located midway in the cavity. Many species also build a thin paper wall called an involucrum around the brood combs. The extent to which the involucrum covers the brood combs is often used as a taxonomic feature.

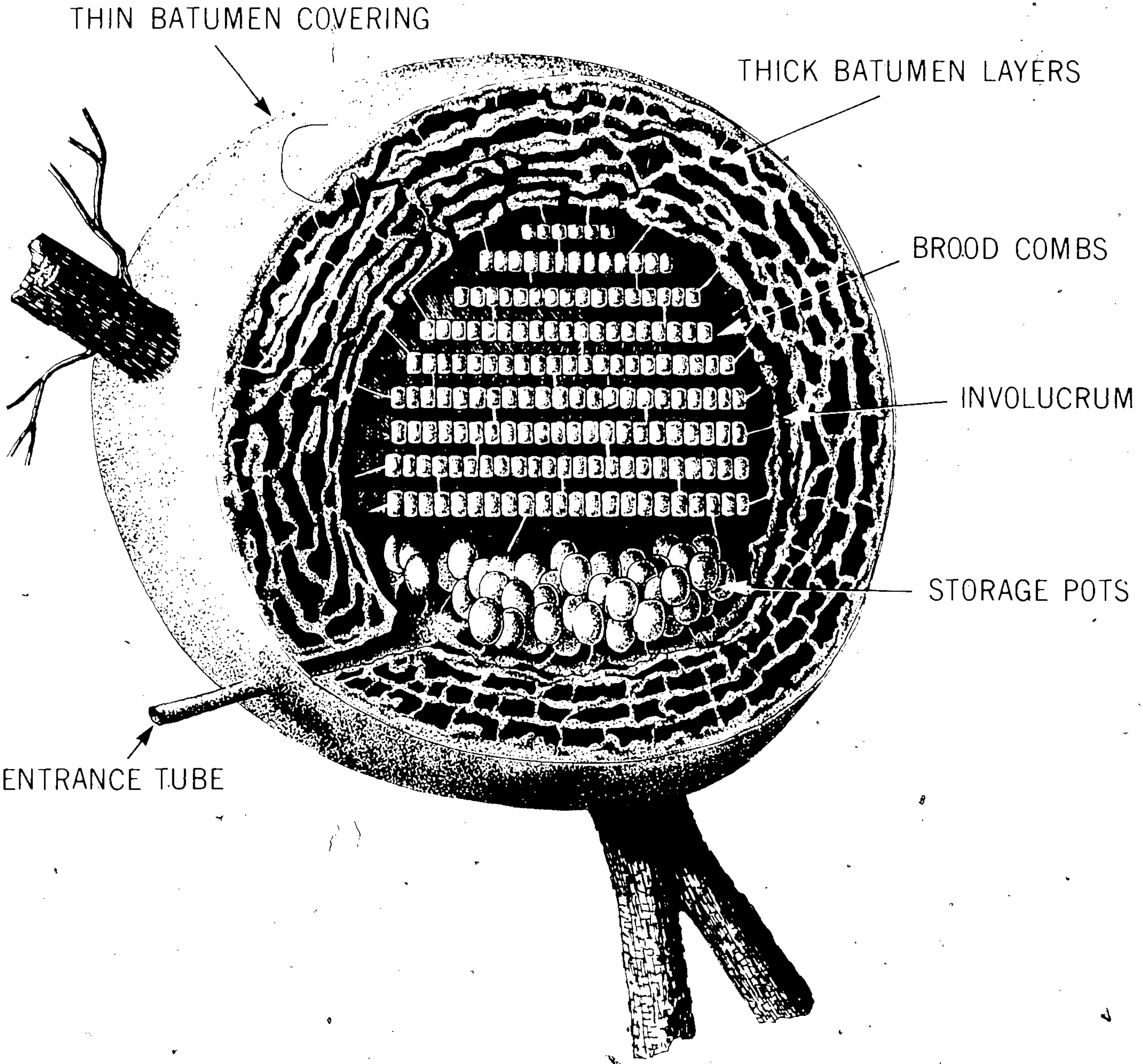
There is no apparent preference for nesting sites in different tree species. However, the cavity size is of importance, and corresponds to the nest size characteristics of each species.

The nest of wild *A. mellifera* (Wilson 1971) is normally also found in the cavity of a hollow tree and is relatively simple. The major components are vertically hanging combs which have cells on both sides, quite different from meliponinid nests in which the combs are, with one exception, always horizontal and have cells only on the upper surface. Usually horizontal supports are built to hang the combs from. There are no storage pots, all honey and pollen is stored in the comb. There are no batumens, walls are erected only to seal unwanted entrances to the nest, the combs are not covered with an involucrum and there is only one entrance hole.

Among the many species of Meliponini nesting in tree trunks, only *M. beecheii* is economically important.

The exposed, aerial nest is considered the most highly evolved form in the Meliponini (Fig. 3). All *Trigona* species of economic importance have aerial nests. Species building such nests must be

Fig. 3 An aerial stingless bee nest similar to that of *T. corvina*.


THIN BATUMEN COVERING
THICK BATUMEN LAYERS
BROOD COMBS
INVOLUCRUM
STORAGE POTS
ENTRANCE TUBE

capable of withstanding temperature extremes, but benefit in that there is no limitation of nesting sites. Any large tree can support one or more nests (Wille 1966a). These bees face greater problems in defending against predators because of their exposed nests.

There are only 25 known aerial nesting species in Central America (Wille 1966a). The most common type of nest is a fully exposed ball shape which encircles a branch, as in the nest of *T. corvina*. The other type, represented by the nest of *T. silvestriana*, is wrapped, as a thick band, around the trunk of a large tree. Commonly, it surrounds a crotch or a depression in the tree.

The aerial nest contains all of the structures common to other stingless bee nests. The brood combs are found in the center, surrounded by an involucrum. Above or below the combs are storage pots. Batumen fully surrounds the nest, usually making a very hard thick husk. In the case of the band nest wrapped around a tree, the batumen covers only the exposed surfaces. The entrance tube is usually near the bottom and extends as a tunnel to the brood combs.

Architecture

In this section the general nest components and their variations in meliponinid nests are described with examples.

The brood combs of the nest are the most important and complex structure. All of the comb is used for brood rearing; honey and pollen are stored elsewhere. The brood combs are always in the center of the nest, and are always on a horizontal plane (Moure *et al.* 1958). There are 3 basic comb arrangements: horizontal discrete layers, a single spiral, and a cluster arrangement in which discrete groups of brood cells are arranged as horizontal discs placed randomly in the brood chamber. The brood cells are only on the upper surface of the comb. The most common cell shape is cylindrical, but it tends towards hexagonal in some of the spiral combs and towards spherical in the cluster combs.

One exceptional African meliponinid, *Dactylurina standingeri* Smith, builds cells and combs like those of honeybees which hang vertically as discrete layers with both sides of the combs containing hexagonal cells. *D. standingeri* is considered to be closely related to bees in the genus *Trigona* (Moure *et al.* 1958).

The size and number of comb layers in a nest varies greatly from species to species. *T. (Tetragona) buchwaldi* Friese, a ground nesting Costa Rican species has a brood chamber measuring 7 to 9 cm in diameter with about 10 discrete comb layers (Wille 1966b). *T. (Tetragona) carbonaria* Smith, a hollow trunk dweller in Australia, has a brood chamber measuring 10 to 16 cm in diameter with a spiral brood comb forming about 10 layers (Michener 1961). *T. corvina,* an aerial nester of Costa Rica, has a brood chamber measuring 5 to 15 cm with between 10 and 30 spiralling comb layers (Table 2) (J.F. Henigman, unpublished data). Measurements of many Australian *Trigona* nests are given by Michener (1961), and Schwarz (1948) has recorded some nest dimension statistics. There is no obvious evolutionary trend consistent with these measurements.

Table 2. Dimensions of 3 *T. corvina* nests[a] measured at Turrialba, Costa Rica, in 1972.

Measurements	Nest 1	Nest 2	Nest 3
Age of nest	5 years	2 years	2 years
Volume	55,000 cc	24,000 cc	18,800 cc
Volume of Comb	28,800 cc	7,300 cc	2,100 cc
Total weight of Nest	20.6 Kg	0.35 Kg	0.57 Kg
Comb weight as a % of total weight	10%	6%	13%
Pollen and Honey weight	5.5 Kg[b]	little	little
Number of Bees	5,400	2,000	2,000
Number of larval Cells	33,000	2,300	1,273

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[a] Colonies were killed with aldrin dust and then the nest dissected.

[b] The pollen to honey ratio was estimated to be approximately 9:1.

The surface areas of the comb layers are largest in the middle of the brood chamber and smaller above and below because of the spherical nature of the chamber. Many of the comb layers are only partially built at any one time and thus are smaller than their full diameter. They are supported and attached to each other by small vertical pillars, 2.5 to 3 mm long and 0.5 to 1.0 mm in diameter (Michener 1961). All of the comb layers contain holes which serve as passage ways from one comb layer to the next.

The brood cell size varies with each species. Generally they are from 2.5 to 3.5 mm in diameter and from 4 to 7 mm deep (Michener 1946, 1961). By comparison, the brood cells of *A. mellifera* are 6 mm by 7 mm (Imms 1964). As in *A. mellifera* some brood cells of *Trigona* species are relatively large and are used for the development of queens and males. In the genus *Melipona*, there is no size difference between castes, and all brood cells are of equal size (Schwarz 1948, Wille 1963). The number of brood cells in the combs varies enormously between and within species. Normally, however, the number is extremely large relative to the number of adults in the nest (Table 2). In a nest of approximately 7,000 adult *T. corvina* there were 82,000 brood cells (Michener 1946).

The brood combs and pillars and several other parts of the nest are made of a dark brown to black wax mixture. It is a mixture of approximately 50% beeswax and 50% propolis, a mixture of resin and plant wax. The exact mixture varies with the species. In contrast, the honeybee constructs its nest using only pure beeswax.

Surrounding the brood chamber, in most species of Meliponini, is an involucrum made of cerumen. The involucrum probably acts to maintain a constant temperature within the brood chamber (Moure *et al.* 1958). In species which build nests, the involucrum normally is thick, brittle and completely surrounds the brood chamber. In species nesting in well protected places, the involucrum is thin, soft and often does not completely cover the brood chamber (Moure *et al.* 1958). Species having cluster brood combs usually do not have an involucrum. The involucrum in *Trigona* species usually has 10 or more concentric layers, and in *Melipona* species has only 2 or 3 concentric layers (Schwarz 1948).

The food storage area of the nest is either outside or inside the involucrum depending on the species. In this area are up to 200 storage pots made of soft cerum which contain either pollen or honey. They are usually spherical or ellipsoid with a capacity of between 30 and 40 cc varying with the species. They are usually concentrated above or below the brood chamber, and are anchored by cerumen pillars to each other and to the outer walls of the nest.

The outer walls of the nest are called batumen. In *Trigona,* batumen is made with propolis or with cerumen containing only a small amount of beeswax, whereas in *Melipona,* it is made of mud (Wille 1963). The extent of the batumen surrounding the nest varies with the nesting site. Hollow tree trunk nests usually have quite thick batumen layers above and below the nest, sectioning off the cavity. Covering the cavity walls is a very thin layer of cerumen batumen. Subterranean nests usually have 3 to 5 mm thick propolis batumen completely surrounding the nest. Propolis batumen is normally brittle and water resistant. The batumen covering is most developed in aerial nests. *T. corvina* and

T. silvestriana do not have entrance tubes; however, fine strings of propolis hang down around the entrance hole appearing like a beard. The entrance tube extends inside through the batumen layers into the brood chamber. Normally the entrance hole is just large enough to allow the passage of one bee at a time.

Building techniques

Once a nest has been built the only structures which are continually rebuilt are the brood combs. All other parts are carefully maintained.

In all the Meliponini, once a brood cell has been used it is dismantled and the reclaimed cerumen is used to form new cells. There are 2 directions of growth of the brood combs. A brood comb layer is built from the center out laterally, with eggs being deposited in completed cells as the building progresses. As a comb layer is completed laterally, a new comb layer is started above it. Once the uppermost layer is completed, construction will begin again at the lowest level (Michener 1961).

There is no good documentation of the building techniques involved in the construction of the batumen, storage pots or the entrance tube. However, many authors indicate that these structures, if damaged, are very quickly repaired (Salt 1929, Schwarz 1948, Michener 1961). In the case of *T. corvina*, the batumen layers are very extensive and must consume much time and energy in construction. Although the building sequence is unknown, I suggest that it is a continuous process. *T. corvina* uses leaf mulch as part of the building material of the batumen. Established nests have a very thick batumen, but I have observed that bees of those nests were still actively foraging for leaves.

Social Life

In this section an overview of the colonial life of the Meliponini is presented. The social life of only a few species of the tribe has been intensively described, however many general phenomena apparently apply to all species. Generally stingless bees have a social organization similar to *Apis* species. The important differences between Apini and Meliponini are dealt with in detail. Where possible the social life of the more economically important stingless bee species is emphasized.

Division of labor

Worker female meliponinids carry out almost all of the work of the hive. As in the Apini, the workers' duties change with age (Table 3). The duties of stingless bee workers, as described in the literature, imply that the division of labor is highly structured and that duties change abruptly. In the honeybee, the transition is very gradual (Lindauer 1952, Ribbands 1964).

The transition of duties in the Apidae appears to be a direct response to the development and degeneration of various glands in the worker body. For example, the young adult stingless bee has an operative pharyngeal gland and can feed larvae with its secretions. After 15 days, this gland degenerates and brood tending by the worker ceases. Wax glands become active about the 22nd day and degenerate at about the 28th day. During those few days that worker produces wax intensively and works with cerumen. The latter part of a worker's life is devoted to foraging. This duty starts about the 37th day and

Table 3. Age and sequence of duties in *M. quadrifasciata* Lepeletier and *T. (Scaptotrigona) xanthotricha* Moure[a].

Stage	Duties	Stage of life in days[b]	
		T. xanthotricha	*M. quadrifasciata*
1	Emergence and resting.	1	1
2	Incubation of brood; work with wax in brood chamber and later in all nest; occasionally feed queen.	2-11	2-11
3	Construction, filling and sealing cells; feeding young adults and queen; cleaning nest; incubation.	12-21	12-21
4	Feeding queen and young adults; cleaning nest; making cerumen.	22-26	22-26
5	Work with cerumen; construction of comb and involucrum; receiving nectar; storing food; guarding entrance.	27-34	27-35
6	Transition to foraging.	34-37	?
7	Foraging.	36-death	35-death
8	Trail marking.	?[c]	?

[a] Compiled from: Bassindale (1954), Moure *et al.* (1958), Hebling, Kerr and Kerr (1964), and Cruz-Landim and Ferreira (1968).

[b] The average life span of *M. quadrifasciata* is 43 days, and of *T. xanthotricha* is 97 days.

[c] *T. (Scaptotrigona) postica* Latreille marks trails from the 43rd-54th day of its life.

continues until death. On about the 43rd day, the mandibular gland becomes active and for a period of about 10 days the stingless bee can mark trails and is capable of communicating with other bees. During the final days of the worker's life, it forages but is incapable of initiating foraging in other workers (Schwarz 1948, Cruz-Landim and Ferreira 1968).

Fertile castes

Males are not always present in stingless bee colonies. Their production commonly coincides with the production of virgin queens, though males may remain with the nest for periods up to 8 months. In a nest of *T. corvina,* a total of 5,201 adults were counted, 417 were males and 2 were virgin queens (Schwarz 1948).

A very common observation, is the occurrence of small clusters or swarms of male bees around nest entrances (Salt 1929, Michener 1946, Schwarz 1948). Although the function of this swarm has not been demonstrated, I hypothesize that these males are awaiting the exit of virgin queens.

Drone honeybees apparently contribute nothing to the colony except for fertilizing the queen. In Meliponini the drones can produce wax in the same way as the workers. The ability of stingless bee drones to carry out worker duties in the nest is disputed. According to Schwarz (1948) some naturalists during the 1800's claimed to have seen males building comb cells. No literature has been found to support that drones are capable of such work. Moreover the anatomy of the drone is not compatible with worker functions. The combs and spines of the drone tibia are not well developed, and it is unlikely that it could remove the secreted wax platelets from its abdomen. Moreover, the mandibles are not developed to facilitate working with wax (Schwarz 1948).

Stingless bees engage in a drone slaughter once a year. The honeybee drone slaughter always occurs in the fall before the colony begins to overwinter, apparently as an adaptive mechanism which ensures winter food for essential colony members. Although stingless bee species do not experience winter in the tropics they do go through quiescent periods during dry seasons or between flowering of forage plants. The drone slaughter in the stingless bees does not occur abruptly, as in *A. mellifera,* but gradually over weeks or months. There does not appear to be any particular time of year when all species would have such a slaughter (Schwarz 1948), and it is not known whether it correlates with adverse periods each species may endure.

Meliponinid and apinid queens share very similar roles in the colony. The meliponinid queen is the egg layer. Her presence prevents worker females from laying eggs. There is only one gravid queen in any stingless bee nest. However, unlike *A. mellifera* colonies, a few virgin queens may be present in the nest and are tolerated by the gravid queen.

Colony swarming in stingless bees occurs once or twice a year (Moure *et al.* 1958). The method by which swarming occurs is very different from the Apini. In the honeybees, the mature gravid queen leaves the nest with a portion of the colony's workers and sets up a new nest. The break from the old nest is abrupt. Queen larvae are developed in the old nest. When a virgin queen emerges she will kill all other queen larvae and then mate. The old nest will have a single young queen.

Shortly before colony swarming, worker meliponinid bees will begin transporting building material and food to a new nesting site. Over a period of a few days a group of worker bees emigrates from the old nest to the new nesting site. A virgin queen from the old nest will then leave, and in the company of workers and males, fly to the new nest. Fertilization of the virgin queen apparently occurs during this flight. The new colony will continue to be supplied with food and building material from the old nest until it is self-sufficient (Moure *et al.* 1958).

The mature stingless bee queen is incapable of surviving apart from the colony. She has only short wings which become frayed soon after maturity and her abdomen is very distended. Her mandibles are so small that she must be fed by workers.

Fecundity of stingless bee queens varies from 4,500 eggs/month by *T. (Plebeia) minima* Gribodo to 1,000 eggs/month by *T. lineata* (Schwarz 1948). The meliponinid queen can lay eggs year round. Comparatively, the honeybee queen can lay up to 1,500-2,000 eggs/day during the productive season, and may produce up to 16,000 eggs/month averaged over a year (Ribbands 1964).

Brood incubation and preadult development

The development of the preadult stages in stingless bees follows a unique pathway relative to that of the honeybee (Michener 1964). The major difference in brood incubation is that the eggs are sealed in their cells with enough food for development to pupation. There is no continuous feeding of larvae as in the honeybee. Before an egg is laid in a cell, workers fill the cell approximately three-quarters full with a mixture of honey and pollen. The queen deposits an egg and the cell is sealed with cerumen. Egg laying on a comb layer proceeds from the center out to the margins. Development from egg to emerged adult takes about 32 days, varying slightly with each species. The egg, larval, prepupal and pupal stages last about 5, 10 and 16 days respectively, 10 days longer in development than that of *A. mellifera* (Ribbands 1964). The newly-emerged callow adult is white. Over about 15 days the pale color will turn usually to black (Schwarz 1948, Michener 1964).

The egg floats on the semiliquid food in the cell (Bassindale 1954). The larva consumes all of the food in the cell. Before pupation, the prepupa constructs a cocoon and discharges the meconium into the bottom of the cocoon. As pupation proceeds, workers begin to dismantle the cerumen cell and at the time of emergence little except the cocoon surrounds the developing bee. This cerumen will be either stored, or immediately used to build new cells.

The nutritional content of the larval food is not well known. It is a semiliquid mixture composed mainly of honey and pollen. However, salivary secretions of workers also are thought to be included. These secretions may be analogous to honeybee royal jelly, which is a complex mixture of water, sugars, proteins and fatty acids such as 9,keto-*trans*-decenoic acid and 10 hydroxy-*trans*-2-decenoic acid (Wilson 1971). It is initially fed to all larvae. After about 4 days royal jelly is withheld from worker larvae and is given only to larvae developing into queens or drones (Wilson 1971). In the meliponinid bees, all royal secretions must be placed in the cell before it is capped and likely the predetermined amount would determine the development of a queen, drone or worker. The chemical composition of meliponinid "royal jelly" is unknown.

The evolutionary significance of mass provisioning of food and sealing of brood cells in the Meliponini is obscure. The habit of sealing cells is not directly analogous to the similar habits of more primitive non social bees of the family Halictidae, which do not have social castes. Sealing brood cells however does appear to have some positive advantages. The survival of stingless bee larvae is less impaired by social and external environmental factors. In the honeybee, maintaining the correct humidity in the nest to prevent desiccation of exposed larvae is a major necessity. Also, during times of low food reserves, honeybee workers can cannibalize up to 50% of the eggs previously laid (Michener 1964).

Communication

The Meliponini have evolved unique methods of communication between individuals (Lindauer and Kerr 1960). They have no behavior resembling the waggle dance of the honeybee. However, unlike the honeybee, they employ trail marking pheromones.

Foraging workers of most stingless bee species, between the ages of 40 and 55 days, have the ability to leave scent markers. In *T. (Tetragona) subterranea* Friese, the trail-marking substance has been identified as citral (3,7-Dimethyl-2,6-octadienal, geranial, neral). It and other alcohols and ketones are found in the mandibular gland. (Table 4) (Blum 1974, Weaver, Weaver and Clarke 1974). The foraging bee, once it discovers a foraging source, will collect a load of nectar and return to the nest, marking a trail about every 2 m with the mandibular secretion. The trail usually is a zigzag from the forage source to the nest, it can be laid on the side of a tree or a cliff although not over water. The trail will end approximately 8 m from the nest ensuring that it will not be crossed by another trail close to the nest. The scent path of a foraging *T. postica* described by Lindauer and Kerr (1960) had markers every 2-5 m over a distance of 50 m, mostly placed on blades of grass. Each scent mark appears to last about 15 minutes and the scent is thought to be species specific (Lindauer and Kerr 1960, Cruz-Landim and Ferreira 1968).

Citral is one of the major components of the Nassanoff gland secretion of honeybees, and its isomers are produced by many social Hymenoptera. It is a common alarm pheromone or defensive allomone, and in the Meliponini, it also functions as a trail marker (Blum *et al.* 1970).

On the return of a foraging bee to the nest, it engages in ritual alerting signals (Moure *et al.* 1958). The worker bee, laden with pollen or nectar, will enter the nest running in a zigzag pattern and jostling other workers. Simultaneously, it will emit a high pitched

Table 4. Chemical compositions, in addition to citral, of the mandibular gland secretions of three *Trigona* species (From Blum 1974).

Compound	Species *T. postica*	 *T. xanthotricha*	 *T. spinipes*[a]
2-Heptadecanol	1[b]	-	-
2-Heptanol	3	2	2
2-Nonanol	-	1	1
2-Pentadecanol	1	-	-
2-Tridecanol	1	2	1
2-Undecanol	1	-	-
2-Heptadecanone	1	-	-
2-Heptanone	2	2	-
2-Nonanone	1	-	-
2-Pentadecanone	2	2	-
2-Tridecanone	3	3	-
2-Undecanone	1	1	-
Hexadecenyl acetate	3 (2 isomers)	3 (1 isomer)	-
Tetradecenyl acetate	3 (2 isomers)	1 (2 isomers)	-
Benzaldehyde	2	2	-

[a] *T. (Trigona) spinipes* F.

[b] Numbers from 1 to 3 indicate in ascending order the relative activity of the chemical in bioassay.

buzzing sound, the frequency of which may indicate the richness of the forage (Lindauer and Kerr 1960). Periodically, it will stop and offer some of the forage for inspection. The bees can thus communicate the existence of the type and richness of a forage source. Initially the trail marking bee, after alerting the nest, will guide foragers over the trail to the forage source. Thus initiated, foragers can easily find their way. Once they arrive at the source they can visually recognize it and then find their own specific foraging site (Lindauer and Kerr 1960).

Stingless bees are apparently not capable of communicating the distance of the forage source. Possibly this information may come indirectly from the frequency of returning foragers. Large numbers of foragers returning quickly would indicate a close source. However, the existence of a marker trail would at least partially preclude the need for an indication of distance to the source. It would also provide a means of indicating height and allowing orientation in dense jungle in which the sky is not visible, a requisite for the waggle dance of *A. mellifera* (Lindauer and Kerr 1960, Wilson 1971).

Mechanisms of communication within the stingless bee colony which result in the ordered functioning of the colony are not well understood. For example, the queen has an odor which prevents worker females from laying eggs, and each colony apparently has a distinct odor. However, other than citral, no chemicals have been identified which regulate social activity in the Meliponini. In the honeybee, 9, keto-*trans*-decenoic acid is produced by the queen and apparently controls some of the worker's activities (Wilson 1971).

Foraging and forage materials

At a forage site, bees quickly begin loading and transporting forage (Table 5) back to the nest. Their behavior is very similar to that of the honeybee, and they are not easily diverted from it.

Stingless bees load and transport materials in the same way as honeybees. The material is collected by the mandibles and, with the fore tarsi, is placed on the tibiae of the mesothoracic legs. It is then pasted on the corbiculae of the hind legs. Pollen, nectar, mud, soft resin and all other soft forage materials are loaded in this manner. If the material is hard or not sticky, the bee can carry it in its mandibles, supporting it with the fore tarsi.

Different meliponinids have definite preferences for food type and construction materials. Food preferences change through the year as various forage plants flower. A preferred construction material will usually be foraged year round if available.

Most of the pollen and nectar collected by meliponinids comes from wild flowers. Lists of plant species and their respective bee foragers are not available. Many of the plants known to be visited by stingless bees grow only sporadically through the jungle and are of minor importance economically. Michener (1946) recorded observations on 2 stingless bee species which tends to confirm that species preference varies as particular plants flower. He found that *M. favosa phenax* F. foraged on a small unidentified flowering bush 60 m from its nest. Three meters from the nest there was a blooming *Solanum* bush and at 30 m a flowering tree of the genus *Dalbergia*, neither of which was foraged by this species. Another species, *M. interrupta triplarides* Latreille, foraged on both the *Solanum*

Table 5. Types of forage materials collected by stingless bees.

Forage	Forage Sites	Selected References
Food		
Honeydew	Homopterans	Hood (1952)
Nectar	Flowers	Michener (1946), Schwarz (1948), Wille (1965)
Pollen	Flowers	Michener (1946), Schwarz (1948), Wille (1965)
Sugar	Rotting fruit, sugarcane, honey	Schwarz (1948), Wille (1965), Freire and Gara (1970)
Construction material		
Animal fat	Dead carcasses	Schwarz (1948)
Leaf mulch	Wild and crop plants	Michener (1946), Schwarz (1948), Wille (1966a) Camacho (1966)
Manure	Pastures	Schwarz (1948)
Mud	Local area	Schwarz (1948)
Resin	Trees	Myers (1935, 1937, Schwarz (1948), Wille (1966a), Freire and Gara (1970)
Tar and grease	Offered sources	Michener (1946), Schwarz (1948)
Wax (beeswax and paraffin)	Leaf surfaces, offered sources	Michener (1946), Schwarz (1948), Freire and Gara (1970)

and the *Dalbergia*. Within 2 months of these observations, *M. favosa phenax* had changed to another flowering plant; the original plant had become dormant.

In some cases where stingless bees forage on crop plants, the result is either pollination or a pest problem. The bees are considered primary pollinators of the vanilla plant, *Vanilla plantifola* Andrews. However, bees foraging on species of *Citrus, Musa, Macadamia, Eucalyptus, Hibiscus, Cajanus* and *Quassia* usually cause damage to the plants.

Some meliponinids have very unique methods of obtaining pollen, nectar or resins from plants. *M. beecheii* is capable of vibrating narrow throated flowers such that the pollen is ejected onto the petals where the bee then collects it (Wille 1965). *T. silvestriana* obtains tree resin by cutting a hole through the bark and collecting the exuding resin. The holes are usually cut when the shoot is young and may be maintained open for years. *Macadamia, Citrus* and *Eucalyptus* trees are commonly damaged in this way. Most species of the subgenus *Trigona,* including *T. corvina* and *T. silvestriana,* obtain pollen and nectar from flowers by cutting a hole in the base of the corolla. This usually kills the blossom. *Macadamia* and *Citrus* trees apparently suffer this damage.

Stingless bees seem to be attracted to any sweet, fermenting or resinous material. Rotting fruit, sugarcane and even honeydew-producing homopterans can become forage sites (Hood 1952). The honeybee is similarly attracted to such sites. The attraction appears to be dependent on the resources needed by a colony. I have observed that foragers of a colony, in need of food (a sugar source) or construction material would collect honey or wax offered to them. If, however, the substance offered to them was not of their immediate need, they would pass it by.

Most species of stingless bees that have been studied forage for the complete photophase period of the day. In Costa Rica sunrise is about 0530 hr and sundown is about 1800 hr. *T. silvestriana*, *T. cupira*, *T. testacea* and *T. ferricauda* all start foraging about 0600 hr and terminate about 1800 hr. *T. silvestriana* is most active about 0800 hr and the other species have 2 activity peaks, one at 0600 hr and another at 1700 hr (Freire and Gara 1970). The amount of material foraged per bee appears to vary directly with size. The smaller bees usually make more forage trips than the larger bees.

Defence

There are 2 basic types of defence mechanisms in all colonial insects. One involves the bodily weapons of the individual bees such as the sting or the mandibles. The other is the architectural defence offered by the nest.

The key to the successful defence of a colony is the alarm signal which appears to be the citral pheromone which is also used to mark trails (Blum 1974). When citral is used as an alarm, it is placed on the intruder in relatively high concentrations. Other bees of the colony respond to the odor aggressively and in the process leave more citral on the intruder. The resultant effect will be a large number of bees swarming on the intruder (Blum *et al.* 1970, Blum 1974).

Normally any insect attempting to enter the nest or any large animal, including man, which comes within a few meters of the nest will be mass attacked. I have personally noted that I could stand within 1 to 2 m of a nest of *T. corvina* for a few minutes unmolested. Once one bee had landed on me, bitten me and left an orange sticky fluid, many other bees would be actively massing on me within 15 to 20 seconds.

Citral, in extremely high concentrations appears to disorganize the colony of most meliponinid species. The robber stingless bee, *Lestrimelitta limão* (Smith), makes use of this phenomenon to disarm victim colonies of *Trigona* and *Melipona*. The attacking *L. limão* literally fumigates the nest with citral and causes most of the colony to evacuate (Blum *et al.* 1970, Weaver *et al.* 1974).

The major physical defence method is biting. The individual bite of the species of bees I experienced was not terribly painful but a mass of biting bees quickly became intolerable! Meliponini have a vestigal sting which is not used in defence. The lack of a sting does not appear to diminish their ferocity. The severity of the attack varies with the species and with the strength of the particular colony. Some species, such as *T. corvina*, *T. fuscipennis* and *T. silvestriana* are very aggressive and will attack from up to 5 m away. Others such as *T. (Cephalotrigona) capitata* Smith will not attack even when its nest is broken open (Michener 1961, Johnson and Hubbell 1974). *Trigona* species of the subgenus *Oxytrigona*, in addition to biting, leave a very caustic fluid which can cause severe burns (Schwarz 1948). The chemical constituency of the fluid and method of deposition are unknown.

Insects intruding into the nest are usually mass attacked, most commonly by biting (Schwarz 1948). *T. (Tetragona) jaty* Smith, a very small bee, normally concentrates its mass biting in an effort to cut off its adversaries' wings. In this way intrusion by wasps or honeybees can be turned back. *M. fasciata scutellaris* Latreille has a unique defence involving gluing intruders to death. The bees follow the intruder about placing sticky fluid on it but generally do not fight with it. Soon the intruder is rendered immobile by the fluid and is removed (Schwarz 1948). It is not known what the sticky fluid is although resin propolis seems likely to me.

The nests of most stingless bee species afford a high degree of protection from intrusion. The nests of ground-nesting species are almost impenetrable. Bees of these species are usually nonaggressive. Aerial nesting species are more vulnerable, and more aggressive.

The nest entrance tube is usually very narrow, wide enough for only one bee to pass at a time. The entrance is guarded at all times, and is commonly plugged with propolis at night. Large wasp intruders would have difficulty even entering the nest. The batumen of aerial nests is normally very thick and difficult to penetrate. The outer layer of batumen however is usually very thin and easily broken. If an intruder broke this outer layer the colony would become quickly alarmed.

Ants, especially of the genera *Atta* and *Solenopsis*, are major predators of stingless bee colonies. To thwart the advance of a column of ants, stingless bees, such as *T. corvina*, deposit a band of sticky resin around the branches holding the nest (Schwarz 1948, Wilson 1971).

In the case of *T. (Scaptotrigona) compressa* Latreille, defence of the nest is guaranteed by a species of ant, *Crematogaster stolli*

Forel (Mercado 1962). The nests of these 2 insects are closely associated and when either nest is disturbed, the ants, which are very aggressive, swarm out in attack. It is unknown if the association is mutualistic, since the ants derive no known benefit.

Within the nests of most species of Meliponini are usually found many insects and mites which are seemingly ignored by the bees. Lists of these parasites and commensals are found in Salt (1929) and Myers (1935). None appear to harm the bee colonies severely. The occurrence of disease in stingless bees is not well known. Foul brood and the bee louse, *Braula coeca* Nitzseh, which can be devastating to the honeybee are not found in stingless bees (Schwarz 1948).

Inter and intraspecific competition occurs (Johnson and Hubbell 1974). In defending a sugar bait forage source, *T. silvestriana* was most aggressive followed in order by *T. corvina, T. testacea* and *A. mellifera.* I observed *T. corvina* foragers attempting to forage resin from holes cut in macadamia trees by *T. silvestriana. T. silvestriana* was easily able to defend its holes. Bees of the 2 species would lock together biting each other until 1 of the species retreated. In another case, I offered resin to foraging bees. Both *T. corvina* and *T. silvestriana* aggressively fought over it. Within a day, the 2 species had adopted compatible behavior which resulted in no observable competition. *T. silvestriana* foraged resin from about 0700 hr to 1000 hr and *T. corvina* foraged it for the rest of the day. I noticed no competition between bees of the same species; however, intraspecific competition between colonies of *T. corvina* is known to occur (Johnson and Hubbell 1974).

ECONOMIC IMPORTANCE OF THE STINGLESS BEES

In this section the first attempt to assess the economic significance of stingless bees to tropical agriculture is made. With essentially similar life histories as the honeybee, stingless bees are a potential source of honey, and serve as important pollinators to some tropical crops. Thus they represent both a detriment and benefit to tropical agriculture. Bees of the same species may serve as a major pollinator of one crop and yet severely damage another. Both pollination and damage may occur even within the same crop.

Economic Benefits

The importance of meliponinid bees as pollinators of both crops and ornamental flowers is documented by Schwarz (1948), Wille (1965, 1966a) and Freire and Gara (1970). No comprehensive list of crops pollinated by stingless bees is available. However Schwarz (1948) cites vanilla, *V. plantifolia;* cacao, *Theobroma* spp.; and banana, *Musa* spp. as being pollinated by meliponinids. When vanilla was introduced into Haiti in the 19th century, stingless bees also had to be introduced to pollinate it. However commercially grown vanilla now is normally artificially pollinated. Both vanilla and cacao are native to the neotropics. Although stingless bees frequent many other crops, proof that they act as major pollinators is lacking. A critical survey of stingless bees as pollinators might reveal that they are a valuable and unrecognized resource.

The use of stingless bees as a commercial honey source also has not been well explored, although the honey has been used in the past and its potential for use today is recognized (Schwarz 1948). During the pre-Columbian era and for about 200 years after the coming of Europeans to the new world, stingless bees were the only source of honey. Sugarcane was not then cultivated in the Americas. Many Indian cultures were known to utilize both honey and wax from various species. The honey was used extensively as a sweetener of food and in the preparation of medicine. Two species of bees seemed to have been most preferred, *M. beecheii* found from southern Mexico south to Panama and *M. interrupta* found in Columbia. *M. beecheii* was kept by Mayan Indians in specially built hives for domestic honey and wax production.

The quality of stingless bee honey varies enormously between species (Table 6), depending on species-specific forage plants. Some honeys are sweet, clear, and good tasting, while others are watery, acid or even intoxicating. According to Schwarz (1948), most species of the genus *Melipona* produce palatable honey. Honey yields vary with species and colony size, and average yield of 2 to 3 Kg/year is normal for most species (Schwarz 1948). Yields of up to 16 Kg from *T. capitata* and 45 Kg from *M. beecheii*/year have been recorded under domesticated hive conditions. A domesticated colony of *A. mellifera* can produce between 40 and 90 Kg of honey/year (Ribbands 1964).

Unlike the pure wax found in *A. mellifera* nests, stingless bee wax is mixed with vegetable waxes, clay or resins to produce the cerumen used for construction (Michener 1946, Schwarz 1948). Impurities in the wax, ranging from 10 to 90%, cause it to appear dark brown or

Table 6. Summary of the palatable quality of the honey of some species of stingless bees.

Species and region	Honey taste and quality	References
Central and South America		
Trigona fuscipennis	Very fermented taste	Salt (1929), Wille (1966a)
T. silvestriana	Dark, sweet, acid	Myers (1935
T. fulviventris	Good taste, slightly acid	Salt (1929), Wille (1966a)
T. capitata	Good taste, slightly thin, acid	Salt (1929)
T. corvina	Varying quality, often acid	Personal observation
Melipona interrupta	Excellent taste	Salt (1929)
M. favosa	Good taste, thin	Salt (1929)
M. beecheii	Excellent taste, consistent quality	Schwarz (1948)
Australia and New Guinea		
T. (Plebeia) australis Friese	Sweet, viscous	Michener (1961)
T. (Plebeia) cincta Mocsary	Sweet, viscous	Michener (1961)
T. carbonaria	Sour, liquid	Michener (1961)
T. (Tetragona) genalis Friese	Sour, liquid	Michener (1961)
T. (Tetragona) hockingsi Cockerell	Sour, liquid	Michener (1961)
T. (Tetragona) iridipennis Smith	Sour, liquid	Michener (1961)
T. (Tetragona) wybenica Cockerell	Sour, liquid	Michener (1961)

black, and be softer than beeswax. Unlike the valuable wax of the honeybee which is used to make candles, high grade polishes and some types of water-proofing products, stingless bee wax is of little commercial use because of the large amount of impurities found in it. Purifying the wax may be possible through distillation but would be costly.

Historically, stingless bee wax has been used where honeybee wax was not available. Pre-Columbian Indians used stingless bee wax to make moulds for casting gold, to wax rope, and to calk boat hulls. Indians of Indonesia used wax of *T. iridipennis* in the making of batiks. After the arrival of the Spaniards to the neotropics, stingless bee wax was used to make candles. Candles of this wax are usually soft and burn with much smoke. They have become of religious significance to some Indian tribes and are highly prized by them (Schwarz 1948, Gross 1972).

For use in apiculture, for honey and wax, stingless bees do not appear competitive with the *Apis* spp. which are now found in all regions of the tropics with the possible exception of dense jungle rain forest areas (Smith 1953, Crane 1973). *A. mellifera* var. *mellifera* or var. *ligustica* are not indigenous to the tropics, although other varieties and other *Apis* species are. The varieties *capensis* and *adansonii* are indigenous to Africa. Both are successful in the wild state and can also be used in apiculture. *A. indica* F., indigenous to India and the Far East, is commonly kept as a commercial honeybee. Thus, it would appear that the commercial demands for honey and beeswax in the tropics can be met by members of the genus *Apis*.

Meliponinid bees have one other competitive disadvantage. It is apparently impossible to acclimatize them to non tropical climates, restricting their use as pollinators to the tropics. Most neotropical species appear to prefer a nest temperature of approximately 30°C. At 25°C they are visibly slowed in their activities, at 15°C they cease flying and at 10°C they will die (Schwarz 1948). Unlike *A. mellifera*, stingless bees do not cluster at low temperatures. *A. mellifera* initiates winter clustering at 18°C and at 13°C clusters are well formed. The cluster can maintain a livable temperature for the bees at below zero air temperatures (Ribbands 1964). Australian meliponinids may be more cold tolerant. Michener (1961) reports that *T. carbonaria* is able to survive a winter temperature of 0°C. A more complete study of the cold tolerance in this and other related species would be of interest.

Economic Damage

Published accounts of stingless bees as pests of agricultural crops are fairly numerous. The information is usually in the form of small annotations in taxonomic papers. Commonly it is mentioned that a particular *Trigona* species is an important pest of perhaps citrus or banana crops. Occasionally the type of damage is mentioned but rarely is its extent reported. To date, no published report exists appraising the economic damage to crops caused by stingless bees. Following is a summary of the published reports of stingless bees as pests. I have added my own subjective descriptions of the damage caused by 2 additional species. Only a few species are pests, and all are in the genus *Trigona* (Table 7).

Table 7. Summary of the pest species of stingless bees.

Species	Range	Crops Damaged	References
Trigona corvina	Mexico, Central America (C.A.)	banana	Schwarz (1948), Buddenhagen and Elsasser (1962)
		citrus	Schwarz (1948), Michener (1961), Wille (1966a), personal observation
		macadamia	personal observation
T. cupria	C.A.	eucalyptus	Freire and Gara (1970)
T. ferricauda	Panama, Costa Rica, Ecuador	eucalyptus	Freire and Gara (1970)
T. fuscipennis	Mexico, C.A., Brazil, Paraquay, Bolivia, Peru, Ecuador	banana	Salt (1929)
		citrus	Schwarz (1948), Wille (1966a)
		macadamia	Wille (1965), Camacho (1966)
T. hyalinata	Brazil, Paraquay, Bolivia	Caribbean pine	Wille (1966a)
T. nigerrima	Mexico, C.A., Columbia	citrus	Wille (1966a)
T. ruficrus	Brazil	citrus	Schwarz (1948)
T. silvestriana	C.A.	banana	Schwarz (1948)
		citrus	Wille (1966a)
		eucalyptus	Salt (1929), Freire and Gara (1970)
		macadamia	Wille (1966a), personal observation
T. testacea	Costa Rica, Peru, Panama, Ecuador, Chile	eucalyptus	Freire and Gara (1970)
T. trinidadensis	Northern South America, Trinidad	citrus	Myers (1935, 1937), Schwarz (1948)

Most stingless bees damage crops as a result of their foraging for construction material. Some also damage crops as a result of their foraging for nectar and pollen. Pieces of leaves, plant waxes and resins are most commonly collected. Members of all species listed in Table 7, with the exception of *T. ferricauda*, build exposed or aerial nests. *T. ferricauda* builds its nests in hollow trunks. Since exposed nests require relatively large amounts of building material, these species may be expected to forage heavily on their preferred forage plants. That these bees prefer commercial crops distinguishes them as pests.

There are five types of notable damage caused by stingless bee pests.

Cutting holes in tree bark

Some species cut holes 1-2 cm in diameter through the bark of forage trees in order to collect resin. Usually these holes are started on small branches or in branch crotches where the bark is relatively soft, and as the branch grows large the wound hole is maintained open. The affected trees will become unthrifty from a constant loss of sap and are constantly open to infection by disease organisms.

Hole-cutting damage occurs to macadamia, citrus and eucalyptus trees. In Costa Rica, macadamia nut trees are severely damaged by *T. silvestriana* (Wille 1966a). Within a plantation of 200 macadamia trees, I have found some damage on at least 80% of the trees with the heaviest damage on the edge trees. Some edge trees appeared more favored than others. On some occasions these trees seemed to be raining resin from the many holes, pools of resin forming beneath them.

At present in the neotropics, macadamia nut trees are being grown only in Costa Rica as an experimental crop. In the near future they will likely be planted throughout the neotropics, possibly inviting many other stingless bee species to become hole-cutting pests.

Hole-cutting damage to citrus trees appears very similar to that occurring to macadamia. All types of citrus seem attractive to stingless bees. In Costa Rica I have seen bee damage on grapefruit, orange, tangerine and lemon trees, but have no record of their specific name varieties. There are a number of published accounts of stingless bees hole-cutting on citrus trees, none of which mentions the species or the varieties of the citrus. Within Central America, *T. silvestriana* appears to be the only hole cutting species on citrus. Both Schwarz (1948) and Wille (1966a) consider this bee one of the worst pests of citrus in this area. In Costa Rica, I saw bees of no other species cutting holes in citrus trees. In Trinidad, citrus tree hole-cutting is attributed to *T. trinidadensis*. Myers (1935, 1937) considered this species the major citrus pest on the island. *T. trinidadensis* is still an important pest of citrus there (F.D. Bennett, personal communication)[1], but its damage impact remains unknown.

Stingless bees also cut holes in eucalyptus trees in Central America. *T. silvestriana*, *T. cupria*, *T. testacea* and *T. ferricauda* cause damage (extent not reported) to plantations of *Eucalyptus citriodora* Hook (Freire and Gara 1970). It is not clear whether or not these stingless bees are pests.

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[1] Entomologist-in-Charge, Commonwealth Institute of Biological Control, Gordon Street, Curepe, Trinidad, West Indies.

Wille (1966a) states that *T. hyalinata,* in Brazil, causes significant damage to pine seedlings, *Pinus* spp., by girdling the stem in order to collect resin. I observed stingless bees, which I tentatively identified as *T. silvestriana,* girdling seedlings of *Pinus caribea* Morelet on the east coast of Costa Rica, but could find no affected trees in the interior.

Defoliation

At least 3 species, *T. corvina, T. fuscipennis* and *T. ruficrus* defoliate citrus and macadamia trees (Schwarz 1948; Michener 1966; Wille 1965, 1966a; Camacho 1966). The bees cut the leaves from the margins in toward the midrib. Each bee cuts off a small piece of leaf, masticates it into a ball and places it on its hind legs. The leaf material is used to build the batumen. Young tender leaves and stems are preferred. Foraging bees may also collect wax and ooze from wounded leaves (Michener 1946). Considerable damage can occur to trees through a constant defoliation of new leaves and stems. Older trees, under constant attack, are badly stunted and unproductive. Seedlings can be killed by the defoliation.

Defoliation by *T. corvina* on macadamia in Costa Rica is very severe. All trees, left unprotected, would soon be defoliated of young leaves and stems. In my opinion, no macadamia trees could survive naturally in the presence of this bee. Wille (1966a) and Camacho (1966) give similar descriptions of stingless bee damage on macadamia. Camacho concurs with me on the severity of the problem.

Stingless bee defoliation of citrus trees occurs to a lesser degree than on macadamia. Michener (1946) reports that *T. corvina* defoliated citrus trees in Panama severely enough to inhibit their growth. In addition to *T. corvina*, *T. fuscipennis* and *T. ruficrus* also defoliate citrus trees (Schwarz 1948). In Costa Rica I observed orange tree plantations partially defoliated of young leaves by *T. corvina*. The older leaves were not badly damaged. Other orange trees, which were growing adjacent to 2 nests of *T. corvina*, were not defoliated. Near a severely defoliated plantation of macadamia trees were tangerine and grapefruit trees untouched by the bees. My impressions are that some varieties of citrus trees may be more attractive as forage than others to the bees, and that macadamia trees are much preferred over citrus trees.

Cutting flowers

Some species of stingless bees cut into flowers in order to forage pollen and nectar. *T. silvestriana* and *T. fuscipennis* forage on wild *Cassia biflora* L. (Wille 1965). The bees cut a hole in the flower at the base of the petals and remove the nectar and pollen. The flower dies soon after with no seed being produced.

T. silvestriana and *T. fuscipennis* are reported by Wille (1966a) as cutting macadamia and citrus flowers. Although I was informed by Costa Rican plantation owners that stingless bees cut these flowers, I did not observe such damage even though both crops flowered during my observations. Moreover, the flowers of both macadamia and citrus trees are shaped such that pollen and nectar could be foraged by the bees without cutting. Therefore, it seems doubtful that meliponinids will be serious flower pests in these crops.

In Guatemala, the flowers of the legume, *Crotalaria agatiflora* Schweinfurth, are severely cut by *T. nigerrima*. This plant is used as a cover crop for cinchona from which quinine is extracted (Schwarz 1948).

Scarring fruit

Salt (1929) and Schwarz (1948) state that in Columbia, *T. fuscipennis* cuts small holes in banana fruit and collects sap from the wounds. Only immature fruit are attacked. The severity of this damage is not reported by either author. Scarring fruit may be of importance, however, in the vectoring of disease by stingless bees to crops.

Vectoring disease

By causing various types of wounds in plants, stingless bees are potential vectors of disease to the crops on which they forage. For example, a foraging bee may collect the sugary juice of a rotting fruit on the ground and soon after collect resin from a wound on the trunk of a tree. As a result any plant pathogen may easily be transmitted to the tree.

Moko disease of bananas in Honduras and Costa Rica is vectored by *T. corvina* (Buddenhagen and Elsasser 1962). This disease, caused by the bacterium *Pseudomonas solanacearum* Smith can kill all types of banana plants. The Bluggoe cooking banana variety appears to be the most susceptible. The initial symptoms of the disease are blackening and shrivelling of the flower bud, pedicel and fruit. Once the bacteria have infected a few plants within a plantation, it can spread rapidly to other plants systemically through root grafts. The disease can also be spread by cultivation or rain. The bacterial ooze must be transmitted to an open wound on a healthy plant.

According to Buddenhagen and Elsasser (1962) a small area in Honduras of 1-2 Km in radius, where the disease was known to be endemic, increased to an area of 96 Km radius within 2 years. *T. corvina* was apparently effective in bypassing most quarantine blockades set up. After spreading through an area the disease becomes endemic in the surviving banana plants. These plants can serve as new sources of infection via bee vectoring.

The possibility that stingless bees can vector diseases of other crops such as macadamia or citrus has not yet been investigated.

PEST CONTROL METHODS FOR STINGLESS BEES

There are numerous ways of controlling stingless bees; the methods vary in sophistication, cost and practicality. Of the control methods available, some of the simpler have been attempted under field conditions. Most of the sophisticated methods are as yet experimental.

Control has been restricted by the criterion that the pest species should become the control target. To interfere with non pest species would threaten the balance of tropical ecosystems as well as cause the loss of pollinators to agricultural crops. Control must also be selective, since a pest of one crop may be a pollinator of another.

Locating Nests and Destroying Them

Finding the offending nests and destroying them is, by far, the simplest method of eliminating bee damage. Bee foragers seldom fly more than 700 m to their forage plants and most species do not fly more than 300 m (Wille 1966a). The destruction of all nests by fire or with insecticides (Table 8) such as carbaryl or diazinon within a radius of 300 to 700 m of the crop will eliminate the pest problem. In many cases, the pests can easily be located by following the flying bees which generally follow a direct path to and from their nest.

The major difficulty with nest destruction is that often the nest is not easily found or accessible. It may often be 50 m high in a large tree. In many other cases the bees cannot be followed because of the rough terrain or dense undergrowth. In one case, I was unable to reach a nest I had located in a tree because the tree was in the middle of a sugarcane field. The sugarcane was 4.5 m tall and full of poisonous snakes.

Table 8. Common names and chemical formulae of insecticides used, tested or considered for control of stingless bee pests.

Common name	Chemical name
Aldrin	1,2,3,4,10,10-Hexachloro-1,4,4a,5,8,8a-hexahydro-endo-1,4-exo-5,8-endo-dimethanonaphthalene
Carbaryl	1-Naphthyl methyl carbamate
Carbofuran	2,3-Dihydro-2,2-dimethyl-7-benzofuranyl methylcarbamate
Chlordane	1,2,4,5,6,7,8,8-Octachloro-2,3,3a,4,7,7a-hexahydro-4,7-methanoindene
DDT	2,2-Bis(p-chlorophenyl)-1,1,1-trichloroethane
Dieldrin	1,2,3,4,10,10-Hexachloro-6,7-epoxy-1,4,4a,5,6,7,8,8a-octahydro-1,4-endo-5,8-exo-dimethanonaphthalene
Demeton	0,0-Diethyl-0,2-(ethylthio)ethyl phosphorothioate
Diazinon	0,0-Diethyl-0-(2-isopropyl-4-methyl-6-pyrimidinyl) phosphorothioate
Dicrotophos	3-(Dimethoxyphosphinyloxy)-N,N-dimethyl-*cis*-crotonamid
Fenthion	0,0-Dimethyl-0-[(4-methylthio)-m-tolyl] phophorothioate
Malathion	0,0-Dimethyl S-1, 2-di(ethoxycarbonyl) ethyl phophorodithioate
Methoxychlor	2,2-Bis(p-methoxyphenyl)-1,1,1-trichloroethane
Monocrotophos	*cis*-3-(Dimethoxyphosphinoxy)-N-methyl-*cis*-crotonamide
Trichlorfon	0,0-Dimethyl(1-hydroxy-2,2,2-trichloroethyl)phosphonate

Treatment of Affected Crops with Insecticide

Using insecticides (Table 8) on crops to kill meliponinid foragers is the most common method now used to reduce bee damage (J.F. Henigman, unpublished observation). In some cases insecticides may protect crops effectively.

Only Camacho (1966) has recommended insecticide sprays against stingless bees on macadamia as follows:

a. Methoxychlor, 1.7 Kg/hectare
b. DDT, 11 Kg/hectare
c. Dieldrin, 0.28 Kg/hectare

Other insecticides, such as diazinon or malathion, have not been tested.

I have found spraying insecticides against stingless bees fraught with problems. In spraying a crop, such as macadamia or citrus, the edge trees should be especially well covered because the bees tend to attack them most. The insecticide must remain effective on the crop year round. Even with persistent insecticides, many sprays/year are necessary at a relatively high cost of time and money. During the rainy season, which may last 4 to 8 months depending on the location, the insecticide will be quickly washed off the leaves and trunk of the trees, adding to the number of sprays needed and the resultant residues. The crop cannot be sprayed during flowering, which in the case of citrus and macadamia, may last many months. With the amount of insecticide needed for continuous protection, beneficial insects, such as parasites of other pests, may be severely harmed.

Seedlings and small trees may be protected with systemic insecticides (Ripper 1959, Saito 1969). In small trees, systemics can be adequately translocated through the trunk and to the leaves. In larger trees, the movement of the systemic is usually not even and the large dosage required may be phytotoxic. Fruit harvested from treated trees should be checked for insecticide residues (Ripper 1959).

One of the major problems with systemics in the tropics is that the chemical in the soil is leached away. Recently on an experimental basis, systemics have been released in the soil from controlled release carbon chips. These chips are water resistant and slowly release insecticide to the roots of the plant, resulting in protection for up to a year (Allan, Gara and Wilkins 1970). Thus, fruit trees could be protected in the future from bees and other pests for the first 4 years after planting. As the first few years of growth in fruit trees are very important to the future form and productivity of the tree, this sort of protection would prove very beneficial.

Attractants and Repellents

Attractants and repellents can be used to control bees either by themselves or in conjunction with insecticides (Freire and Gara 1970). These substances may range from crude extracts to synthesized pheromones or host plant attractants or repellents.

I have found many natural attractants for stingless bees, e.g. honey, macadamia or citrus leaves, and various tree resins. Freire and Gara (1970) also list some substances, such as eucalyptus leaf extract or vegetable oil which when placed adjacent to a nest or forage plants, usually attract some bees. The attractiveness of the substance varies a great deal depending on what the foraging bees are engaged in collecting. For example, if bees are foraging leaf material for construction, it is not practical to use honey or sugar as an attractive bait. None of the natural attractants with which I am acquainted will out compete the forage crop. Simple diversion of the bees away from the crop with these substances is not likely to work.

Growing highly attractive noneconomic plants as a trap crop has never been tried, and there are no recorded wild plants which are more attractive than the crop plants. However a search for such plants may be worthwhile.

Citral and some alcohols and ketones (Table 4) at low concentrations can be highly attractive to stingless bees (Blum *et al.* 1971, Blum 1974, Weaver *et al.* 1971). As each species has its own specific pheromone, the attractive chemical bait should match the species involved. It is not clear that all the bees foraging in a plantation could be diverted quickly with a pheromone but it would appear that the chemicals are very attractive under most conditions. In the simplest case a plantation could be surrounded with bee traps baited with pheromone. The pheromone evaporates quickly so that some method of controlled release, such as formulations in plastic (Fitzgerald *et al.* 1973) may be necessary. Although higher concentrations of citral cause alarm and aggressiveness, still higher concentrations are apparently repellent (Blum 1974). To repel bees from a plantation with citral appears rather impractical and expensive.

Attractants could be used in conjunction with insecticides in a number of ways. The insecticide could be mixed with the attractive bait in lethal or sublethal concentrations. Foragers would be killed, or could accumulate insecticide in their nest until the whole colony is poisoned. The method of application could be by using bait stations or by spraying a mixture of attractant and insecticide on a wild or cultivated trap crop.

The way in which attractant-insecticide mixtures are used depends primarily on the type of attractant. Many natural forage substances can easily be mixed with insecticide so that the mixture can be collected and transported by the bees back to the hive. Resins and waxes are best for this because insecticides will dissolve in them and are not washed away by rain. Resins are also not likely to be attractive to non-target insects. Since the bait is not likely to attract all of the bees foraging in a plantation, the preferred strategy is to use a sublethal dose of insecticide which, after a period of time, would kill the whole colonies. Regardless of whether a bait station or spray application is used, it is important that the bees be able to forage the mixture in large amounts so that the insecticide is quickly accumulated in the nest.

If pheromones are used as the attractant, the optimal strategy would be to incorporate a lethal dose of insecticide. The pheromone should be able to attract enough of the foraging bees to kill them as they are attracted. An effective application method might be to set up pheromone bait stations around a plantation with insecticide placed either in a bee trap or on a landing platform. Care should be taken that the insecticide does not interfere with the pheromone odor. While this method is unlikely to completely kill the offending colonies of bees, it will kill those foragers damaging the crop.

The type of insecticide to use with the bait will vary with the application method. When the mixture is sprayed on plants, a non residual insecticide such as carbaryl (Table 8) should be used. With bait stations, more residual types such as DDT or chlordane (Table 8) would be preferable. The insecticide used must not taint the bait such that the bees are repelled or the attraction diminished. Dosage and palatability of insecticides must be ascertained through bioassays before more detailed recommendations can be given.

Biological Control

Control of stingless bee pests through parasites, predators or diseases has never been investigated. The bees are native pests and most of the organisms potentially controlling them may already be present. Salt (1929) and Myers (1935) both compiled extensive lists of stingless bee-associated arthropods and found none which cause great damage to the bees.

It is possible that parasites or diseases attacking stingless bees of other continents could be utilized. However the threat to beneficial species as well as to honeybees will probably preclude introduction of pathogens.

Exploitation of competition between bee species is a possible method of control. If commercial hives of honeybees were placed within plantations to be protected, it is possible that stingless bees may be displaced. Schwarz (1948) states that in some areas *A. mellifera* has displaced stingless bees (species not indicated) through competition. However, Johnson and Hubbell (1974) have found that the pest species *T. silvestriana*, *T. corvina* and *T. testacea* can out compete *A. mellifera*.

Physical Controls

The use of changing light regimes, sound frequencies or simple barriers do not seem applicable as control measures against stingless bee pests. However, if plants, such as ornamental flowers, could be put in enclosures practically then this prophylactic control would be quite satisfactory. Esch (1967) found that by playing tape recordings of bee buzzing sounds to a colony of *M. quadrifasciata*, he could, to some extent, direct the flight of foragers. No experiments were made to assess the potential of using buzzing sounds to manipulate bees around forage plants.

SUMMARY OF A PROJECT TO CONTROL STINGLESS BEE PESTS DAMAGING MACADAMIA NUT TREES

For 6 months, during 1972 in Costa Rica, I attempted to control 2 species of meliponinids causing damage to macadamia nut trees in the Turrialba Valley of Costa Rica. Since practical control methods were found, the project was successful.

During the project, I had only a rudimentary understanding of the bionomics of the bees, little access to reference material, and no research facilities. These factors, together with time constraints, made the collection of quantitative data difficult. Therefore, the results described herein are primarily qualitative.

Macadamia trees were introduced into Costa Rica in 1951 (Anon. 1972). However, only recently has there been a concerted effort to propagate the trees as a crop, in addition to the other major crops, sugarcane, coffee and bananas. Macadamia trees have approximately the same growth requirements as coffee plants and it is hoped to diversify the Costa Rican agricultural economy with them. In the Turrialba Valley, a major coffee growing area of Costa Rica, a project to breed and propagate macadamia trees is funded by the Food and Agriculture Organization of the United Nations and is under the direction of Dr. H. Barres[2].

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[2] Director, Diversificacion Agricola, Apartamento 25, Turrialba, Costa Rica, C.A.

A detailed analysis of the horticulture of macadamia trees is given by Woodroof (1967). The trees being bred are clones of *Macadamia integrifolia* Maiden and Betche grafted on *M. tetraphylla* L.A.S. Johnson root stock (H. Barres, personal communication)[2]. In plantations, the transplanted trees start bearing fruit after the third year, yielding initially about 0.45 Kg of nuts annually. Yields increase to 54 to 68 Kg annually after 13 to 15 years. The tree is evergreen and produces about 3 flushes of new leaves/year. At maturity the tree is normally 9 to 12 m high with a crown of about the same diameter. In Costa Rica there are about 800 hectares of macadamia trees at present. Most of these trees are under 5 years old.

Macadamia nuts are a luxury food and as a crop give a very high cash return. An economic marketing study in the United States disclosed that the demand for macadamia nuts was at least twice the world production. The grower could expect at least $1.32 U.S./Kg for shelled nuts (Scott 1969).

Problems involved in growing healthy macadamia trees include the demand for fertilization, and the control of weeds, fungi and insects (H. Barres personal communication)[2]. The most important single biological factor limiting an expansion of this crop in Costa Rica has been stingless bee attack (Camacho 1966, H. Barres personal communication)[2].

Pest Species and Their Damage

I found 2 species of bees causing damage to the macadamia trees, these were identified by Dr. A. Wille (personal communication)[3] as

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[3] Professor, Departamento de Entomologia, Universidad de Costa Rica, San Jose, Costa Rica, C.A.

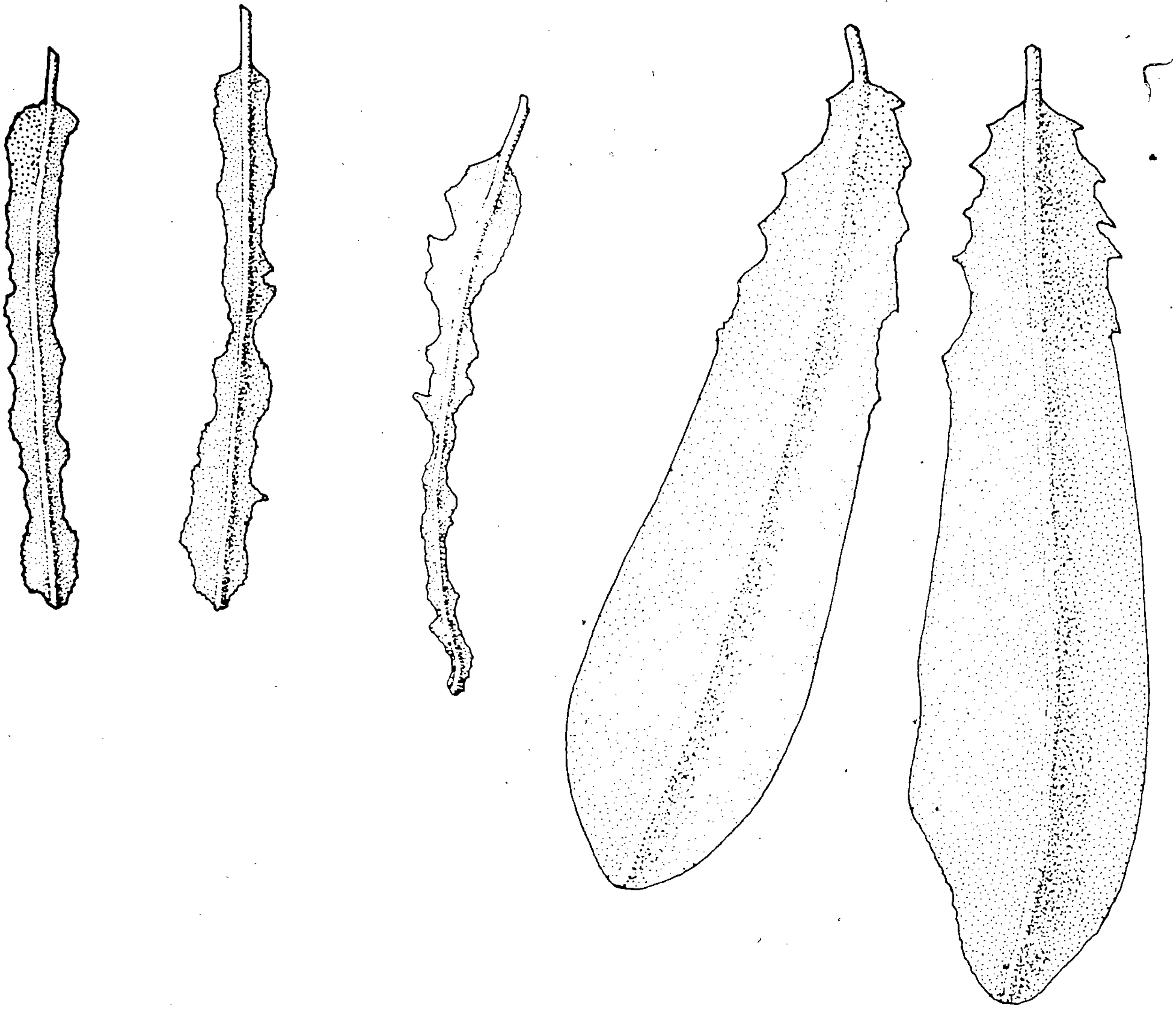
T. corvina and *T. silvestriana*. *T. corvina* cut young leaves and stems, and reportedly flowers as well. *T. silvestriana* cut holes in the trunk causing bleeding of sap. All of the trees in the Turrialba Valley, except 2 plantations of trees which were continuously protected with insecticide sprays, were severely damaged. They were generally defoliated of most new foliage and had many open wounds on the trunks. Older leaves had been damaged to various degrees. Damaged and undamaged leaves are shown in Fig. 4. The 2 plantations which were sprayed once a week with fenthion (Table 8) were virtually undamaged. These trees were used for promotional purposes. New growth on branches of these trees was approximately 0.9 m/year and on unprotected trees growth was 0.3 m or less/year, varying with the severity of damage.

Around the major plantations, in which I did much of my work, I found 3 nests of *T. corvina* and 2 of *T. silvestriana*. None of the nests were more than 300 m away from the edge of the plantation and all of them were high up in trees and very difficult to reach. The bees concentrated most of their foraging on the 2 outside rows of trees in the plantation. This plantation, containing about 100, four year old trees, had been protected with insecticide sprays until 3 months prior to my arrival. The trees were in good condition with much new growth, and the bees were just beginning to damage them.

Development of Practical Control Methods

Most of the work in developing a practical control method was directed at finding a suitable forage attractant into which insecticide could be mixed. It was hoped that the bees would forage on the mixture and take back to their nest enough insecticide to accumulate a lethal

Fig. 4 Tracings of bee-damaged and undamaged leaves of *M. integrifola* from a plantation in Turrialba, Costa Rica. All of the leaves are approximately the same age. The 3 leaves to the left have been cut down to the midrib by *T. corvina*.



dose for the whole colony. Many materials, as listed by Freire and Gara (1970), were tried as attractants without much success. These materials included: sugar, stingless bee honey, animal and vegetable fats and oils and banana. In 3 days of observation, bees would occasionally forage on all of the materials but none consistently.

Domestic bee honey was also studied as an attractant. It proved impractical for many reasons. Bees in the plantation would bypass the honey for the macadamia leaves. Honey was easily washed away by rain, insecticides would not dissolve in it well, and in the hot climate it would quickly ferment. However, using honey as an attractant, I was able to study the palatability and toxicity of several insecticides to the bees. Aldrin, DDT, Diazinon, carbaryl and trichlorfon (Table 8) were palatable as a 2% mixture in honey. All insecticides tried in concentrations over 2% were not palatable. Carbaryl caused behavior changes such as involuntary twitching 5 minutes after exposure to a 2% mixture. Death occurred within 30 minutes. The other insecticides did not affect the bees after 4 hours of observation.

A major difficulty in developing a bioassay with the bees is that if the subject bees are caged, preventing them from contact with their nest, they quickly become hyperactive and die within 8 hrs from apparent exhaustion. This problem restricted insecticide toxicity studies.

In desperation, I eventually asked some of the local Indian people if they knew of or could locate any substances which would attract the bees. I gave them each some money and asked them to bring me anything that they could buy or find that they thought would work. They returned with many items including: ink, a pork chop, wine, various types of pastry, oranges, lemons, sugarcane, putty and goma pez. All were placed on a table in the plantation open to the bees. Those items containing sugar did occasionally attract some bees. One substance, goma pez, a resin mixture extracted from pines, *P. caribea* or *P. oocarpa* Schieda, proved very attractive. It was in the form of a small block of wax resin, and is used by local shoemakers to wax thread.

Goma pez was an excellent forage attractant in all required respects. Both species of bees would forage it apparently as much as the tree leaves or resin. No other insects, particularly honeybees, foraged it during the 2 months of field testing. It is water insoluble and insecticides can be dissolved in it in high concentrations. It has a melting point of about 58°C. Goma pez was not eaten by the bees, but carried back to the nests in their corbiculae. By coloring the resin with wax crayon dye, I was able to trace the resin to the combs of one nest which I dissected.

Small cups, with a capacity of 45.5 g, were filled with a mixture of goma pez and one of the following insecticides: DDT, carbaryl, aldrin and diazinon (Table 8). Insecticide concentrations of 25 and 50% by volume of resin were initially used. Although this is a very high concentration, I wanted to allow the bees to quickly accumulate as high a dosage of insecticide as possible in their nests. Five cups of each insecticide at the 2 concentrations were made. Four replicates, of 10 cups each, were randomly hung on the plantation fence at 3 m intervals and were observed for 3 days. Bees foraged most from the DDT and carbaryl cups, and were killed on contact with the carbaryl. I reduced the dosage of carbaryl to approximately 5% but still was not confident that the foragers were ~~able to~~ return to their nests. For convenience sake, I picked DDT to use. At a concentration of 50% DDT, foragers were killed while at 25%, they were able to transport the mixture to their nests.

Over a period of 2 months, bees continuously foraged on the goma pez offered them in the plantation. During 38 flying and foraging hours, over a 4 day period, the bees collected an average of 70 mg goma pez/hr/cup from a total of 20 cups hung on the fence. These cups contained no insecticide. The mean load weight per bee of 20 bees weighed was 3.50 mg (range = 1.2 to 4.3 mg) of resin. Thus, approximately 20 bee visits/hr/cup were occurring.

I was not able to prove that bee colonies were actually killed from exposure to the DDT-goma pez mixture. However, after 1 month, the foraging by bees in the plantation decreased dramatically, and there was little damage occurring to the trees. The bees have been kept away from the trees with the DDT-goma pez cups for at least a year following the end of my study in January of 1973 (H. Barres personal communication)[2]. A complete kill of the bee colonies apparently did not occur. It has been necessary to keep the cups around the plantation on a relatively continuous basis to control the bees. To preclude the development of resistance to DDT, I suggest that other effective insecticides be used in the cups on a yearly rotational basis.

Additional Pest Control Methods

Systemic insecticides

Four different systemic insecticides were applied to the roots of macadamia seedlings. These were: carbofuran, demeton, dicrotophos and monocrotophos (Table 8). Eight seedlings were treated with each systemic, with a dosage of 0.5 gm of active ingredient per tree. Forty seedlings were kept as controls. The seedlings were observed daily for bee damage over a 30 day period.

Results of this experiment were not conclusive or particularly promising. The control trees sustained bee damaged for 15 days and only dicrotophos and moncrotophos apparently reduced bee damage, with 8 and 10 days of bee damage, respectively. It was not possible to determine the uptake of the insecticides into the seedlings.

Synthetic attractant bioassays

I received 14 different candidate chemicals and traps from Dr. H.G. Davis[4] of the U.S. Department of Agriculture as possible stingless bee attractants. They were: butyl benzoate, propylene valerate, butyl 2-ethylhexenoate, heptyl butyrate, octyl butyrates, heptyl valerate, 2,4-hexadienyl butyrate, pivalic acid nonyl ester, nonyl isobutyrate, heptyl isovalerate, octyl 3-chloropropionate, nonyl 2-methylbutyrate, nonyl tiglate and 2,2,4-trimethylpentyl valerate. The attractants had originally been developed for yellow jacket wasps, *Vespula* spp. None were

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[4] U.S. Department of Agriculture, Entomology Research Division, 5544 Air Terminal Dr., Fresno, California 93727, U.S.A.

attractive to stingless bees. I was unable to obtain any citral pheromones or their analogues, which possibly may have proven attractive.

Genetic clone preference

In the plantation where most of the work was done, there were 3 different clones of *M. integrifolia* represented in equal numbers. There was a great difference in the number of days of bee damage sustained by the trees of each group. Over a 5 week period, with observations made once a week for 4 hrs, clone No. 508 sustained a total of 5 attacks, clone No. 333 sustained 14 attacks and clone No. 246 sustained 44 attacks. However, too few observations were made to show definite preferences. Furthermore, the trees of the 3 clones were not planted randomly. Nevertheless, further studies to select trees less attractive to the bees may be warranted.

CONCLUSIONS

Pest management of stingless bees presents some unusual problems. Only a few of the species are pests and the rest are beneficial insects, primarily as pollinators. The pests should be controlled but not at the expense of beneficial species, including honeybees. Most conventional control methods, such as insecticide sprays, will interfere with non pest species. Therefore, controls should attempt to exploit the unique adaptations of the pest species, thereby achieving species specificity.

The bionomics of Meliponini are not comprehensively understood.. Almost no information is available concerning the plants visited by the different bees, particularly the economic species. Since these bees are important pollinators of wild and crop plants of the tropics, a host plant survey is essential. Many questions also arise. What would be the effect of an ecological disruption which resulted in the erradication of stingless bees from an area? As jungle areas are cleared for agriculture, what effect will this have on the bees? I suggest that where jungle areas are disrupted without prior investigation or precautions, many bee species will become very significant pests. Also, jungle adjacent to agricultural areas could deteriorate for lack of pollinators.

The population dynamics of stingless bees should be studied in detail. Once an area has been cleared of bee pests it is obviously important to be able to estimate their potential for reinvasion. When an area is developed for agriculture, the local populations of bees will probably change. For both the pollinating and the pest species, it is important to understand the nature and rate of change. For example, if new land is cleared and planted to macadamia seedlings, agricultural planning must consider the possibilities of bee infestations.

Building techniques used by the bees may be turned against them. All of the pest species build large aerial nests with thick husks. Bees foraging for leaf mulch to build the nest husk or resin to make propolis create a major pest problem. My observations indicate that the nests are continuously expanded as the colonies grow. Thus, even established colonies should be susceptible to pesticides applied to their forage plants. However I do not know if foraging for construction materials declines as the colony matures. It is possible that the majority of the bees foraging on citrus and macadamia leaves are members of new colonies.

Biochemical studies could aid the development of control methods for the bees. The chemical composition of meliponinid "royal jelly" should be described. It is possible that these chemicals or their analogues could be used to disrupt the development of bee colonies. Citral, the trail-laying and alarm pheromone of stingless bees, has already been described specifically for several species (Blum 1974, Weaver *et al.* 1974). If more field studies are made with citral to find the correct concentrations to use, and to develop reliable pheromone release systems, it could be applied extensively as part of a pest management programme. It could be used as a bait, as a trail disruptor or even as a repellent. Other pheromones, for example those used to keep order within the colony, should also be described, since many pheromones are species-specific, they may provide control methods which will conserve beneficial species. The plant chemicals which cause crops such as macadamia and citrus to be so attractive should also be investigated. If these substances were known they could be used as detection, survey or control tools. It might also be possible to selectively breed unattractive plants. The cost of producing and registering pheromones and host compounds may present many problems and impede their adoption as pest management tools (Djerassi, Shih-Coleman and Diekman 1974).

Vectoring of disease by the bees to their forage crops is not severe at present compared with defoliation. Moko disease is the only meliponinid-vectored disease known (Buddenhagen and Elsasser 1962). However, other diseases may also be traced to bee vectors.

Spraying insecticides on crops affected by bees is the most common method employed now (J.F. Henigman, unpublished observation). This method generally is expensive and impractical. Because of the year-round growing season and periods of heavy rain, an excessive number of sprays are necessary. Contamination of the harvest and surrounding environment as well as resistance to the insecticide can be expected with this method.

At present, the 2 best methods available to control stingless bees are to find and destroy all nests in the area of the crop, or to attract bee foragers to a bait containing insecticide. For the small farmer, finding and destroying nests can be an excellent inexpensive method. It involves only time and work. In rough terrain or for large acreage plantations, this method is not as practical as killing bees after attracting them to a bait or killing the colony though sublethal doses of insecticide in a bait. The attractant could be either a pheromone or a more common forage material such as goma pez. The type of insecticide and concentration to be used must be studied further. I recommend an insecticide with residual qualities of at least 2 months under field conditions. Carbaryl in low concentrations may be acceptable. DDT could be used if necessary because little environmental contamination would occur with this method (Table 8).

The pest control method which I developed in Costa Rica using a pine resin (goma pez) and insecticide mixture has kept bee damage to a minimum in macadamia plantations for over a year. The method is inexpensive and easily applied. However, more work is necessary to perfect this method. While bee foragers in the plantations have been reduced to the extent that economic damage no longer occurs, the colonies have not been killed. I hypothesize that either the insecticide is killing the foragers before they can transport sufficient insecticide back to the nest, or it is being trapped in the resin and is unavailable to kill the bees fast enough. This problem should be easily overcome though it is not actually crucial to the short term economic control of bee damage. However, if a colony is not killed rapidly, the development of resistance should be expected. Therefore, additional research must be done to develop an arsenal of pesticides which may be substituted on a rotational basis before resistance can develop.

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APPENDIX 1

Glossary of Terms

Allomone: A chemical substance produced or acquired by an organism, which, when it contacts an individual of another species in the natural context, evokes in the receiver a behavioral or physiological reaction adaptively favorable to the emitter.

Batumen: A protective layer of propolis or hard cerumen that encloses the nest cavity of a colony of stingless bees.

Cerumen: A mixture of wax and propolis used for nest construction by social insects.

Corbiculae: A smooth area on the hind tibia, bordered on each side with a fringe of long curved hairs which act as pollen baskets.

Glabrous: Smooth, without hairs.

Hamuli: Minute hooks, a series of minute hooks on the anterior margin of the hind wing, with which the front and hind wings are attached together in Hymenoptera.

Involucrum: A sheath of soft cerumen surrounding the brood chamber in a nest of stingless bees.

Meconium: Drops of liquid discharged from the anus, representing the waste products of pupal metabolism.

Pedicel: Stalk of an individual flower of an inflorescence.

Pheromone: Any substance produced by an organism that serves, upon contacting another member of the same species to induce behavioral or developmental responses adaptive for that species.

Propodeum: In higher Hymenoptera, the first abdominal segment when it is fused with the mesosoma of the thorax.

Propolis: A collective term for the resins and waxes collected by bees and brought to their nests for use in construction and in sealing fissures in the nest wall.

Pterostigma: A thickened opaque spot along the costal margin of the wing, near the wing tip.

Storage pots: Containers made of soft cerumen for the storage of food in the nests of social bees. Some pots contain only pollen and others only honey.

Tessellate: Chequered.

CURRICULUM VITAE

John Frank HENIGMAN

July, 1975

PERSONAL INFORMATION

Canadian; Age: 27; Born: October 12, 1947; Single;
Height: 5'10"; Weight: 140 pounds; Excellent health.

SPECIAL FIELDS OF INTEREST:

Pest Management and Insect Pathology.

ADDRESSES:

Home: 320 Nootka Street,
New Westminster,
British Columbia,
Canada
Telephone:
(604) 521-6439

Office: Pestology Centre,
Dept. of Biological Sciences,
Simon Fraser University,
Burnaby, B.C. V5A 1S6
Telephone:
(604) 291-4220

EDUCATION:

Secondary School, 1960-1966. New Westminster High School, New Westminster, British Columbia, Canada.

B.Sc., 1966-1970. Simon Fraser University, Burnaby, British Columbia, Canada, emphasis in Ecology, Entomology and Bacteriology. Completed 71 course hours in Biological Sciences, achieving an A average (85%).

M.P.M. (Master of Pest Management), 1973-1975. Simon Fraser University, Burnaby, British Columbia, Canada. The M.P.M. program requies intensive study in evaluation and management techniques of insect, animal, and plant pests. The summer semester involves 12 weeks of combined lectures and field work, and provides invaluable practical experience in insect, animal, and plant pest management.

AWARDS:

Tuition Waiver Scholarships, from the Government of British Columbia, 1967, 1968, 1969.

The Sidney Hogg Memorial Scholarship, 1973.

The Simon Fraser University Alumni Scholarship, 1973.

The President's Research Grant, 1974.

Curriculum Vitae
John Frank HENIGMAN
- page 2 -

RESEARCH AND FIELD EXPERIENCE:

Research technician in population dynamics, summer 1973. The larch casebearer, a pest of larch, was studied to project its population densities. Supervisors: Dr. A.L. Turnbull and Professor T. Finlayson.

Manager of a pest control project, 1972. I planned and carried out a control program for Tropical Black Bees, a pest of Macadamia nut trees, in Costa Rica, Central America. Funds were obtained from the Government of Canada and advice was given by Dr. H. Barres.

Research technician in biochemistry, 1970-1971. I assisted Dr. J.S. Barlow in researching fatty acid metabolism and protein synthesis in insects. Experimentation involved the use of radioactive materials, gas and column chromatography and other related techniques. My duties also included management of the laboratory and helping graduate students with their research.

Research assistant in microbiology, spring 1970. In conjunction with Dr. L. Albright, I carried out research on coliform and marine bacteria, measuring their sensitivity to pressure and salt concentrations. This research was financed by the National Research Council.

Research technician in population dynamics, 1969-1970. As part time employment, I monitored insect and spider populations in the University of British Columbia Research Forest using pit fall traps. All specimens were identified to family. Supervisor: Dr. A.L. Turnbull.

INDEPENDENT RESEARCH:

Population dynamics study, spring 1970. European marsh cranefly populations were monitored in local dairy pastures for their population densities to project future damage to turf by this insect.

Pathology study, summer 1970. Two bacteria were studied as potential pathogens of the European marsh cranefly in an attempt to control this insect. Assistance and advice was received from Drs. L. Albright and J.H. Borden.

Plant pathology study, summer 1970. Field studies on white pine blister rust were made on a stand of western white pine at the University of British Columbia Research Forest to describe the rust life stages and relationships with its host. Histological preparations of the rust were also made.

PUBLICATIONS:

Albright, L.J. and J.F. Henigman. 1971. Sea water salts-hydrostatic pressure effects upon cell division of several bacteria. Can. J. Microbiol. 17: 1246-1248.

MEMBERSHIP IN PROFESSIONAL ASSOCIATIONS:

The Entomological Society of Canada
The Entomological Society of British Columbia

LICENCES HELD:

Pesticide Applicator and Dispenser Certificates issued by the Government of the Province of British Columbia in the following categories:

Agricultural crop pest abatement
Forest or forest product pest abatement
Landscape and garden pest abatement
Mosquito and Biting Fly abatement
Non agricultural, non forestry vegetation control
Pesticide Dispenser, Class A
Product Fumigation

REFERENCES:

Dr. J.H. Borden, Associate Professor, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C. V5A 1S6

Dr. A. L. Turnbull, Professor, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C. V5A 1S6

Work references may also be obtained from:

Dr. L.J. Albright, Associate Professor, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6

Dr. J.S. Barlow, Professor, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6

Dr. H. Barres, Food and Agriculture Organization Expert, Diversificacion Agricola, Turrialba, Costa Rica, Central America.

Professor T. Finlayson, Associate Professor, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6