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Effects of invasive Africanized honey bees (Apis Mellifera Scutellata) on native stingless bee populations (Meliponinae) and traditional Mayan beekeeping in Central Quintana Roo, Mexico

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EFFECTS OF INVASIVE AFRICANIZED HONEY BEES (*APIS MELLIFERA SCUTELLATA*) ON NATIVE STINGLESS BEE POPULATIONS (*MELIPONINAE*) AND TRADITIONAL MAYAN BEEKEEPING IN CENTRAL QUINTANA ROO, MEXICO

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Christine Elizabeth Cairns

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To: Dean Arthur W. Herriott
College of Arts and Sciences

This thesis, written by Christine Elizabeth Cairns, and entitled Effects of Invasive Africanized Honey Bees (*Apis mellifera scutellata*) on Native Stingless Bee Populations (*Meliponinae*) and Traditional Mayan Beekeeping in Central Quintana Roo, Mexico, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this thesis and recommend that it be approved.

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The thesis of Christine Elizabeth Cairns is approved.

Dean Arthur W. Herriott
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Dean Douglas Wartzok
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Florida International Unviersity, 2002

DEDICATION

I dedicate this thesis to John M. Fortuin, who pushed me to go farther when I thought I was at the end of my rope, whose ideas were instrumental in shaping this project, and whose love and support helped make this project a success.

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ABSTRACT OF THE THESIS

EFFECTS OF INVASIVE AFRICANIZED HONEY BEES (*APIS MELLIFERA SCUTELLATA*) ON NATIVE STINGLESS BEE POPULATIONS (*MELIPONINAE*) AND TRADITIONAL MAYAN BEEKEEPING IN CENTRAL QUINTANA ROO, MEXICO

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The Maya of the Yucatan region have a long history of keeping the native stingless bees (subfamily *Meliponinae*). However, market forces in the last two decades have driven the Maya to favor the use of invasive Africanized honey bees (*Apis mellifera scutellata*) for producing large quantities of high quality honey which has an international market. Furthermore, the native bees traditionally used by the Maya are now disappearing, along with the practice of keeping them.

An interdisciplinary approach was taken in order to determine the social factors behind the decrease in stingless beekeeping and the ecological driving forces behind their disappearance from the wild. Social research methods included participant observation with stingless beekeepers, *Apis* beekeepers, and marketing intermediaries. Ecological research methods included point observations of commonly known melliferous and polliniferous plants along transects in three communities with different degrees of human induced ecosystem disturbance.

The stingless bee species most important to the Maya, *Melipona beecheii,* has become extremely rare, and this has caused a breakdown of stingless beekeeping tradition, compounded with the pressure of the market economy, which fuels *Apis* beekeeping and has lessened the influence of

traditional practices. The community with the heaviest amount of human induced ecosystem disturbance also had the lowest degree of bee diversity, while the area with the most intact ecosystem had the highest diversity of stingless bees, though *Apis mellifera* was still the dominant species. Aggressive competitive behavior involving physical attacks by *Apis mellifera* against stingless bees was observed on several occasions, and this is a new observation previously unreported by science. Human induced disturbance of the ecosystem and competition with the Africanized honey bee are affecting the diversity and abundance of various bee species.

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The landscape of the lower Yucatan consists of lowland semi-evergreen and sub-deciduous tropical forest, and is characterized by thin, rocky soils over limestone shelves pockmarked with numerous sinkholes (*cenotes*) and seasonally flooded areas with no surface rivers (Hawthorne and Huges, 1997). The Maya who are the primary inhabitants of this region live mostly in small, nucleated rural communities. During the agrarian reform movement after the Mexican Revolution, land ownership was passed to the peasants as agrarian communities known as *ejidos*. The *ejido* system is a collective land tenure system in which common pool resources are communally managed, although agriculture is individually appropriated. Today, an estimated 80% of Mexican forests are on *ejido* lands (Galletti, 1998).

The predominant production system of the Maya has been a shifting cultivation agricultural system known as the m*ilpa*. In addition to agriculture, many forest-based resources are exploited such as game hunting, chicle extraction[1], logging, and beekeeping; but these are normally used as a complement to the milpa rather than in place of it. Although the *hacienda* plantation system rose during the 1800s, the *milpa* has still been the dominant agricultural system from the time of the ancient Maya (Ewell and Merrill-Sands, 1987).

Under the *milpa* system, soils are given time to increase nutrient stores during fallow periods. However, due to the recent dramatic increase in population in the region, at an annual rate of >7% since the 1970s[2], pressure on agricultural resources has increased substantially and caused *milpa* farmers to decrease fallow periods, causing soils to wear out faster with associated declines in food crop yields. These historic declines in yields of the *milpa* have been documented in various

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[1] Chicle refers to the latex of the *Manilkara zapota* tree, which is used to make chewing gum.

food crop yields. These historic declines in yields of the *milpa* have been documented in various sources (Figure 1) (Ewell and Merrill-Sands 1987; Sullivan, 1987). Optimal productivity requires a fallow period between 16 and 25 years. Statistics from 1984 showed that the fallow periods had dropped to an average of about 5 to 10 years. This dramatic drop in fallow periods is thought to be due mostly to increased population and increased pressure on the land and resources (Mukul, 1997).

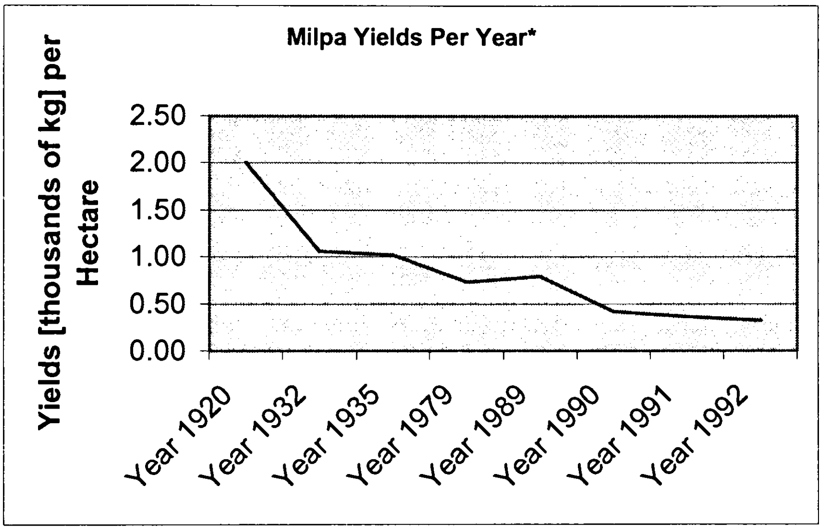


Figure 1: Milpa Yields Per Hectare Per Year [3]

Because of these declining yields and new consumption demands, small farmers have become more dependent on alternative income sources. Rural development programs and training have led to an increase in diversified uses of the land including sustainable logging and non-timber forest product (NTFP) extraction. Under an initiative called the Plan Piloto Forestal (PPF), communities set aside permanent forest areas (PFAs) that are communally managed for forest products including timber and NTFPs (Galletti, 1998). Multiple income sources from chicle,

[3] The years listed are only years which have data and which were not drought years. In some cases, yields were expressed for first year milpa, in other cases second or third year. Sources for chart data: Ewell and Merrill-Sands, (1987) and World Bank Report No. 13114-ME, (1995)

logging, agriculture, honey, and other NTFPs, has increased economic security in an often uncertain environment. Having multiple land uses is potentially less stressful to the ecosystem as well. Dependence on one single production system means increased pressure and possible overuse of a single resource, leading to degradation. Multiple land use options decreases stress on any one individual component of a system. (Ewell and Merrill-Sands, 1987; Neugebauer, 1988).

Beekeeping is worthy of in-depth study due to its economic and ecological importance in the region, and due to the fact that it is a low impact land use and NTFP. Bees are important pollinators and are known to be useful in helping fallow plots regenerate and increasing yields of various food crops. Honey is one of the major NTFPs[4] that is used to provide additional economic gains for families and communities. Honey is also very important to both the national and regional economy. Mexico is the fourth largest producer and second largest exporter of honey in the world, and the majority of honey from Mexico is produced by small farmers in the Yucatan region (Sanchez Vazquez & Colli Ucan, 1992; Hostettler, 1996). Thus, beekeeping is a naturally low impact land use that does not compete with other land uses such as agriculture and logging for capital, due to the fact that an apiary requires very little land and can contribute pollination services to farmers and the natural environment (Ewell and Merrill-Sands, 1987).

This research is divided into two parts: a qualitative social analysis and a quantitative ecological analysis. The qualitative analysis focuses on social factors related to beekeeping with two types of bees: Africanized honey bees and native stingless bees, and the effect of Africanized honey bees on beekeeping practice and management in the region. The quantitative ecological analysis

[4] I am here classifying honey as a non-timber forest product even though it must be recognized that it has different qualities from other NTFPs, since it is not directly extracted from the forest by the producers. It might be thought of as a forest-derived non-timber product.

focuses the effects of Africanized honey bees on diversity and relative abundances of native bees in three areas with varying degrees of forest degradation. The study as a whole is based on the methodological and theoretical framework that a multidisciplinary approach is necessary for effective problem solving of complex environmental issues. The problems associated with the effects of the invasive Africanized honey bees on the ecosystem and on the practice of traditional beekeeping is taken as a problem in ecosystem management. *Ecosystem management* is a concept which, in its broadest view, looks at the connections between abiotic, biotic and social aspects of an ecosystem at multiple scales, and attempts to manage these often complicated inter-relationships as a unit. Thus the ecosystem is seen and managed as a whole entity, inclusive of its human elements, rather than as the sum of its separate parts (Franklin, 1997). Management of a specific species or single natural element in an ecosystem does not always work, since, in the contemporary period, human values, policies, and economic incentives affect ecosystems in subtle and dramatic ways and human disturbance of natural ecosystems has been occurring for thousands of years. Thus in order to develop responses to environmental degradation, it is necessary to examine and come to an understanding of how the social and ecological systems interact on small and large scales. Once the interactions are understood, the best courses of action are those which ensure as much as possible the continued processes of the ecosystem taking into account the human disturbances as part of the ecosystem. Humans are part of ecosystems, and thus some human disturbance of ecosystems is expected and may even form an integral part of "natural" ecosystem processes. However, if human pressure on the ecosystem becomes too intense, the ecosystem could loose its ability to produce and regenerate, and thus begin to deteriorate. This is what needs to be avoided, not human interaction itself but those activities and processes which lead to ecosystem deterioration. It is important therefore to determine the land use practices which are economically and ecologically optimal.

In order to practice ecosystem management for any land use system, integration of ecological knowledge and understanding of economic forces which drive land-use decisions is necessary. Using an adaptive management model can also be beneficial when working with systems that have multiple influences which can often cause surprise elements to enter into and alter the ecosystem processes. *Adaptive Management* is a process of integrating scientific research and sustainable management practice. Science and management have traditionally been at odds with each other, as scientists require proof of hypothesis before implementing any action (which often requires more time than managers have to make decisions) coupled with the fact that the final data presented from scientific research often involves no clear application to actual problems which managers had to deal with. Adaptive management creates a framework that encourages scientists and managers to work together to solve problems. In this way, the management polices should be regarded as hypotheses, as in scientific experiments, and if the policy does not have the desired outcome, then a new hypothesis is applied and tested. This creates flexibility within a managed system, and allows for resilience in the face of surprise by adjusting management and policy decisions on the basis of scientifically based monitoring (Lee, 1993). This process also implies the development of "social learning" whereby human institutions absorb lessons and implement new policies and management strategies on the basis of lessons learned from previous experience and experiments. Neither ecosystem management nor adaptive management have been explicitly applied by managers in the case of beekeeping or other land use practices in central Quintana Roo. Nevertheless, the multiple land use practices developed by local peoples, and some encouraged by government programs, can be interpreted as efforts to more productively and sustainably manage the entire ecosystem. Producers, civil society organizations and government have also been at least informally engaged in adaptive management and social learning on these land use practices, as they try to learn from past mistakes and projects that have not had the desired results. The role of scientific research in these processes is to shorten the

feedback loops from lessons that can be derived from research and practice to the implementation of new possibly more sustainable practices. Thus, the creation of Mexican government sponsored cooperatives supporting local farmers using *Apis mellifera*, the common honeybee, in the 1960s can be seen as a policy experiment in raising small farmer incomes with what was perceived to be a benign use of natural resources. The unforeseen introduction of the more aggressive and invasive Africanized honeybees *(Apis mellifera scutellata)* can be seen as a "surprise" in the adaptive management sense. in the early 1980s, the agricultural secretary - Secretario de Agricultura, Ganadería y Desarrollo Rural (SAGAR) - helped prepare beekeepers for the event of the Africanized honeybee's coming by informing locals about their eminent arrival and advising the beekeepers on simple management methods to help them cope (Echazarreta et al., 1997). Therefore, the surprise factor of the arrival of Africanized honey bees did not lead to collapse of beekeeping practice as it might have otherwise, thanks to foresight and appropriate action on the part of the Mexican government. The ecological consequences of the Africanized honeybee's arrival, however, was not foreseen, especially their effects on the native bees and pollinators of the region. Even as stingless bees began disappearing, especially the species *Melipona beecheii* which is the major species of stingless bee domesticated by the Maya for honey, no management plans were enacted to cope with the problem, and thus it has led to a collapse of stingless beekeeping practice. This research contributes to a more explicit ecosystem and adaptive management model which mitigates the current problems related to the loss of native stingless bees and associated traditional beekeeping practice with *Melipona beecheii*. The research questions asked here are: what are the driving forces behind the decline in beekeeping with *Melipona beecheii* and the rise of beekeeping with *Apis mellifera*? What are the institutional and ecological constraints related to beekeeping with *Melipona beecheii* and how can the current social systems adapt to those constraints? For the ecological portion of this research, my research questions are: what are driving forces behind the decline in *Melipona beecheii* populations? What

are the current species distribution patterns and level of diversity of stingless bees and other bees, and what is the current relative abundance of the Africanized honeybee in three areas with varying levels of human induced ecosystem disturbance?

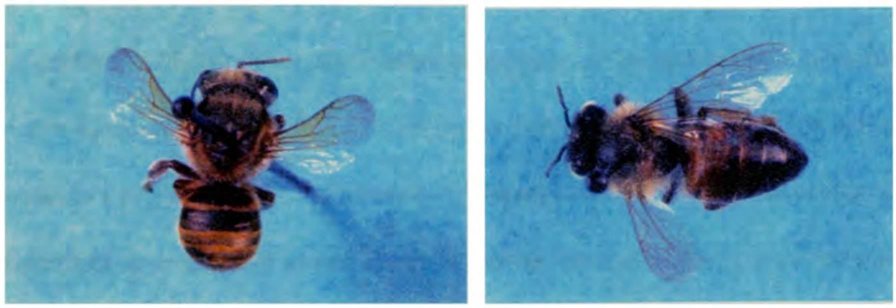


Figure 2: *Melipona beecheii* and *Apis mellifera*.

Chapter II: Beekeeping in Mayan Communities

From Meliponiculture to Apiculture

The Maya have a rich cultural history of beekeeping dating back to the times of the ancient Mayan empire. The ancient Maya domesticated the native stingless bees of the region, that belong to the subfamily *Meliponinae*, most often using bees of the species *Melipona beecheii*. Their honey was traditionally used as part of religious rituals for planting and harvesting celebrations and is a key ingredient in fermented beverages used in these celebrations (*balché*), as well as an ingredient in traditional sweets made from sweet potatoes and yucca and a sweet drink made from maize called *tsacab*. The honey produced from bees of the *Meliponinae* has medicinal qualities and has long been used by the Maya for treatment of ocular conditions such as cataracts and conjunctivitis as well as laryngitis, sore throats, colds and coughs. The wax of the stingless bees has been used to make candles for ceremonies and has therapeutic uses for treating small external wounds and for removing ectoparasites such as ticks (Sanchez Vazquez & Colli Ucan, 1992; De Jong, 1999). The native stingless bees have traditionally been kept in hollow logs called *jobones* which are usually maintained very close to the home in the *solar* (Maya home garden), or sometimes near the *milpa*, in an attempt to provide the bees with ample forage. The bees presence have the added effect of benefiting the crop yields and/or pollinating plants and trees in the home garden. These *jobones* are stopped up on either end with a round piece of wood and sealed with mud; these ends can then be taken off to harvest honey at the appropriate time. Stingless bees store their honey and pollen stored in pots made from wax and resin, and their brood is kept in horizontal combs layered on top of one another. To harvest the honey, the beekeeper reaches into the hive and breaks open the pots containing honey. The jobones are often kept in a "bee house," which consists of a palm thatched roof supported by small wooden poles, like a small open air *palapa* (traditional polewood and thatch sheds) (see figure 3) (De Jong, 1999). The bees produce a very sweet, light colored honey that has a slightly higher water

content than *Apis mellifera* honey (Sanchez Vazquez & Colli Ucan, 1992). Thus, bees and the products they produce have always had an important place in the Maya culture.


Figure 3: Stingless Bee *Jobones*
Top left: sealing end of log with mud. Top right: the bee house. Bottom left: Honey pots. Bottom right: Brood.

In the past century significant changes have dramatically altered beekeeping in Mayan communities. The change began in the late 1800's or early 1900's when the European honey bee (*Apis mellifera)* was introduced to the region of the Yucatan. Initially, it was the land owning elite who experimentally fostered a new beekeeping industry in the Yucatan with *Apis mellifera*, and controlled the industry until the 1960s. Mexico's export market for honey was developed originally around the time of World War II, when sugar shortages in the USA caused a New York based trading company to become interested in Mexico's honey. This company helped capitalize the honey industry in Mexico, which at this time was still controlled by the land owners. When this happened, the capitalist honey producers began hiring Mayan peasant farmers as laborers to

feed the new export demands. Thus the Maya began to learn the technology of beekeeping with *Apis mellifera*. By the 1960's, the large scale capital enterprises had given way to an explosion of small scale peasant operations. This remarkable transition from large scale capital-intensive apicultural enterprises to small-scale labor intensive small farmer operations was facilitated by the *ejido* system, which gave the peasants the ability to assert control over their land and allowed them to restrict the commercial enterprises from the use of their forests and their floral resources. Large producers were forced to remove their apiaries from *ejido* lands. Peasants stopped working as laborers for the large producers and began using their newly acquired knowledge to produce their own honey. These actions effectively killed the large scale honey enterprises. Today, commercial honey is still largely controlled by small farmers on *ejido* lands. The Mexican government stepped in in the late 1960s to aid these small scale operations and began two export co-operatives representing the interests of 8,000 peasant producers. Government agencies were also responsible for some apiary training programs in the 1970s, but the majority of small scale beekeepers learned their trade from friends and relatives (Echazaretta et al., 1997).

Part of the knowledge the Mayan farmers had acquired was use of moveable frame technology, which made it easy to exploit the *Apis* honey bees. The moveable frame works well with the *Apis* bees' nature to build combs vertically - as opposed to the *Melipona* which build honey pots on a more or less horizontal plane (Crane, 1992). The moveable frame technology uses parallel wood frames which are inserted into a box hive. The bees then build their combs vertically from the top of the wood frame down. The frames are easy to remove with the combs attached (see figure 4) (Crane, 1983). The practice of European beekeeping for export markets became widespread in the Yucatan Peninsula and Quintana Roo. With these new methods and new bees with a honey that had global markets, honey production in the Maya communities became for the first time a cash oriented activity (Hostettler, 1996). Small farmers had a new income source that was a very

low impact land use that also had apparent ecosystem service benefits through pollination. Virtually unnoticed, since it had only restricted local markets, was the fact that cash cropping of European bees was gradually contributing to a decline in stingless beekeeping, although it continued to hold on because of its importance in traditional religious and curing activities. The new system of European beekeeping, after several decades of apparently problem free integration into the economy and ecology of local communities, eventually ran into a "surprise".

Figure 4: Moveable frame

The Africanized Honeybee Invasion

The surprise was the invasion of Africanized honeybees. The invasion of this aggressive subspecies of *Apis mellifera* would have great effects on the practice of beekeeping in the Yucatan. In 1957, 21 queen bees of the subspecies *Apis mellifera scutellata* escaped from an apiary in Sao Paulo, Brazil where Dr. Warwick Kerr was conducting experiments with the imported African bees. Commonly known as "killer bees," the new subspecies subsequently spread throughout South America and arrived in the Yucatan in 1986 (Villanueva et al, 1991). Part of the reason for their swift spread has been due to their rapid reproductive rates, which are four times higher than the European bee. Swarming and absconding behaviors are also more common among the Africanized bees. Swarming occurs when the colony produces a new Queen bee and half of the colony forms a swarm to travel with the old queen to form a new colony. Absconding occurs often during dearth periods of flowering, when a colony will abandon the hive

looking for more resources. European bees rarely abscond, and swarm four times less often than Africanized bees. Because of the Africanized honeybee's tendency to abscond, it is much harder to control the bees and prevent them from forming feral colonies. Thus, Africanized honey bees have successfully in penetrated the forest and established wild colonies in a way that European honeybees never did (Villanueva and Colli-Ucan, 1996; Porter, 2001).

These behavioral differences have caused dramatic changes beekeeping practice in the region of Quintana Roo. Because the Africanized bees are more aggressive than the European bee, some apiculturists stopped their beekeeping activities altogether. Others have been able to adapt to the new more aggressive subspecies, but protective gear has to be worn while working with the Africanized bees, and hives have had to be placed much farther from home and livestock (Hostettler, 1996). Because of the increased swarming and absconding behaviors, beekeepers tend to loose their colonies more often, which makes managing colonies difficult. Beekeepers have had to modify their practices in order to adapt to the behavior of the new bees. Beekeeping has become a more labor intensive activity than previously, as beekeepers have to make more visits to apiaries and have had to learn how to re-capture escaped colonies (Sanchez Vazquez & Colli Ucan, 1992). Beekeepers are also learning to select out the most aggressive colonies by re-queening with milder tempered queen bees. There is a wide range of characteristics in the Africanized honeybee populations. As European and Africanized colonies mix, traits and behavioral characters begin to vary from colony to colony – with some colonies being more aggressive than others (Porter, 2001).

An additional problem that has come along with the introduction of the Africanized bee is the possible displacement of native bee species. European honeybees may have had some effect on native species as well, but Africanized bees are more threatening because of they are more

invasive and tend to be better competitors for resources than the native bees. This coupled with their reproductive habits and their tendency to abscond and thus create feral colonies in the forests can have implications for conservation. A change in pollinator makeup could have effects on vegetation, though the full effects are currently unknown. The Africanized bee is very good at exploiting resources, and uses many of the same nectar resources as the *Meliponinae* bees, but this does not necessarily mean that the Africanized bees are as effective in pollinating native flora as the native bees which have evolved within the ecosystem (Porter, 2001; Meffe, 1998).

Pests and Plagues

Beekeepers also have to protect managed colonies from natural enemies, and bee pests can often effect quality and production of honey. Various pests are prone to attack hives of Africanized bees and stingless bees. The introduced parasitic mite *Varroa jacobsoni* infests the thorax region of *Apis mellifera* during the larva stage. Not all the larvae are killed by the mites and many reach adulthood, but will often have deformities of the wing which can significantly hinder the performance of a worker bee and thus effect the colony's production (Morse, 1978). The mites first seem to have appeared in the region around 1992. The use of pesticides for control of *Varroa* is not recommended because of the effect on honey quality (Echazarreta et al., 1997). Africanized colonies show lower infestations of *Varroa* than European colonies. The Africanized bee may have more efficient grooming methods, which helps remove the mites or the *Varroa* may be less attracted to the Africanized bee. In parts of Brazil where the levels of Africanization are essentially 100%, there are very low levels of *Varroa* (Echazarreta et al., 1997).

Another pest of the honey bee are army ants (of the subfamily *Ecitoninae*) which tend to attack during the rainy season. According to Echazarreta et al. (1997), 80% of beekeepers in the Yucatan region report attacks by these ants during the rainy season. The extent of damage can

vary, but generally the ants attack the brood and can even cause the colony to be abandoned. The effects and losses due to these ants has not been studied in depth. *Melipona beecheii* can also fall prey to the army ants of this sub-family (De Jong, 1999).

Major pests to the *Melipona beecheii* bees include mainly Phorid flies or humpback flies (*Pseudohypocera kertez*), which will enter the hive and oviposit in the brood. The larvae then hatch and feed off of pollen and brood. Many beekeepers in the region have lost hives of *Melipona* to this pest. The traditional method of control is to use crushed leaves of the *Chakah* plant (*Bursera simaruba*) which are placed in the hive or rubbed on the inside of the hives and is though to repel the flies (De Jong, 1999). Modern methods include using vinegar mixed with a bit of pollen to make a trap for the flies. The pollen of the *Melipona* is very acidic, like vinegar, and thus the flies are attracted to the acidic mixture, which leads them to fall in and drown in the vinegar (A. Parra Canto, personal communication). In any case, making sure the hive remains properly sealed on either end of the log, and not leaving the hive open for long except when necessary to harvest is important to avoid infestation. Some *Melipona* beekeepers will not open their hives unless they have *Chakah* leaves present. Opening the hives in the middle of the rainy season is considered particularly dangerous, as this is when fly infestations are most likely to happen. A well sealed hive should be safe from the flies, since the entrance hole is consistently guarded by vigilant guard bees who are capable of protecting the hive from the small flies (De Jong, 1999).

Chapter III. Ecology of Bees in Quintana Roo

General Ecology and Flowering Phenology of Quintana Roo.

The state of Quintana Roo is located in the eastern part of the Yucatan peninsula between the latitudes 17° 49" and 21° 35" north and longitudes 86° 42" and 49° 25" west. The eastern border is the Caribbean sea. Soils form a thin layer over limestone and the terrain is flat and barely above sea level. Slight changes in elevation will influence the vegetation makeup dramatically. The terrain is considered karstic, with no surface rivers, fast-draining permeable limestone and many sinkholes in the limestone (commonly referred to as *cenotes*). The climate is Awi type, or sub-humid with seasonal rains. Annual rainfall fluctuates between 1,100 and 1,200mm, with 70% of the rainfall occurring between the months of May and October. Mean annual temperature is 26° C, and the average elevation is 10m (Olmsted and Durán, 1990; Hawthorne and Huges, 1997).

The dry season consists of two parts; from November to February, the early part of the dry season, is characterized by intense flowering of herbs in secondary vegetation. Although only a few species are in bloom during this period, many of the species are weedy and therefore extremely abundant and melliferous, providing ample foraging opportunity for bees. The latter portion of the dry season, from March into May, is characterized by increased flowering of trees in mature forest, and decreased herbaceous plant flowering. Peak flowering (the most species flowering at once) happens in the late part of the dry season and early part of the rainy season, starting in approximately late April and continuing into May and early June. Flowering then drops back in the late part of the rainy season, and a flowering dearth period begins often around late August or early September and continues through October and early November (Porter, 2001 and Villanueva, personal communication).

Vegetation in Quintana Roo includes a mosaic of various types, influenced by elevation, soil type and salinity[5]. Tropical forest types include sub-deciduous and semi-evergreen (*subcaducifolia* and *subperennifolia*) forests. Dominant species of trees in semi-evergreen forests include *Manilkara zapota, Brosimum alicastrum* and *Talisia olivaeformis.* Dominant sub-deciduous species include *Bursera simaruba, Caesalpinia gaumeri, Vitex gaumeri* and *Metopium browneii* (Olmstead and Durán, 1990). Whether a forest is semi-evergreen or sub-deciduous can depend on a combination of factors, including rainfall and soil type. Though generally areas with heavier rainfall will favor semi-evergreen forests, soil type can override this general pattern. In areas where soils are thin and made up of more than 50% limestone outcrops, sub-deciduous forest will prevail (Hawthorne and Hughes, 1997). Low seasonally inundated forests (*selva baja inundable*) occur in low lying areas and are dominated by species such as *Haematoxylon campechianum, Bucida buceras, Bucida spinosa,* and *Dalbergia glabra.* Other ecosystem types include *pantanos*, or low seasonally flooded plains dominated by graminoids (mainly sawgrass, *Cladium jamaicensis*), some of which may include scattered individual palms (mainly *Acoelorraphe wrightii*) or other small trees and shrubs. These *pantanos* have been compared to Florida's Everglades, which is a valid comparison in terms of the general landscape appearance, though the species makeup of the plant communities are slightly different. Mangroves and salt marshes prevail closer the Caribbean sea, where salinity obviously increases (Olmstead and Durán, 1990).

Phylogeny and relationships of tropical stingless bees (Hymenoptera: Apidae: Meliponinae)

The known bee fauna of Mexico consists of 8 families including 153 genera and 1,589 species. The stingless bees, of the subfamily *Meliponinae*, are found throughout the tropics of the

[5] It is important to note that all forest and plant communities have been historically impacted by regular disturbances such as hurricanes, fires, and extensive deforestation in the ancient Mayan period, not to mention slash and burn agriculture practices of the present era. There are no "virgin" forests in this part of the Yucatan.

Americas, Africa, Asia and Australia. This unique subfamily belongs to the family *Apidae*, which includes bumblebees (*Bombinae*), orchid bees (*Euglossinae*) and the widely known honey bees (*Apinae*) (Ayala et al. 1993; Sakagami, 1982). The subfamilies *Meliponinae* and *Apinae* are the only groups which exhibit highly eusocial behavior. Worldwide, there are as many as 400 to 500 species of stingless bees, 300 of which are found in the neotropics. In Quintana Roo, around 90 species of bees have been described. These include 15 species of stingless bees (Roubik et al. 1990; Roubik 1992). The Maya of this region recognize 12 species of stingless bees, several of which have traditionally been exploited for honey, though by far the most important in terms of honey production for the Maya has always been the species *Melipona beecheii* (Ayala et al 1993).

The *Meliponinae* are divided into two tribes; *Meliponini* and *Trigonini*. The *Meliponini* are represented by one genus in the neotropics, *Melipona*, while tribe *Trigonini* contains 50 genera and subgenera (Roubik, 1992). In Quintana Roo, two species of *Melipona* are described - including the species *Melipona beecheii* - and thirteen species of *Trigonini* are described including the following 7 genera: *Trigona, Scaptotrigona, Nannotrigona, Partamona, Lestrimelitta, Trigonisca* and *Plebia* (Roubik et al. 1990). Subfamily *Apinae* has significantly less diversity than the stingless bees. *Apinae* contains one genus, *Apis*, with only seven species. All *Apis* bee species are distributed naturally in the old world – Asia, Europe and Africa - where they are native, and are not limited to the tropics. *Apis mellifera* is the only *Apis* species now found in the new world (O'Toole and Raw, 1991; Sakagami, 1982).

Pollination services

Many local and economically important crops such as citrus, coconut, squash, watermelon, avocado, mamey sapote, mango, and sapodilla are mostly or partly dependent on bees for pollination and many must be cross pollinated (Adey et al. 1986; Roubik, 1995). The ecosystem

service of pollination is thus recognized as part of the economic equation of agriculture and fruit production in the tropics, as stimulating pollination services can lead to higher yield and increased income (Roubik, 1995).

Some evidence has been presented which suggests that Africanized honey bees may not be as effective at pollinating some plant species as native bees (Aizen and Feinsinger, 1994a; Roubik 1996). A study by Osorio-Beristian et al. (1997), found that even though *Apis* bees delivered less pollen grains per visit to *Kallstroemia grandiflora*, they visited flowers more frequently than the native *Trigona* and therefore were still effective pollinators. Roubik (1996) found correlation between honey bee dominance of *Mimosa pudica* and lower seed set. It is yet unclear what the impact the Africanized honey bee will have on pollination and seed set in the ecosystem overall, and/or what the possible economic effects may be if native pollinators are pushed out. It is known that 90% of tropical plants need to out-cross for successful pollination, and the majority are pollinated by bees (Kerr et al., 1999). Dramatic changes in the population makeup of bees therefore can potentially have dramatic effects on plant biodiversity and ecosystem health overall.

Competition

Competitive interactions are defined as any type of interaction between species that negatively influences the population growth and abundance of one or both species. A variety of interactions can constitute competition, for example use of a shared resource such as food (exploitation competition) or territorial behavior which reduces the exploitation efficiency of another species (interference competition). Interference competition may evolve under conditions where exploitation competition becomes severe (Gotelli, 2001).

Competition between Africanized honey bees and stingless bees has been studied (e.g. Roubik, 1978, 1980, 1982, 1991, Roubik and Wolda 2001, Roubik and Buchmann 1984, Roubik et al. 1986, Menezes and Carmago, 1991, Sommeijer, 1983). Africanized bees share a large proportion of resources with other types of small and medium sized bees, including the *Meliponinae*, though not many with larger bees such as *Centris, Bombus*, or *Euglossa* (Roubik, 1982). Roubik, (1978, 1982), found that stingless bees in French Guiana were less abundant at flowers and harvested less resource when African hives were experimentally introduced near flowers. This suggests the competitive superiority of the Africanized honeybee and possible resource shifts by stingless bees to escape competition, though during 75 hours of observation in the above mentioned study, no physical aggression was observed on the part of the Africanized honeybees. It has thus been observed, until now, that exploitation competition was the type of competitive interaction which occurred between African and stingless bees, and interference competition was only incidental. Displacement of stingless bees from flowers and resource shifting was due only to a perceived decrease in resource abundance by the stingless bees.

What is it about the biology of the African honeybee that makes it a superior competitor? The Africanized bee has a larger colony size of up to 60,000, where the largest stingless bee colonies have around 2,000. Africanized bees produce more offspring in much shorter periods of time, and Africanized honeybee queens and workers mature three times faster than in stingless bee colonies (A.R. Parra Canto, personal communication). These demographics alone allow the Africanized honeybee to numerically dominate ecosystems in short periods of time, and explains its rapid spread from Brazil to Mexico in less than 30 years. In addition to these factors it is also known that *Apis* bees have more effective communication tools for recruiting other colony members to floral resources than stingless bees. Thus they are more skilled at finding and dominating the richest resources in an area through recruitment (Kearns and Inouye, 1997), and

they have a larger flight range for foraging. The largest flight range of the stingless bees is around 3km, compared to 10km for *Apis* bees. The smaller stingless bees, mainly the *Trigonini*, will have smaller flight ranges of 1km or less (Roubik et al. 1986). Some species of *Trigona* exhibit physically aggressive behavior while foraging, and although the literature indicates that Africanized bees do not exhibit the same kind of aggression, they are impervious to aggression from other *Trigona* species (Roubik 1991).

Foraging

Most foraging by *Apis* bees occurs at an intermediate distance from the nest, so that the area immediately adjacent to neighboring nests may not be the area of most intense competition. For *Apis* bees, the area of most intense foraging is 2-4 km from the nest, though they can go as far 10 km, and over half of all foraging flights are within 2km of the nest. The reason for this is that while the probability of foraging will decrease with increasing distance, the foraging area will increase arithmetically with increasing distance from the nest. Thus, the area where the most intense foraging occurs is not adjacent to the nest, nor far from the nest, but at an intermediate distance of 2 to 4 km from the nest. The same concept holds true for stingless bees, although their maximum foraging ranges are smaller (Roubik, 1991).

Though bees may be found foraging during most of the day excluding the hottest hours of the afternoon, generally speaking, maximum daily nectar harvest will occur in late morning or early afternoon for most species and maximum pollen harvest in early morning (Roubik and Buchmann 1984). A resource harvest peak is defined by Roubik et al., 1986 (p. 106), as "...a period in which the number of returning foragers per unit time exceeds the mean return rate by at least three standard deviations." Peaks average only 4% of total foraging time, but during these brief peaks, 28% of the total resource harvest occurs. This holds true for all the eusocial bees. It was found

that competition with *Apis* bees causes a reduction or total elimination of the stingless bee's peak foraging periods. Competition with *Apis* bees does not abolish profitable foraging by the stingless bees altogether, but with an elimination of peak foraging the bees would only collect 75% of their normal harvest (Roubik et al. 1986). If we can assume that brood production is correlated with resource harvest, it could easily be predicted that populations would be effected by this foraging competition.

The Disturbance Factor

Given these various demonstrations of resource competition, the natural conclusion to be drawn is that the *Meliponinae* should show a substantial decrease in population size, however a recent long-term study by Roubik and Wolda, (2001) indicates the opposite. The study took place over a 17 year period in Barro Colorado Island, Panama, starting seven years before the invasion of Africanized bees and observing changes in bee populations for ten years after their arrival. The study aimed to show a population-level impact on stingless bees, but failed to find any significant changes to populations of various species after the arrival of the Africanized honeybee. Several species in fact increased in population, including *Trigona fulviventris*. It is possible that population effects will not be seen for several more years or decades, and it is important to realize that this study took place in mature, undisturbed and biologically diverse lowland tropical forest. The picture changes in disturbed habitats.

Human alteration of landscapes through agriculture, habitat fragmentation from development, cattle ranching and other activities has repeatedly been correlated with changes in native pollinator densities in various regions of the world from Europe to Africa to Central and South America (Janzen, 1974; Williams, 1986; Jennersten, 1988; O'Toole, 1993; Gess and Gess, 1993; Vinson et al. 1993; Aizen and Feinsinger, 1994b, Kearns and Inouye, 1997). A study by Aizen

and Feinsinger (1994b) in Northwestern Argentina showed correlation between habitat destruction and dominance of the Africanized honeybees over native bees. This study found that honeybees were more abundant in fragmented habitats, where native bees were more abundant in diverse and intact habitats, though it found no evidence of direct interaction between native bees and honeybees. Kerr, et al. (1999) sites five specific reasons for declines in *Meliponinae* populations in Brazil, all having to do with human activity: agricultural clearing, honey collection, inadequate protected areas, habitat destruction due to timber extraction in old growth habitat, and general deforestation. Many of these are contributing factors in central Quintana Roo as well. Stingless bees are especially susceptible to fire due to the fact that the queens do not fly and cannot escape in a fire (Kerr et al., 1999). Likewise, honey harvest from wild colonies is often destructive. In my fieldwork I observed one instance of a wild hive of *Trigona (Cehpalotrigona) capitata* that had been clearly destroyed by a person harvesting honey, and heard accounts from a few individuals that they harvest this way from wild colonies (though generally wild harvest is done with stingless bee species other than *Melipona beecheii*) (see figure 5). Timber harvest is also an issue in Quintana Roo since many stingless bees need large diameter trees to nest in. It is possible that this decline in population of *Melipona beecheii* in Quintana Roo is due to human interference with the ecosystem in addition to the invasion of the Africanized bee. I would postulate that stingless bees may be able to adapt to the Africanized bees presence in mature and diverse ecosystems, but a synergistic effect occurs when competition with the Africanized honeybee is compounded by habitat destruction, agricultural burning, timber harvesting in old growth forest, and over-harvesting of honey by humans. Hence, ecological and social factors need to be examined to determine the root of the problem and begin to find a solution.

Figure 5: The Disturbance Factor

Top: Area of forest burned for agriculture. Bottom: a wild hive of *Trigona (Cehpalotrigona) capitata* destroyed by a honey harvester.

Chapter IV Social and Management Aspects of Beekeeping with Africanized Honey Bees and Stingless Bees.

The goal of this portion of the study was to conduct a qualitative analysis of the status of beekeeping and honey marketing in the region and the effects of the Africanized honey bee on beekeeping practice and management, determining in the process what the driving forces are behind the decline in stingless beekeeping over the last two or three decades, as well as what the institutional constraints and market potential are for stingless bee honey. This was accomplished thorough participant observation and semi-structured interviewing with a small sample of both *Apis* and stingless beekeepers, as well as semi-structured interviews with workers at honey processing plants and honey intermediaries.

Field Methods

My sample of beekeepers included six *Apis* beekeepers from two communities (Betania and Kampocolche), eight stingless beekeepers from six communities (Betania, Santa Maria, Kampocloche, Tuzik, San Hermengileo, and the Sian Ka'an Biosphere Reserve) and a group of stingless beekeepers in the town of Felipe Carrillo Puerto with an organization called the *Organización de Médicos Indígenas Mayas*, (Organization of Indigenous Mayan Medicine Men), sponsored by a government agency called the *Instituto Nacional Indigenista* (INI) (See appendix VII for map of the study area and communities). I also spent time in the community of Dzulá, where a group of women were involved in a training program to learn about keeping stingless bees. The women did not make good informants since they were just learning how to keep stingless bees, but it was informative to spend time participating in the program and I was able to learn some details about stingless bee colony management along with the women. I was forced to go to more communities to find stingless beekeepers, since they are rare and difficult to find. The information I got from some stingless beekeepers was very limited, a clear indication of the

decline in traditional knowledge on this subject, so I sought out every stingless beekeeper I was able to identify and locate in order to compensate and compile more information. On the other hand, Most *Apis* beekeepers knew a great deal and I was able to get a wealth of information from each of the six informants, plus four of the six informants were part of organized cooperatives and thus able to give me an idea of the issues on a regional scale. As mentioned, I was not always able to get such good information from stingless beekeepers and I will discuss this phenomenon in more detail later.

For marketing research on *Apis* bee honey I visited two honey processing plants, one in Felipe Carrillo Puerto (Ch'ilan Kabbo'ob), which I made several visits to, and one in Jose Maria Morelos, which I visited once. These processing plants are where most beekeepers in the region sell their honey, so they act as intermediaries between the honey producer and the next steps in the commodity chain. I also interviewed two independent middlemen. Investigating stingless bee honey markets was more difficult. Despite asking around, I was unable to uncover any retail sales points for stingless bee honey in Felipe Carrillo Puerto or anywhere in central Quintana Roo. Marketing of stingless bee honey in central Quintana Roo is very informal and localized within communities. I interviewed Ana Rosa Parra Canto, a meliponiculture specialist from Merida, Yucatan who has worked with various programs, including the one in Dzulá, promoting *Melipona* beekeeping. She was able to give me some information about the limited marketing programs in the States of Yucatan and Campeche.

Effects of Africanization on Management of Apis Bees:

The arrival of the Africanized honeybee greatly effected beekeeping in the region. All bees in this region are now considered Africanized to some degree, and there do not appear to be any pure European honeybees left. Managing Africanized honeybees is more difficult not just

because of their aggressive nature but also because they swarm and abscond more often and many beekeepers have lost numerous hives due to this. All informants indicated that to prevent swarming, hives need to be split more often, as swarming occurs when the colony gets crowded. To prevent absconding, the bees must have sufficient food sources all year round. Informants indicated that the nature of the Africanized honeybee is nomadic, they will leave once resources are scarce and look for greener pastures. The beekeeper has to prevent this by making sure the have adequate resources constantly, especially during the flowering dearth period of August through October. Protective clothing and use of smokers is necessary, and is consistently used by all *Apis* beekeepers in the region; the smoke calms the bees and makes them somewhat less likely to attack. The arrival of the Africanized honeybee caused many to give up beekeeping completely, and those that held on lost many colonies and have had to make more visits to their apiaries. One beekeeper in Betania who has 15 hives, reports he used to have 80 hives of bees before the Africanized honeybee arrived and lost over half to absconding and swarming. All beekeepers I spoke with claimed to have lost hives due to this. All informants visited their hives on a very regular basis, at least three times a week and some visited every day.

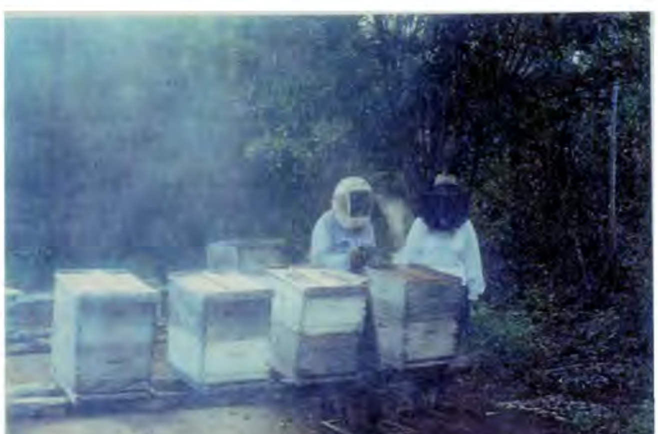


Figure 6: Africanized honeybee apiary

One method of controlling Africanization is through re-queening with European bee queens. This process entails replacing the Africanized queen with a mated European queen, who will begin

laying eggs of pure European decent and thus will temper the colony. This appears to be a tricky process, as the new queen can be rejected by the colony if the timing is not exactly right. Furthermore, it really only solves the problem temporarily since after the European queen dies and a new un-mated queen is born, the new queen is likely to mate with African drones and start the Africanization process all over again. In order for re-queening to effectively combat the problem of Africanization, it needs to be accomplished on a regional scale. Few people appear to be practicing re-queening at this time due to lack of knowledge and resources for obtaining European queens, though most of my informants were anxious to begin. Only one informant, a middleman and beekeeper, had tried re-queening, without any success. The Sociedad Chi'lan Kabbo'ob (a cooperative which runs the honey processing plant of the same name) has plans in the works to start a European "queen farm" and make European queens available to local beekeepers, but at this point it is still in planning stage.

Economics and Honey Production with Apis Bees

As expressed earlier, beekeeping is an important part of the Mexican peasant economy especially in the Yucatan region, and it is a good option for lower income small farmers. From a socioeconomic and labor investment standpoint, Beekeeping works well in combination with the Milpa. The agricultural production of the Milpa has *use value* as well as *exchange value* – meaning the produce from a Milpa plot can be self-consumed (use value) or sold for profit (exchange value) (Ewell and Merrill-Sands, 1987). Honey has mainly exchange value and is used to bring income into the home. In this way, a family can depend on the honey production for monetary income and the Milpa production mainly for sustenance. This takes the pressure off of the Milpa system as a means of generating exchange value, especially as Milpa yields are falling. Three informants who worked with *Apis* bees expressed the desire to increase their beekeeping practice specifically due to the need for increasing household income due to the fact that the

Milpa yields have been dropping recently, and the chicle market, formerly a good source of income for many families in the region, is no longer strong. Timing and labor commitments for beekeeping work well in conjunction with the Milpa. Beekeeping requires minimal land investments and less labor than the Milpa, plus the high season for honey harvest (the months of April and May) are a time when labor requirements for the Milpa are less intense. The Milpa system also provides the bees with plenty of forage opportunities, as many honey sources exist in the secondary vegetation found in fallow. Thus the two systems complement each other well and do not compete for capital. The two systems are also not inter-dependent, so a drop in the yield of one system will not necessarily effect the other. Thus if one system fails one year, the yields from the other can sustain the family (Ewell and Merrill-Sands, 1987).

Marketing

Marketing is usually accomplished through an intermediary who purchases the honey directly from the beekeeper and sells it to other buyers. Some intermediaries will come through communities and buy honey, sometimes a beekeeper will take their honey to town and sell to middlemen, while some sell honey directly to the processing plants. Some honey is even sold at a local level directly from the honey producers, but this amount is fairly insignificant. Recently, some producers have begun to organize into cooperatives, often with assistance of non-governmental organizations (NGO's). The social and economic benefits these cooperatives provide includes technical assistance through the NGO's, help in obtaining government credits, and ability to negotiate directly with markets instead of using a middleman. The Sociedad Chi'lan Kaab'bob is one influential cooperative organization in central Quintana Roo representing apiculturists from 20 communities, including Betania. They have their own honey processing plant in Felipe Carrillo Puerto.

While much of the local honey is bottled in old Coke bottles, Ch'ilan Kabbo'ob gives more value added by using plastic bottles with a nice printed label. There is still a need for better bottling, labeling and branding, and also bar-coding for direct sales to large store chains. Branding the local honey will add value in international markets, as people may pay a premium for "Maya forest honey."

Figure 7: Honey Bottles in Local Store and Ch'ilan Kabbo'ob Honey Processing Plant

Ch'ilan Kabbo'ob also buys and sells beeswax and some pollen, but markets for other bee products, such as propolis and *jalea real* (royal jelly) are not readily available to beekeepers here, or at least many beekeepers are not sure where to sell these products and thus do not harvest them

except for self consumption. I have seen these products for sale only once in a small shop owned by a beekeeper. If beekeepers had markets for these products it could substantially increase their earning potential. Propolis is believed to have immune system stimulant and antibiotic properties; royal jelly and pollen are also thought to have general health benefits. Health food and natural medicine stores in the United States often carry these types of bee products, and they can be found as ingredients in various natural health and beauty products (creams, salves, medicines), but no clear market channels exist for these products in this region.

Most honey producers sell to a middleman, while some sell directly to the local processing plants such as Ch'ilan Kabbo'ob. The honey sold through middlemen can go a number of places. Some middlemen sell directly to buyers such as the companies *Hansa Miel* (a German company) or *Apicola Maya* in Mérida, some middlemen sell to the processing plants. The best deal for the individual beekeeper is to sell directly to the processing plant, or to process it themselves and sell directly to buyers. The latter rarely or never happens except in the case of the middleman who keeps bees himself and sells his own honey plus the honey he buys to the buyers. Most of the honey ultimately gets exported to Europe, especially Germany. According to Güemes Ricalde and Villanueva (2001), 70% of honey from the Yucatan region ends up in Germany, with the rest going to other European countries and the United States. The biggest apparent problem with marketing is that beekeepers, even those in cooperatives such as Ch'ilan Kabbo'ob, get a very low price for their honey compared to what it is sold for to the end buyer. In fact, most beekeepers are unaware of what price their honey sells for in the end market in Europe. It is clear that the more steps that can be eliminated between producer and buyer the better it will be for the beekeeper. Several beekeepers have mentioned to me that the cost of getting the honey to a processing plant is expensive and for some it is near impossible. A beekeeper may harvest 50 or more kilos in one harvest. This is a lot of honey to get to market, especially from the more

remote villages. It is thus easier and less costly for many beekeepers to sell it to the middlemen who come through the village and pick it up for them, even though they would get a higher price if they were able to take it themselves.

Organic Honey

There appears to be a strong market demand for organic honey in Germany which, as mentioned, is the export destination of most conventional honey from the Yucatan. The organic standards of the European Economic Community (EEC) require chemical residues to be no more than ten parts per billion. Although organic commands a premium price on the market, it is not clear how this higher price is distributed along the commodity chain and the price premium to the producer does not appear to be substantial. One middleman with whom I spoke in Dziuché buys conventional honey for 6.50 a kg and organic for only one or two pesos more (7.50 to 8.50). Although at the honey processing plant of the Sociedad Chi'lan Kabbo'ob organic honey can apparently be sold for as much as 18 or 19 pesos a kilo, and regular honey for 8 to 9 pesos. Obviously the price of honey varies depending on where it is sold, and middlemen are taking advantage of ignorance of prices by producers to significantly lower the producers' net gain. EEC organic certification also requires more than just no pesticide use. The hives must be placed in relatively intact forest (*monte alto*) far from any Milpa lands, to avoid contamination from bees visiting crops treated with pesticides and fertilizers. This is inconvenient and increases cost of production since it takes more time and resources to get the honey from such a remote area to the market. Furthermore, the honey must be extracted and processed in stainless steal, which is a more expensive material than traditional sheet metal. Stainless steel extractors are a hefty investment for local beekeepers as they cost around 4,400 pesos (about US$488), although they can be bought subsidized from Chi'lan Kabbo'ob for 2,200 pesos (US$244).

At the processing level, stainless steel filters and containers are also required for processing, and separate filters must be used for organic and regular honey, which is done at the Chi'lan Kabbo'ob processing plant. One bad batch of honey with some contamination can contaminate the whole plant and could have disastrous consequences; this occurred once at Chi'lan Kabbo'ob when a dose of honey containing antibiotics got into the organic honey vats and ruined the whole batch, making it unmarketable on the organic market.

Quality Indicators

The price of both conventional and organic honey is also determined by quality indicators, with the most important of these being water content. High water content honey will ferment more easily; if honey is greater than 18% water, it is likely to ferment, while at 16% water it is considered safe from fermentation. In the Ch'ilan Kaabo'ob processing plant they use a dehumidifier which heats the honey to reduce its water content. This could be an important step for improving honey quality and a practice that is apparently not observed at the honey processing plant in Jose Maria Morelos[6]. At the producer level, a beekeeper has limited control over the water content of his honey, as it is often affected by the level of atmospheric humidity. Honey is not usually harvested late in the rainy season because the high atmospheric humidity leads to high water content.

I was told by several beekeepers that when larvae get into the honey during the extraction process it increases the water content of the honey and reduces its quality in general. A good way to prevent larvae from getting into honey is to have a queen excluder device, which prevents the

[6] This processing plant in Jose Maria Morelos was not in operation when the visit was made, and it apparently had not been in operation for a while. We talked with someone who seemed to be in charge, and with a secretary but could not get a clear answer as to what was going on there, they were resistant to answering questions, but it was obviously less organized and much dirtier than the Chi'lan Kabbo'ob plant.

Queen bee from entering and laying here eggs in part of the colony. It usually placed between the lower and upper box and the Queen remains in the lower box, leaving the upper box free of larvae. The queen excluder is a very simple device that can have a great effect on honey quality at the producer level, but it appears few local beekeepers are using such a device.

Quality is also affected by things over which beekeepers have no control, such as flowering cycles. When the right flowers are in abundance, such as *Tajonal* (*Vigueira dentata*) or *Tzitzelché* (*Gymnopodium florbundium*), a high quality honey will be produced. It should be noted that the two species mentioned both flower in the dry season and are found mainly in early and secondary succession; they are cited in various sources (Porter, 2002; Salvador Flores, 1990) as some of the most important honey sources in the region, and this has been confirmed by several of my informants. The fact that these honey sources grow in the secondary vegetation has more implications for producers of organic honey, who have to put their hives in *monte alto* (mature, upland forest), were it can be more difficult for the bees to reach flowers growing in early succession. Organic honey producers often have to supplement their hives due to lack of floral resources in the *monte alto* during the early dry season, when most of the flowering occurs in the early succession.

Pest Management

Another issue beekeepers face in this region that effects management and quality is the presence of *Varroa* – the parasitic mites which can infest colonies of African honeybees and cause declines in production. The mite infects the bees in larval stage, but does not necessarily kill the larvae. The infected larvae can become adults but will have deformities which will often render them unable to fly or work. Thus an infestation of these mites can have a severe effect on the colony's production. I found that beekeepers use a number of methods for controlling the mites including

formic acid, tobacco smoke, *copal* resin smoke, or manual removal of larvae infested with the mites. Chemical pesticides are rarely used due to the fact that they can contaminate the honey and have negative affects on the bees.

Ants in some ways pose an even bigger problem than *Varroa*. One bad ant attack can seriously cripple or destroy an entire colony. All beekeepers I worked with took extreme precaution against ant attacks, including keeping hives off the ground on long benches and keeping water around the feet of the benches. Algae must be cleared from the water regularly, or the ants can easily walk over the algae. The area surrounding the apiary up to a ten meter radius needs to be cleared and remain clean and free of too much detritus. At the same time, some shade is good for the hives, so some beekeepers try to balance clearing with the proper amount of shade for the hives. Some beekeepers leave one or two small trees standing near the hives which may provide some shade during part of the day. Others keep the area completely cleared and figure the bees are very efficient at cooling their hives on their own.

Melipona Beekeeping

Although I searched far and wide for *Melipona* beekeepers, interviewing all I could find during the fieldwork period, it was more difficult to get knowledgeable information about stingless beekeeping. This is itself is a significant finding, which has two very different explanations. The first explanation is that it is considered privileged ritual information. The practice of Meliponiculture is steeped in religious and ritual significance and is part of traditional Mayan culture. Therefore, some who still keep stingless bees are very traditional themselves, are very protective of their traditional knowledge and not always open to outsiders. Three informants spoke almost no Spanish and I would not have been able to communicate with them without the help of translators. The second explanation is that some stingless beekeepers do it as a casual

undertaking and seem to have very little traditional knowledge about their management. These beekeepers seemed very willing to share information, but when I began asking questions I found that they actually knew very little. Thus, the stingless beekeepers I interviewed fell into two general categories. The first category is that of the traditional *Melipona* beekeeper, who is generally older (>50 years of age), has several jobones and has kept stingless bees for most of his life, and has continued with a family tradition, reporting that his father and grandfather before him kept stingless bees. Four of my informants (including the group at INI) fit this category. The second category was characterized by 5 younger individuals, in their 20s or 30s, who had come across a colony of *Melipona beecheii* while clearing land for the *Milpa* or while doing other activities in the forest, and decided to bring the hive home and care for it. These individuals all had fathers or grandfathers who they could recall keeping these bees and thus had some knowledge, but were not "keepers of the flame" in the same way as the older, more traditional informants. These men had became stingless beekeepers more by accident than by a conscious choice, and they tended to have much less knowledge overall.

Several common themes arose among all informants during interviews. Every informant who I have talked to lamented that the *xunan kab* (*Melipona beecheii*) bees are almost impossible to find now, and recounted how once the forest was full of them. Most link their disappearance to the appearance of the Africanized honeybee, and one informant linked it also to habitat destruction from poorly managed slash and burn agriculture practices. In all cases, these links were made independently by the informants without my prodding or leading them to think in that direction. Each of the *Apis* beekeepers I spoke with echoed this sentiment as well. I also had a number of informal conversations with people in various villages who were not beekeepers but who were curious about what I was doing, and when I explained that I was studying *xunan kab* would volunteer, again without prompting, that they had noticed a decline in the numbers of

Melipona bees in the wild since the arrival of the Africanized honeybee. All informants with multiple hives who where long-time stingless beekeepers have lost significant numbers of colonies of *Melipona beecheii* over the past two decades, and most blame it on the Africanized honeybee. One informant once had 40 *jobones* of *Melipona beecheii* bees in his care only 20 years ago and now has none, all the colonies having died or absconded slowly over the last 20 years. On the day of the interview, this beekeeper had one colony of *Tirgona (Cehpalotrigona) capitata* and one colony of *Scaptotrigona pectoralis* in his care, but no colonies of *Melipona beecheii.*

Stingless bee management issues

For reasons discussed above, getting a handle on management practices with stingless bees was more difficult than for *Apis* bees. *Apis* beekeepers are organized and most have been formally trained in the past by organizations, relatives, or government programs. Traditional stingless beekeeping knowledge was once passed from father to son and the knowledge was shared among members of a community. Honey produced by the bees served as a link between man and god in religious ceremonies, thereby creating a man-bee-god connection. Bees were thus given a high position in the hierarchy of important animals in the Maya culture (DeJong, 1999). However, traditional religious practices have less and less influence on the society and especially the younger generations, as the culture moves into the market economy and younger people are working in the tourist industry and becoming exposed to modern city living. Various Protestant sects (*evangelicos*) are gaining influence and popularity[7]. In addition, satellite TV is now common in remote villages and brings with it the influences of western culture. In the face of all

[7] Although the Catholic church has traditionally had a stronger influence, the Maya have long incorporated Catholicism into their traditional practices. However, the Protestant church with its increasing inroads into remote villages, promotes isolation of practitioners from community practices and thus contributes a faster breakdown of traditional knowledge and practices (Canby, 1992, and personal communication with local people of various faiths).

these changes, the traditional religious practices and thus the associated meliponiculture practices, are rapidly becoming mere folklore. Today, stingless beekeepers are few and far between. Those that choose to keep the bees therefore have little social capital to draw from, in other words they have a limited or non-existent network of shared knowledge and no organized system for learning what they need to know to keep stingless bees. Most of the younger beekeepers I spoke with were going strictly on recollection from boyhood of their fathers or grandfathers who kept the bees. From these recollections they were able to recall the basics of how to harvest honey, but had lost many of the subtleties of stingless bee management, such as hive division or effective pest control, discussed below.

Pest control

As discussed previously, the major pest threats to stingless bees include Phoridae flies. Traditional methods of control include using leaves of *Chakah* (*Bursera simaruba*), however the majority of my informants used nothing. In fact, a few of the younger informants even claimed that stingless bees have no pests and did not seem to be worried about it. Older informants were very aware of pest threats and would take measures, from not opening the hive during rainy season to using *Chakah* to burying remnants of pollen after a harvest, since the flies are attracted to pollen. Younger informants in my sample who were more ignorant about pests were still mostly aware that it was not good to leave the hive open for long. New methods for pest control being taught to the women in Dzulá included the vinegar trap method, but this method does not appear to be widespread and was not encountered among any of my informants.

Colony Division

Another aspect of management that has fallen out of practice is division of colonies. Only the group at INI was actively practicing hive division, all other informants had little to no knowledge

of how to multiply colonies. At first, so many of my informants had so little knowledge about division, I wondered if it had ever been a part of the traditional practice, or if it was knowledge that had just been lost. It appears that the latter is true. According to informants at INI and an outside informant for a group of Mayan dignitaries who keep stingless bees in the traditional way, hive division was traditionally practiced by the Maya. Dejong (1999) confirms this in her study of religious and ritual aspects of stingless beekeeping. The Mayan dignitary group, called *Macanxoc*, an organization of Mayan religious and cultural leaders whose intent it is to preserve Mayan religious rituals and traditions, divides yearly using *jobones*. When the colony produces a new queen, she is moved to a new *jobon* along with some honey, some brood and some pollen pots. Though it sounds simple enough, it is actually very complicated and if not done properly, the new colony is likely to fail. According to DeJong, (1999) there are different philosophies about timing and method of hive division. Some beekeepers do not worry about whether a new queen has been born, but only if the Mother colony is strong. They then move some brood and honey and pollen to a new hive and assume the colony will create a new queen, which indeed often happens. Some beekeepers are insistent on dividing only when the moon is full, which is when bee larvae are though to attain maturity.

The group at INI divides by moving the new colony to box hives. Box hives make division easier, but are not the traditional method. The box hives are small, rectangular white boxes with removable tops. The box hives make it easy to open the hive and observe and have access to the entire colony, rather than opening a hollow log at one end, where you can only see the activity at that end. Box hives seem to allow easier management due to this, but many traditional groups, such as *Macanxoc*, prefer to keep the traditional ways, even if box hives make division easier. A study by Quezada-Euan and Gozalez-Acereto (1994) suggested that colonies fare slightly better

in traditional log hives than in box hives, but that box hives are still relatively good for colony development and allow for better and easier management.

Marketing of stingless bee honey

The honey of the stingless bees can be sold in local markets for extremely high prices. I was told that the market stand price for this honey can be as high as 600 pesos (US$66) a Kilo, or 60 pesos (US$6) for 100 grams. Because of this very high price and its low production volume, the honey is normally sold in small quantities. However, the few stingless beekeepers I spoke with who actually sold their honey usually sold it for closer to 300 pesos per kilo, and one sold his honey for as little as 30 pesos a kilo. The high market price is somewhat mitigated by the low productivity of stingless bees. A hive of *Melipona beecheii* only produces on average 2 kilos of honey a year while Africanized honeybees can produce around 10 kilos a year. Nonetheless, the high market value suggests that an expansion of Melipona beekeeping could be profitable, although little is known about traditional demand.

Markets for stingless bee honey in Quintana Roo appear to be very informal and localized within villages. People who own *jobones* will sell honey to others in the village, or sometimes honey will be given to others in the village for little or no cost if the person is a relation or friend and needs the honey for medicine, for ailments such as a coughs, colds or conjunctivitis. The honey is also still used by some for religious ceremonies. Most stingless beekeepers do not keep the bees for economic reasons at all but for self consumption, medicine, or for religious or personal reasons. Some stingless beekeepers indicated that they had sold their honey once or twice to someone coming through the village, like a middleman. However, the final consumer of that honey is unknown, and I was unable to locate any middlemen who report dealing with stingless bee honey, and in fact all but one stingless beekeeper who claimed to have sold honey this way

were unable to even tell me the name of the person they sold it to. Obviously, it is not a regular occurrence for outsiders to come in and buy stingless bee honey, although it has apparently happened. When asking around at local markets in Felipe Carrillo Puerto, the largest town in the area, I found that most vendors had no idea what I was talking about when I asked for *xunan kab* honey. A couple of older Mayan women vendors understood what I was asking about and indicated that once and a while they get stingless bee honey from *campesinos* who come to town and sell it, but it is rare. They also confirmed that the honey sells for very high prices, and they do sell it for around 60 pesos for 100 grams.

There are some groups in the state of Yucatan and Campeche which are trying to formally market stingless bee honey (Parra Canto, Interview, May 8, 2002). One group in Campeche actually markets to a natural foods store in France. They also sell their honey at local fairs and events. Another group in Mérida sells stingless bee honey to a market stand which specializes in bee products. There is another group located in Mexico City that specializes in the honey of *Scapotrigona mexicana* and makes medicinal products from stingless bee products, including skin creams and salves. They also market the honey for sore throats, bronchitis and colds, and even honey in an eye dropper for cataracts, conjunctivitis and other eye problems. Thus, there is evidence of small-scale successes elsewhere in the Yucatan region for formally marketing stingless bee products.

Discussion

What happened here? Why has a traditional practice going all the way back to the ancient Maya been almost completely phased out just over the past 20 years? A combination of factors are contributing to the change. One factor is the shift to market economy with *Apis* honey and away from production of honey solely for self consumption and religious or personal reasons. Honey is

now more and more thought of as a way to bring economic gain and less and less as a medicinal or religious product. In other words, honey now has more exchange value than use value. These changing values are compounded by the impact of the Africanized honeybee. It is apparent that the native bees are disappearing, and most local people blame the Africanized honeybee. The next chapter will get into details about the impact of the Africanized honeybee on stingless bee abundance and distribution, but what I found from the social aspect of my research is that there was a clear correlation between the arrival of the Africanized honeybee and the noted decline in *Melipona* in the eyes of all local people. Stingless beekeepers who have kept *Melipona* bees for more than 20 years have indicated that their colonies have been slowly disappearing. Stingless bees do not usually abscond, in fact a colony can inhabit the same *jobon* for decades according to informants. However, when conditions become excessively stressful, colonies will abscond. The fate of the absconded colony is unknown, but most informants postulate that it is death. Absconding of *Melipona* colonies has become increasingly common and has caused stingless beekeepers to loose colonies over the past two decades. Some stingless beekeepers claimed that the Africanized honeybee actually physically attacks hives of stingless bees, but there is no scientific evidence to support this claim. Africanized honeybees are not prone to attacking other colonies, and it is unclear how the individuals who claimed that came to that conclusion. It is clear that the Africanized honeybee is the bad guy in the minds of most stingless beekeepers.

The gradual loss of colonies has led to a breakdown in social capital among Mayan stingless beekeepers. Social capital is defined by Stiglitz (2000, p. 59) as "…tacit knowledge, a collection of networks, an aggregation of reputations and organizational capital." In other words, it is network of shared knowledge of a regular activity; a resource pool of knowledge, conventions, rules and patterns of interactions which allow an individual who has access to that social capital to succeed at a given activity. It is known that social capital wears out with disuse rather than use

(Ostrom, 2000). Social capital of stingless beekeepers was utilized less and less as the bees began their disappearing act, and gradually practitioners began to give up, some probably opting for *Apis* beekeeping instead, leaving the next generation without any social capital to draw from. Thus the newest generation of stingless beekeepers, including all the younger individuals of my sample, is left with limited knowledge and no knowledge pool or network to draw from. This compounds the problem because now younger individuals are more prone to mismanaging colonies, and thus more likely to loose them. Furthermore, the knowledge of how to multiply colonies has all but disappeared, so younger individuals have no knowledge of how to go from having one hive to having many. When that one hive dies, the bees are gone until they can find a new hive in the forest.

As for the older generation, why is it that a few have continued to successfully keep stingless bees for the past two decades while so many have failed? This is an important question which I was unable to solidly answer from my study, however speculation points to the possibility that most older practitioners did not change their management practices when the stingless bees began to be under stress from competition. Obviously something changed in the environment to cause stress to domesticated colonies. Habitat destruction explains why it is more difficult to find wild colonies, but why have domesticated hives been disappearing? It would seem that domesticated colonies could still survive if habitat destruction were the only factor, since human beings were providing adequate habitat. Clearly, some environmental stress caused domesticated stingless bees to begin to struggle, but beekeepers may have been ignorant of it until it was too late. The one stingless beekeeper in my sample, who had lost 40 hives in the past 20 years, admits to having continued to harvest honey very often even after the arrival of the Africanized honeybee. Other more successful older stingless beekeepers have been more conservative and harvested a more limited volume, only once a year and less than the total colony production. Sustainable

harvest levels could account for the difference between successful and non-successful stingless beekeepers. To illustrate these interrelated factors which have contributed to the decrease in stingless beekeeping, see the conceptual model in Figure 8. Here we can examine how the different pieces of the puzzle begin to fit together and produce the outcome of an extreme drop in stingless beekeeping in favor of *Apis* beekeeping over the past 20 years. We also begin to see the institutional constraints to stingless beekeeping and why bringing it back to its previous state will require overcoming numerous ecological and institutional barriers. The bold lines indicate the presence of a negative feedback loop, whereby a breakdown of social capital leads to poor management practices among the younger generation, leading to loss of domestic colonies and further breakdown of social capital.

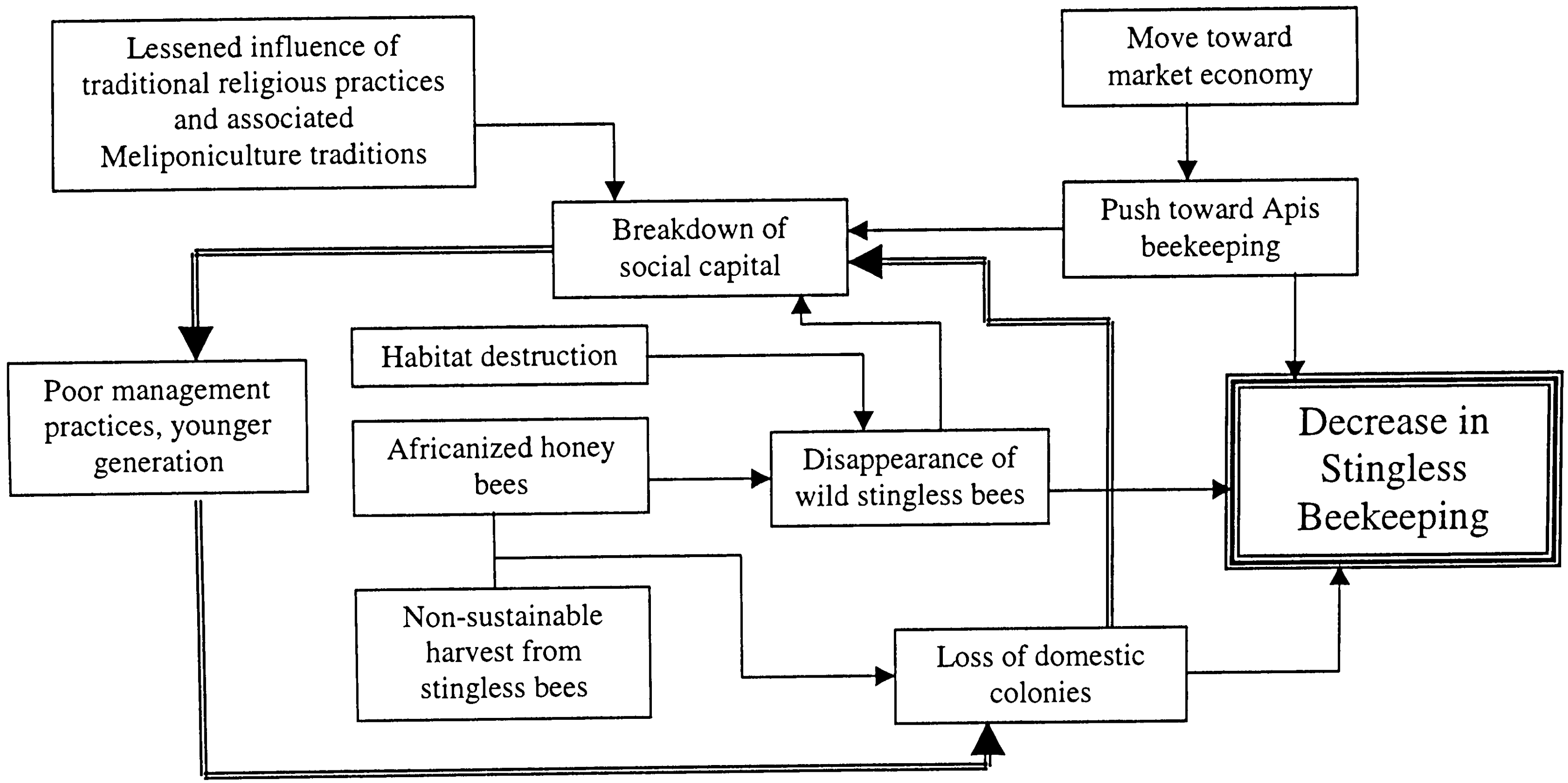


Figure 8: Conceptual Model: factors influencing changing dynamic of beekeeping with stingless bees.

Chapter V: Diversity and Distribution of Bee Fauna in Three Communities

Introduction

The purpose of the diversity studies was to give an overall view of the diversity, abundances and dominance of different bee species and observe significant patterns in diversity of bees in three areas with different degrees of human induced ecosystem disturbance. It was ascertained from interviews that local people have noticed changes in the populations of some stingless bee species, mainly *Melipona beecheii*. The next goal is to determine through ecological research what the actual abundance patterns are and if there are any differences between highly disturbed areas and less disturbed areas. Understanding population structures of the bees which are most commonly exploited for honey can give insight into management alternatives. It was also my intention to observe behavior patterns among bees visiting flowers to determine if any competitive interaction was occurring between different species.

Study Area

Three areas were chosen for the diversity study: the traditional Mayan ejidos of Kampocolche and Santa Maria, and the Sian Ka'an biosphere reserve (see appendix VIII for maps of the study area). In Kampocolche, with an ejido territory of about 10,000 ha, predominate vegetation includes medium sub-deciduous forest, patched with some semi-evergreen and lowland areas. The community is a traditional Mayan farming village, predominate land uses include Milpa agriculture, agroforestry and beekeeping. Timber harvest is mainly restricted to *palizada* or small diameter trees used mainly for housing, some of which is sold commercially. Kampocolche is thought to be to the north of the naturally occurring ranges for mahogany and cedar, the major timber species of the lower Yucatan, and there may not have ever been much of a presence of these timbers in the forest here. Kampocolche does not have an official permanent forest area, as many *ejidos* which practice selective logging do. The forests of Kampocolche are by far the most degraded of the three study areas, with only one or two small patches of mature forest. The forest

here was heavily impacted by a fire in the early 1960s. Santa Maria is also a traditional Mayan farming community, some 30 miles to the south of Kampocolche, with an ejido territory of 9,226 ha. Vegetation in Santa Maria features a large relatively intact forest mass with medium semi-evergreen forests, some seasonally inundated low forests (*bajos*), seasonally flodded grasslands or savannas (*pantanos)* and sub-deciduous patches. Predominate land uses include Milpa agriculture, agroforestry, and logging of mahogany and cedar under government-approved management plans. Beekeeping is not common here. The forests of Santa Maria are remarkably intact, partly due to their designation of permanent forest areas which are used exclusively for managed logging and never burned for agriculture. Thus large tracts of mature forest exist, though there are areas of milpa agriculture and various stages of secondary succession, mainly in the central area of the community surrounding a small lagoon. An examination of satellite images of Kampocolche and Santa Maria, produced by a joint research project between the University of Quintana Roo and Florida International University, quickly reveals the dramatic difference in terms of amount of mature forest cover in the two areas (see appendix IV). Finally, the Sian Ka'an Biosphere Reserve is an UNESCO-registered reserve of 528,000 ha which extends along the eastern coast of the Yucatan, and is mostly composed of various kinds of wetlands with some terrestrial ecosystems. My sampling was done in a small area of the northern portion of the Sian Ka'an, which is characterized by medium sub-deciduous and semi-evergreen forest, with many patches of low forest as well as seasonally flooded *pantanos*. Toward the east there are salt marshes and mangroves as well, which are not seen in either of the other two communities which are farther inland. Few people live in the Sian Ka'an, and those that do are spread out rather than clustered in a single community. Though some agriculture is practiced by the people who live in the biosphere, human population is so low in this area that the mature forests are almost entirely intact. The intention of choosing these three areas was to have one area of low disturbance (Sian

Ka'an), one area of moderate disturbance (Sta. Maria) and one study area of high disturbance (Kampocolche) and see the differences in bee diversity and abundances.

Field Methods

Study period

The field study took place between February and May of 2002, during the dry season. Unseasonably heavy rains characterized the first part of February and made data collection difficult, though by the end of February rains had ceased entirely. Data collection then continued through all of March, April and the first half of May. There was no rain at all during March and April, though a few scattered showers started to occur in late May.

Sampling Procedures

In each of the three areas, nine transects were sampled, each of approximately 2km. Transect walks would begin between 7am and 8am eastern standard time, stopping around noon, and sometimes continuing again from 4pm until sunset. Preliminary observations revealed very little activity between noon and 4pm in terms of pollinator visitation. Along each transect, intensive observation points were taken at flowering patches. The number of points taken along each transect varied depending on how many patches were encountered, averaging about 3 points per transect. My criteria for determining whether points were appropriate for observation included three main factors: 1) it had to be a known melliferous or polliniferous species, 2) it had to be observable and 3) it had to be in or near peak flowering.

First it was determined if the flowering species was one known in the literature to be a melliferous or polliniferous species important to stingless and *Apis* bees (Porter, 2001; Villanueva, 1999, 1994; Rico-Grey et al., 1991; Medellin Morales et al., 1991; Flores, 1990; Suarez Molina, 1981; Souza Novelo, 1981). A Mayan informant from each community was hired

as a guide and to help with local plant identification. When I was not able to identify the species based on my own knowledge I would sample it only if 1) the guide recognized it as an important melliferous or polliniferous species, 2) the flower had an easily recognizable pollination syndrome[8] as a generalist or bee attracting species, and 3) if bees were clearly visiting the specimen in question. Seventy-five percent of the species sampled came from the following six plant families: *Leguminosae, Compositae, Polygonaceae, Anacardiaceae, Malpigiaceae*, and *Verbenaceae* (see appendices V and VI). The second criteria for determining if the point was appropriate for sampling was that the specimen in question needed to be observable, meaning it was possible to reach and see the flowers and observe them comfortably for 20 minutes. Some tall trees were climbed if it was possible, other times the lower branches on a tall tree were doubled over with rope and brought to eye level. When this was done it was appropriate to wait for a few minutes before beginning the formal count, since the effects of climbing or lowering branches would often disturb the bees which were already present, though after a time activity would return to normal. A third criteria was that the flowers needed to be either at peak flowering or just slightly past peak. If flowers were still mostly in bud stage or if fruiting had begun, the flowers were not sampled.

After the initial determination that the point was appropriate for sampling, an informal 5 minute observation period would begin in which I would determine the overall level of visitation activity at that patch, with four categories of intensity of visitation: heavy, moderate, minimal, and no visitation. If, during this initial observation period, no visitors were observed at all, the point would not be sampled under the assumption that that flowering patch was not ideal for sampling if it was not attracting any visitors at that moment. The intention of this was to avoid having numerous data points with zero values. If the initial observation showed minimal to heavy

[8] Pollination syndrome is indicative of specific traits of a flower, such as color, shape, odor, depth, size etc. which to some degree help predict what kind of pollinators are attracted to that flower (Proctor et al., 1996).

visitation, the formal observation period would then begin. The formal observation consisted of two periods of ten minutes each, counting all visitors, and capturing voucher specimens after the count. It was important not to disturb the area of observation during the count by catching specimens. In this way, I was able to sample 26 points along 9 transects in Kampocolche, 22 points along 9 transects in Santa Maria, and 21 points along 9 transects in the Sian Ka'an, for a total of 69 points along 27 transects, and a total of 23 observation hours.

Identification of specimens

Voucher specimens of each plant species sampled were collected. My field identifications were confirmed and unidentified specimens were identified by Odilón Sanchez, botanist at the Colegio de la Frontera Sur (ECOSUR) and deposited in the ECOSUR herbarium (CIQRO) in Chetumal, Quintana Roo, Mexico. Insect specimens were identified or confirmed by Dr. David W. Roubik, entomologist at the Smithsonian Tropical Research Institute (STRI) and deposited in the museum at CIQRO. Some specimens of non-*Apidae* bees were identified to genus level only. Field identification of stingless bees was done using identified vouchers, but to avoid field identification errors as much as possible, I grouped some morphologically similar bee species into a single morpho-species group. The three species of *Plebia* in the region included in my sample are *Plebia minimia, Plebia frontalis* and *Plebia jatiformis*. Because these three are morphologically similar and difficult to distinguish at flowers, they were grouped into a single morpho group. *Trigona corvina* and *Trigona fuscipennis* were grouped together as well, as both are small, entirely black bees of the same size and nearly impossible to distinguish at flowers[9] (figures 9 and 10). All other bees had distinguishing characteristics sufficient enough to make field identification possible, though some identification error cannot be completely ruled out.

[9]The vast majority of my collected specimens for this morpho group fit *Trigona fuscipennis* when identified with voucher specimens, leading me to believe that *T. fuscipennis* is the more common of the two.

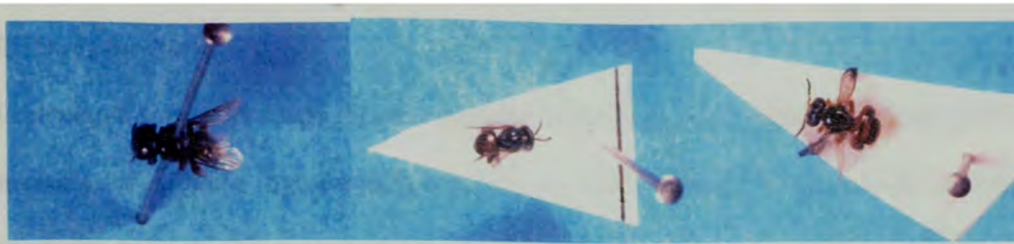


Figure 9: *Plebia frontalis, P. minima*, and *P. jatiformis* as one morpho group.

Figure 10. *Trigona fuscipennis* and *T. corvina* as one morpho group.

Diversity Indices and Statistical Tests

Common diversity indices applied to biodiversity studies include measures of richness, evenness, and dominance. Species richness is defined as simply the number of species in a given sample area or within any number of individuals. Species richness will inevitably increase with sample size. Richness does not consider evenness, a measure of the relative abundance of each species, giving consideration to how many individuals make up each species or what percentage of the total population is represented by one species. In many species assemblages, one species will make up the majority of the total assemblage. Measures which are weighted toward the abundance of the commonest species are considered dominance measures (Magurran, 1988). For comparing the species assemblages of bees in the three study areas, I employed a number of diversity indices to measure richness, evenness and dominance in all three sampling areas and compare the results of different measures.

Richness measures

I calculated species richness (S), the Margalef index (D_{mg}) and the Shannon index (H') as measures of richness. Species richness (S) is a simple whole number indicating the total number of unique species, or morpho-species when appropriate, observed in a given location. Margalef (D_{mg}) is a simple calculation combining S (species richness) and N (total number of individuals overall) (Magurran, 1988):

$$D_{mg} = (S-1)/\ln N$$

The Shannon index, often referred to as the Shannon-Weaver index, is a richness measure that takes into account the proportional abundances of each species. It is given by the equation (Magurran, 1988):

$$H' = -\Sigma p_i \ln p_i$$

Where p_i is the proportional abundance of the *i*th species (n_i/N).

Dominance and evenness measures

I calculated the Simpson index (D), the Berger-Parker index (d) and the Shannon Eveness index (E) as measures of dominance and/or evenness. Simpson's index is a dominance measure that gives the probability that any two individuals drawn at random from a population will be of different species. It is calculated as (Magurran, 1988):

$$D = \Sigma\ (n_i(n_i-1)/N(N-1))$$

Where n_i is the number of individuals in the *i*th species. The inverse of D (1/D) is used to show how evenness and diversity decreases as D increases. The Berger-Parker index (d) is a measure of dominance which expresses the proportional significance of the most abundant species (Magurran, 1988):

$$D=N_{max}/N$$

Where N_{max} = the number of individuals in the most abundant species. Again, the reciprocal form (1/d) shows a trend of decreasing diversity with increasing values of d. Finally, the Shannon evenness index (E), which is an extension of the Shannon index (H') expressed above, will increase with increasing diversity. Although the Shannon index (H') takes into account the relative abundance or evenness of species, the Shannon evenness measure is a way to calculate a distinct additional evenness measure. It measures the ratio of observed diversity to maximum diversity, which would theoretically occur in a population where all species are equally abundant. Maximum diversity or H_{max} = lnS, therefore:

$$E = H'/\ln S$$

Shannon t test

Hutcheson (1970) provided an effective method of calculating a "*t*" statistic for the Shannon index in order to be able to compare two different sampling areas and test for statistical significance. This process uses the variance of H' which is calculated by (Magurran, 1988):

$$\text{Var } H' = [\Sigma\, p_i (\ln p_i)^2 - (\Sigma\, p_i \ln p_i)^2/N] + [S-1/2N^2]$$

Data from two communities is then compared by calculating *t* (Magurran, 1988):

$$t = H'_1 - H'_2/(\text{Var } H'_1 + \text{Var } H'_2)^{1/2}$$

where H'_1 is the diversity of sampling area 1 and H'_2 is the same for sampling area 2. Likewise Var H'_1 is the variance of area 1 and Var H'_2 of area 2. Once a t value has been determined, the correct degrees of freedom then must be calculated in order to utilize a t table. In this case degree of freedom is calculated by (Magurran, 1988):

$$df = [(\text{Var } H'_1 + \text{Var } H'_2)^2] / [(\text{Var } H'_1)^2/N_1 + (\text{Var } H'_2)^2/N_2]$$

I utilized these tests in order to compare my three sampling areas and test for significance. All diversity indices were calculated for all bee species including non-Apidae bees, and for stingless bees only. It should be noted that although Africanized bees share a large proportion of resources with other types of small and medium sized bees, including the *Meliponinae*, they do not share

the same resources with many larger bees such as *Centris, Bombus*, or *Euglossa* (Roubik, 1982). Therefore, this study is biased toward *Apis* and *Meliponinae* bees and toward some of the smaller and medium sized bees of other families, and does not include an accurate depiction of the abundance or distribution of larger bee species.

Goodness of fit test

Rank abundance plots are often used in order to plot species abundance data, and they can reveal a great deal about patterns of dominance or evenness in a species assemblage. Sometimes, however, applying a mathematical model can serve to further clarify apparent patterns. I chose to run a goodness of fit test for the geometric series due to the fact that much of the data appeared to fall in a straight line when plotted on a rank abundance plot. The geometric series is a distribution pattern which is based on a niche pre-emption hypothesis, meaning that the most dominant species pre-empts a proportion of a limiting resource, while the next dominant species utilizes the same proportion of the remaining resource and so on until all species are accounted for. This pattern is most often found in species-poor assemblages and environmental conditions that are harsh or stressful, or in early succession. The species abundance pattern will move away from the geometric series as conditions improve or the species assemblage becomes richer. The abundance of species ranked from most to least abundant in a geometric series will be (Magurran, 1988):

$$n_i = NC_k k(1-k)^{i-1}$$

Where k= the proportion of available niche space occupied by each species, n_i = the number of individuals in the ith species, and C_k is the constant that insures that $\Sigma n_i = N$, given by $[1-(1-k)^s]^{-1}$ (Magurran, 1988).

Statistical tests

After calculating an overall diversity index for each of the three sample areas, in which each individual bee was weighted evenly, ran some more conservative statistical tests in which data from each transect were treated separately, therefore giving equal weight to each transect rather than each individual, resulting in an equal N value of 9 for each community. I calculated the Shannon diversity index, Shannon evenness index and the Berger-Parker dominance index for each transect. These indices were selected because they are the least sensitive to sample size and include one measure of diversity, one measure of evenness and one measure of dominance. S and Margalef do not stand up to this type of test, since the number of species encountered along a transect (S) will be greater in Kampocolche, where there were more bees overall, than in the Sian Ka'an, even though S is greater overall in the Sian Ka'an for stingless bees. I also calculated the percent abundance of *Apis* bees and stingless bees per transect, as well as the percent abundance of *Trigona fulviventris* and percent of all stingless bees minus *T. fulviventris* per transect (due to the dominance of *T. fulviventris* in Kampocolche and Santa Maria). I then ran one way Analysis of Variance (ANOVAs) with these data to compare the difference between communities. Originally I had planned to calculate the percent abundance of *Melipona beecheii* for each transect as well and run tests to see whether there were significant differences in dominance of *M. beecheii*, but to my dismay I only encountered three individuals of *M. beecheii* at flowers in my entire study, making this test impossible. It is sufficient to conclude simply that this species is rare in all areas.

Results

Descriptive Data

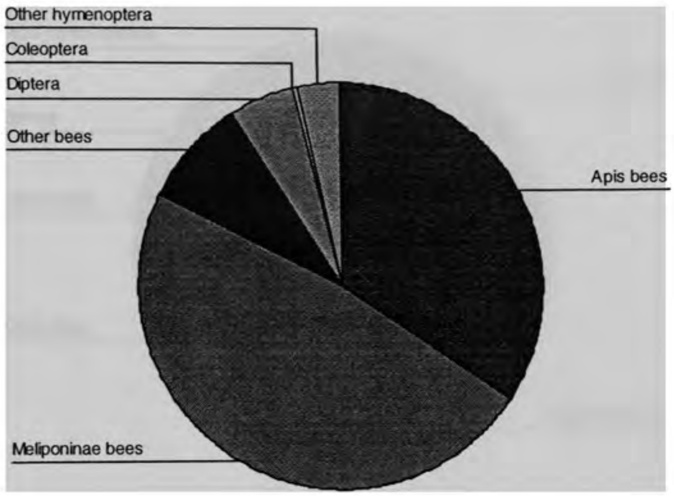
A few trends became immediately apparent during sampling before any formal analysis was carried out. Two species of bees were clearly dominating all floral resources in Kampocolche

and Santa Maria – *Apis mellifera* and *Trigona fulviventris*. In Kampocolche, *A. mellifera* was the more dominant species, making up 39% of all bees observed, where *T. fulviventris* made up 34%. In Santa Maria, *T. fulviventris* was actually the dominant species making up 29% of all bees observed, and *A. mellifera* made up 22%. In the Sian Ka'an, *T. fulviventris* was almost non-existent, but *A. mellifera* was still dominant, making up 31% of all bees observed. *Melipona beecheii* was only observed at flowers in the Sian Ka'an, and made up only 1.7% of the total bees observed there (only three individuals). This is disturbing given that *M. beecheii* used to be a very common species according to local people.

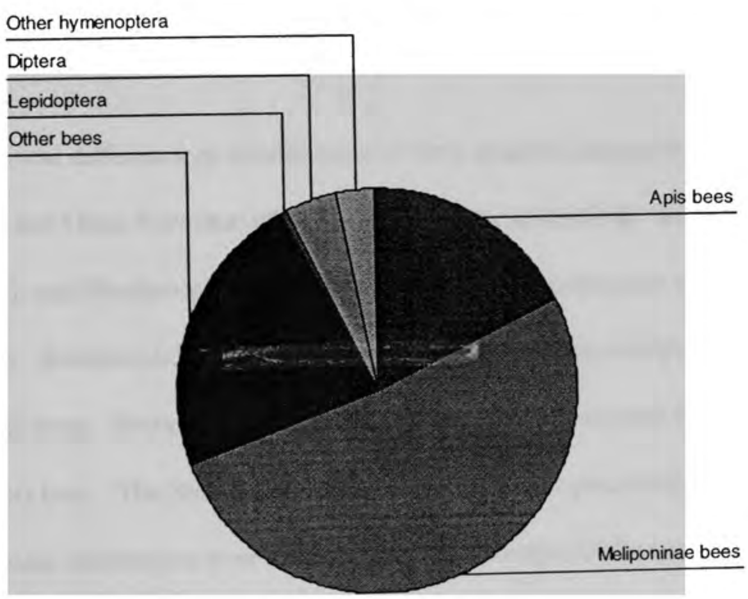
Figure 11: *Trigona fulviventris*

I also observed a greater diversity of pollinator types in the Sian Ka'an, including Lepidoptera, Diptera and other Hymenoptera (wasps and ants), perhaps due to the fact that bees are less abundant in general there and only made up about 75% of the total floral visitors in my sample for the Sian Ka'an, as opposed to 91% bees in both Kampocolche and Santa Maria (see figure 12). The phenomenon of lower abundance of bees in the Sian Ka'an will be discussed in more detail later.

Kampocolche



Sta. Maria



Sian Ka'an

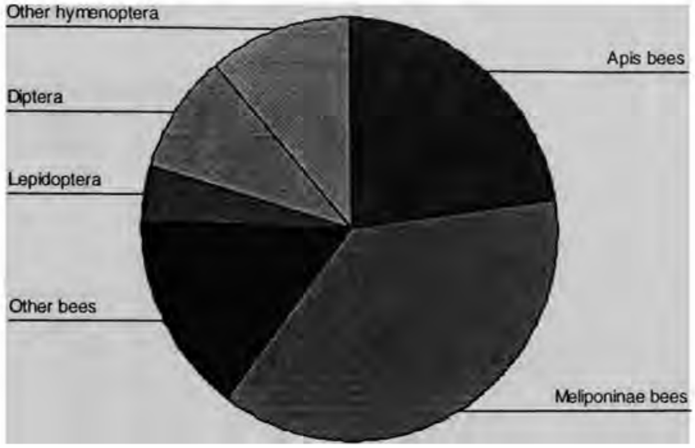


Figure 12: Pie Charts – Distribution of Pollinator Types in Three Sampling Areas

Two way tables reveal difference in distributions of three general categories of bees: *Apis* bees, *Meliponinae* bees and Other bees (see table 1). A chi square test reveals the differences are significant ($P<.05$), and Bonferroni post hoc test shows the differences are significant among all three communities. Kampocolche has the highest percentage of *Apis mellifera* and the lowest percentage of other bees. Santa Maria shows the highest *Meliponinae* and Other bees, and the lowest level of *Apis* bees. The Sian Ka'an shows a slightly lower percentage of *Meliponinae* bees, but a more even distribution over all categories than Kampocolche (see figure 13).

			Community			Total
			Kampocolche	Santa Maria	Sian Ka'an	
Bee Group	***Apis mellifera***	Count	192	90	55	337
		% within community	38.79%	21.79%	31.07%	31.06%
	Meliponinae	Count	262	215	89	566
		% within community	52.93%	52.06%	50.28%	52.17%
	Other bees	Count	41	108	33	182
		% within community	8.28%	26.15%	18.64%	16.77%
Total		Count	495	413	177	1085
		% within community	100.00%	100.00%	100.00%	100.00%

Table 1: Bee Group by Community Crosstabulation

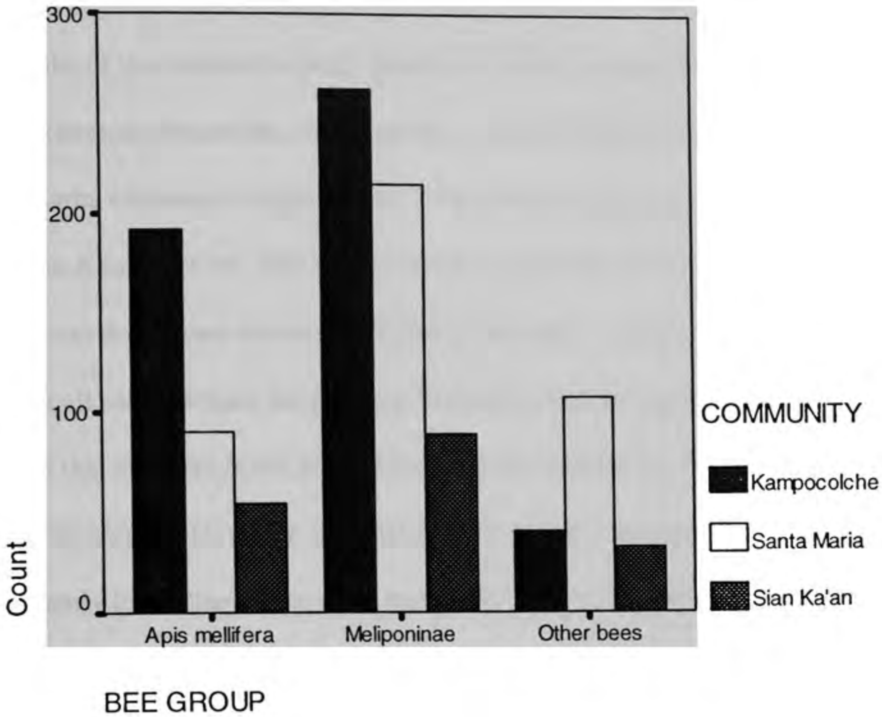


Figure 13: Bee Group by Community

Diversity

The results of the various diversity indices for all bee species observed are summed up in table 2. When examining the results, clear patterns emerge. Richness measures are consistently highest in Santa Maria, evenness is highest in the Sian Ka'an, while dominance measures are consistently highest in Kampocolche. The inverse of the two dominance measures show clearly that diversity increases as dominance decreases. Richness measures were lower in the Sian Ka'an than in Santa Maria in all cases, despite the fact that Shannon evenness was highest in the Sian Ka'an. This suggests that there are fewer actual species in the Sian Ka'an, but those that are there are more evenly distributed. However, the total number of bees observed in the Sian Ka'an was significantly lower than in the other two areas. Where I observed N = 495 and N = 413 individuals in Kampocolche and Santa Maria respectively, I only observed N = 177 individuals in the Sian Ka'an, despite equal sampling effort. It was very that the bee fauna of the Sian Ka'an has lower density than the other two sampling areas. Because the sample size was so much lower in the Sian Ka'an, it is possible the lower richness numbers are due to the smaller sample size, especially in the case of the measures S and Margalef, which are both highly sensitive to sample size.

The Shannon index is less sensitive to sample size and therefore is probably the most accurate of the three richness measures. We can see in the case of the Shannon index that the lowest richness measure is in Kampocolche (1.6), while the measures for Santa Maria and the Sian Ka'an are higher (2.213 and 1.978 respectively). The results of the Shannon index usually fall between 1.5 and 3.5 and are usually normally distributed (Magurran, 1988). Therefore, the fact that Kampocolche is just above 1.5 shows that it is a very low measure on the Shannon index scale.

Name of index	Richness, dominance or eveness	Results		
		Kampocolche	*Sta. Maria*	*Sian Ka'an*
Individuals (N)		495	413	177
S (species richness)	Richness	13	20	12
Margalef	Richness	1.93	3.15	2.13
Simpson (D)	Dominance	0.281	0.159	0.175
Simpson inverse (1/D)	Dominance Inverse	3.563	6.304	5.726
Berger-Parker (d)	Dominance	0.388	0.288	0.311
Berger-Parker inverse (1/d)	Dominance Inverse	2.578	3.471	3.218
Shannon (H')	Richness	1.6	2.213	1.978
Shannon E	Evenness	0.6237	0.7389	0.7961

Table 2: Diversity Index Results – All Bees

From this data it can be concluded that Kampocolche actually has the lowest diversity of the three communities, given that the dominance measures are consistently highest and the richness measure that is least subject to sample size is significantly lower than the other two communities. The t test for the Shannon index confirms this. It showed significance ($p < .0005$) for the difference in diversity between Kampocolche and the Sian Ka'an, and for the difference between Kampocolche and Santa Maria. The difference between Santa Maria and the Sian Ka'an is also significant, but to a slightly lesser degree ($p = .001$). Thus when considering all bee species, Kampocolche is significantly less diverse than the other two areas, and that the Sian Ka'an is significantly less diverse than Santa Maria.

When the same indices are calculated for stingless bees only, the picture changes. Table 3 shows the results of the same indices for stingless bees in the three areas. Examining these results we find that evenness and richness measures are now consistently highest in Sian Ka'an. This time, even the richness measures which are sensitive to sample size are highest in the Sian Ka'an, despite the lower N value. Dominance measures are again consistently highest in Kampocolche but only slightly lower Sta. Maria, and both dominance measures in the Sian Ka'an are close to

40% lower than Kampocolche and around 30% lower than Santa Maria. The major difference in dominance can be explained by one stingless bee species – *Trigona fulviventris* – which was extremely dominant in both Kampocolche and Santa Maria, almost to the exclusion of all other stingless bee species.

Name of index	Richness, dominance or evenness	Results		
		Kampocolche	*Sta. Maria*	*Sian Ka'an*
Individuals (N)		262	215	89
S (species richness)	Richness	6	6	7
Margalef	Richness	0.90	0.93	1.34
Simpson (D)	Dominance	0.460	0.381	0.252
Simpson inverse (1/D)	Dominance Inverse	2.174	2.622	3.968
Berger-Parker (d)	Dominance	0.645	0.553	0.393
Berger-Parker inverse (1/d)	Dominance Inverse	1.550	1.807	2.543
Shannon (H')	Richness	1.076	1.183	1.538
Shannon E	Evenness	0.6006	0.6605	0.7902

Table 3: Diversity Index Results – Stingless Bees

In Kampocolche, *T. fulviventris* made up 64% of the total stingless bee fauna sampled, and 55% in Santa Maria. In the Sian Ka'an, there was no evidence of an extreme dominance of *T. fulviventris,* with this species making up only 2% of the total sample. The morpho group which includes *Trigona fuscipennis* and *Trigona corvina* was the dominant group of stingless bees in the Sian Ka'an, making up 39% of the sample of stingless bees[10] (see appendix VII). With richness and evenness measures highest and dominance measures so much lower in the Sian Ka'an, it appears there is a clear evidence to make the case that there is a higher degree of stingless bee diversity in the Sian Ka'an than in Kampocolche or Santa Maria. The Shannon index t test confirms this. There was significance ($p<.0005$) for the difference in diversity between the Sian Ka'an and Kampocolche and the Sian Ka'an and Santa Maria. There was significance for the difference between Kampocolche and Santa Maria only at the alpha .10 level ($p <.10>.05$). Thus,

[10] It can be noted that all voucher specimens matched with *T. fuscipennis* from the Sian Ka'an, it is thus likely that *T. fuscipennis* is the dominant stingless bee species in the Sian Ka'an.

the Sian Ka'an is significantly more diverse than the other two areas in terms of stingless bees, and stingless bee diversity in Santa Maria is marginally higher than in Kampocolche.

Rank-Abundance and the Geometric Series

Though numbers obtained from diversity index calculations are informative, plotting the data is useful for gaining additional insight into patterns of abundance. The relative abundance of each species is plotted against the species' rank, in order from most abundant to least, on a logarithmic scale (figure 14). A test of fit for the geometric series was applied to all, with very interesting results. I made rank abundance plots of all bee fauna in the three communities, and additional plots for stingless bees only in the three communities. In a total of six plots, three fit the geometric series: stingless bees of the Sian Ka'an, all bees of the Sian Ka'an and stingless bees of Kampocolche. Looking at the plots of expected and observed values (figures 15 and 16) we see that even in the cases where the fit is not statistically significant, it is still very close, meriting further investigation. Dominance still appears to be highest in Kampocolche although the species abundance data does not statistically fit the geometric series. Upon close inspection of the observed and expected plots for all bees of Kampocolche we see that the first points (representing dominant species of *Apis mellifera* and *Trigona fulviventris*) fall above the expected points, but after that most subsequent points fall below the slope of the geometric series line. Thus, the rank abundance plot reveals that dominance is strong in Kampocolche.

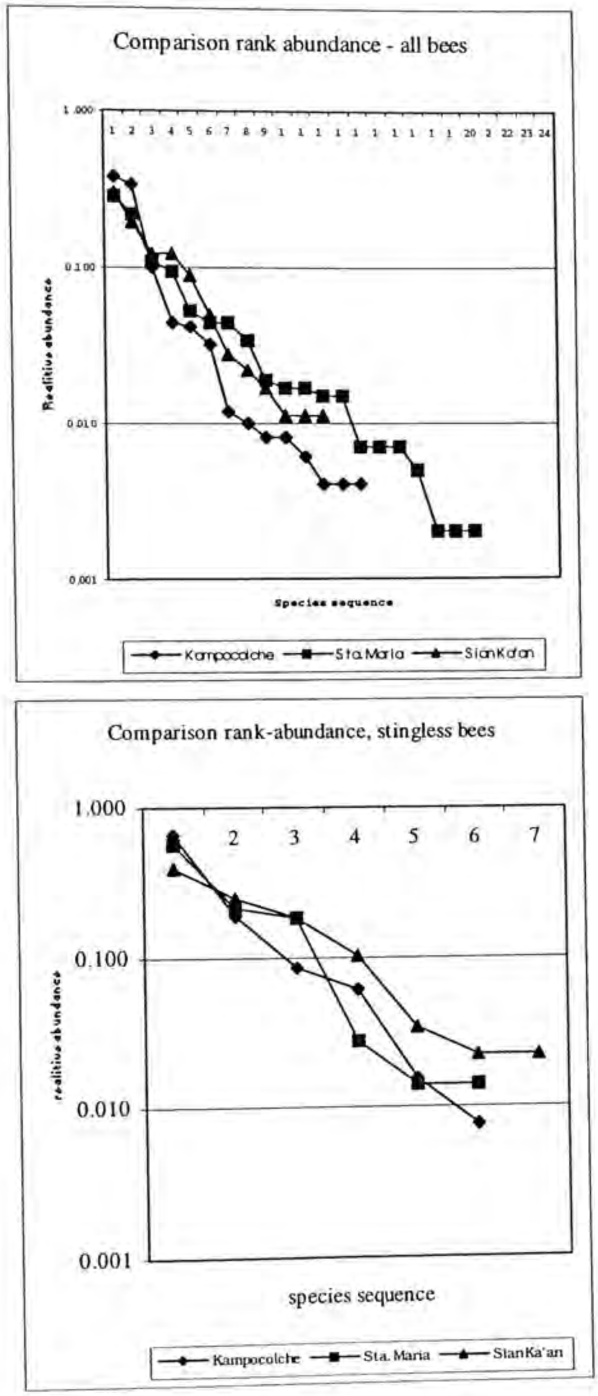
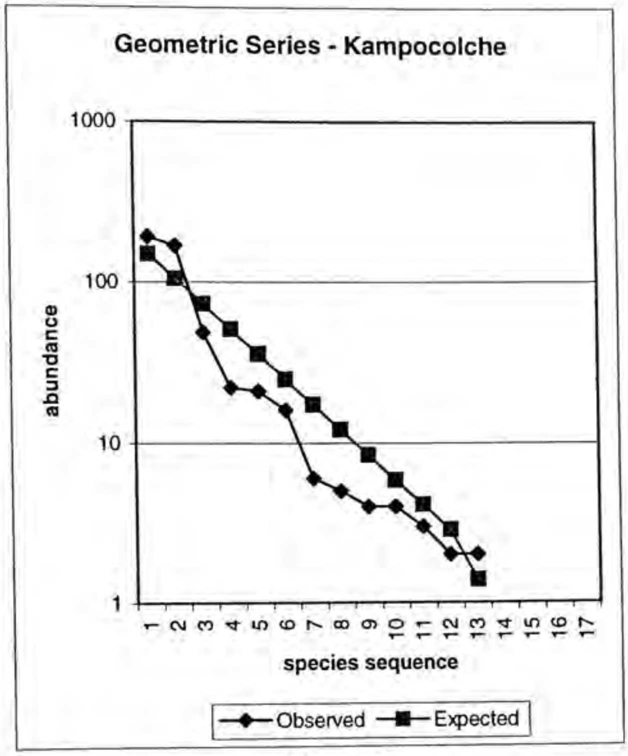
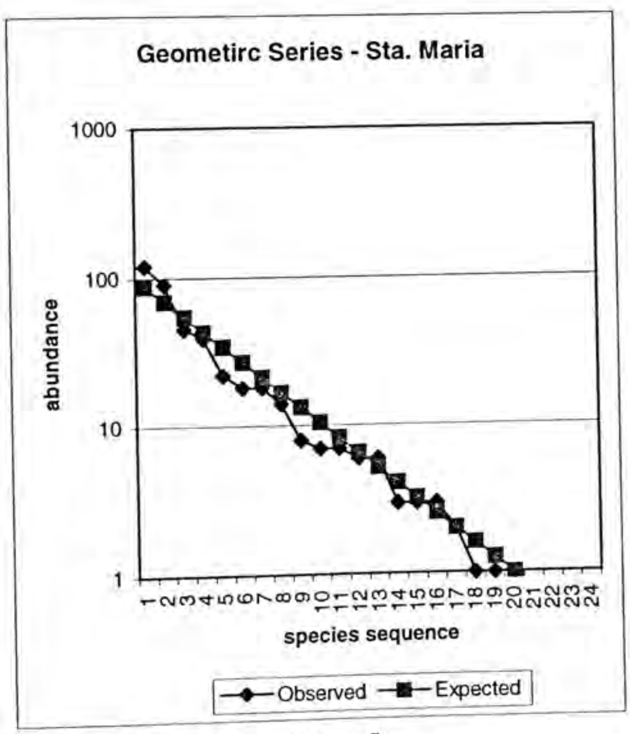


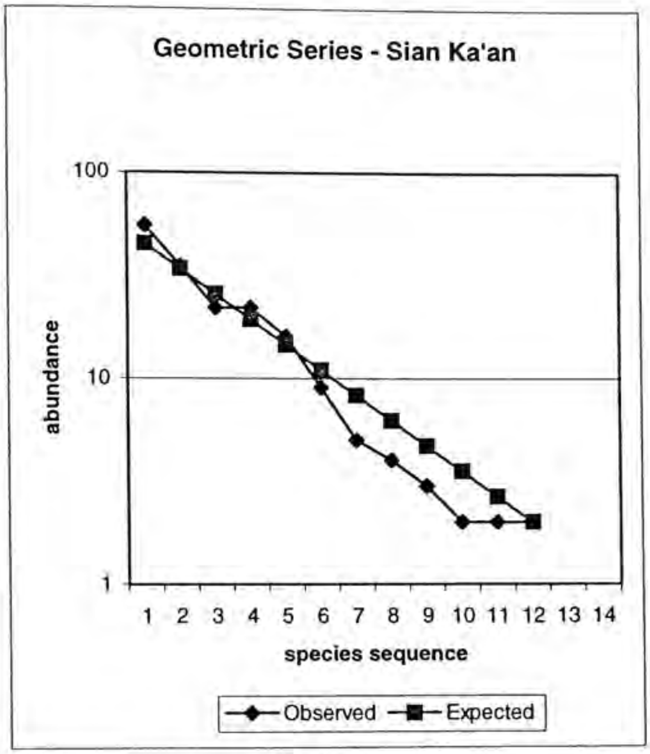
Figure 14: Comparative Rank-Abundance



p<.001: no fit

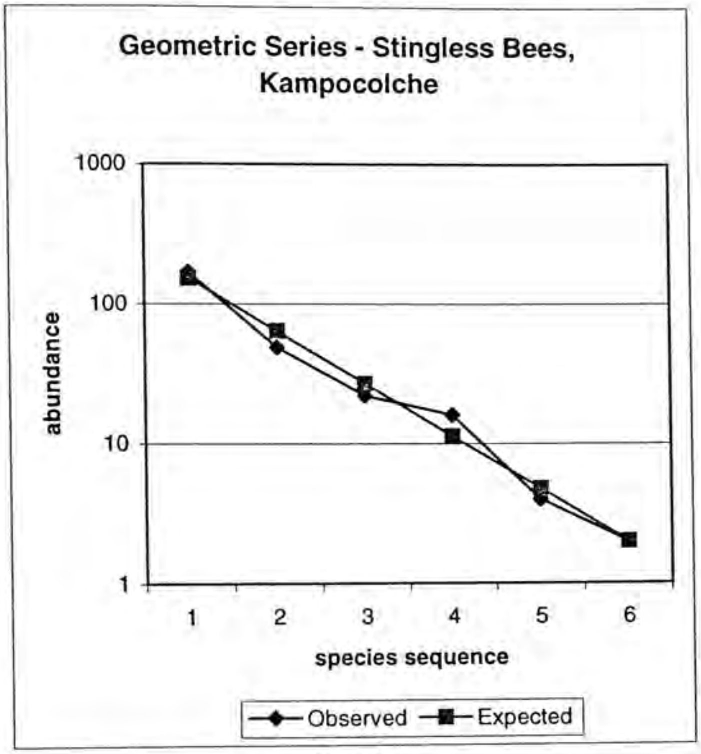


P=.03: no fit

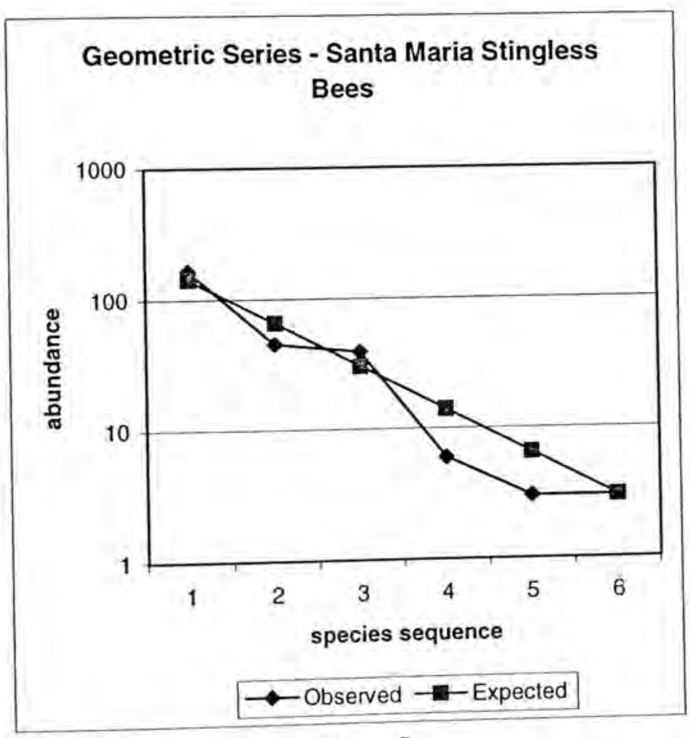


P>.25: fit

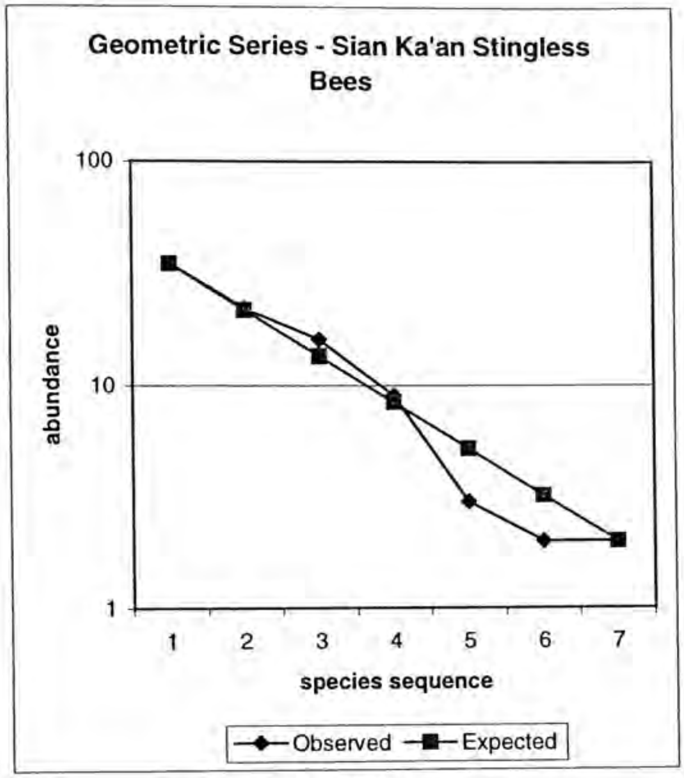
Figure 15: Geometric Series – All Bees



P>.1: fit



P=.03: no fit



P >.25: fit

Figure 16: Geometric Series – Stingless Bees

Statistical results

Results from the series of one way ANOVAs were more conservative and showed less significance overall, but indicated some of the same general trends which appeared in the community level diversity indices. Assumptions of homogeneity and normality were tested in all cases. ANOVAs for all bee species showed marginal significance at the alpha .10 level (p=.07) for the Shannon diversity index. LSD multiple comparisons tests for the Shannon index revealed that Santa Maria was significantly more diverse than the Sian Ka'an (p= .02). Kampocolche did not test significantly different from either Santa Maria or the Sian Ka'an. There was no significance found for the Shannon Evenness measure. Although no significance was detected by the ANOVA for the Berger-Parker dominance index, post hoc multiple comparisons tests revealed significance for this measure, indicating Santa Maria had significantly lower dominance measures than the Sian Ka'an (p=.05). Again, Kampocolche did not test significantly different from either Santa Maria or the Sian Ka'an for Berger-Parker. This reflects the same general pattern presented in table 2. Although Santa Maria never tested significantly different from Kampocolche, the mean of the Shannon diversity measure was less for Kampocolche than for Santa Maria, and Berger-Parker dominance was higher in Kampocolche than Santa Maria (see appendix I).

The same series of ANOVA's run for stingless bees only showed no significance at the alpha .05 level except in the LSD multiple comparisons tests of the Berger-Parker dominance index. The ANOVA for Berger-Parker revealed marginal significance at the alpha .10 level (p=.08). LSD multiple comparisons revealed the Sian Ka'an had significantly lower dominance than Santa Maria (p=.03). The Sian Ka'an also had lower dominance than Kampocolche, but the difference could not be considered statistically significant at the alpha .10 level, though it was close (p=.12), and there was no significant difference between Kampocolche and Santa Maria. Shannon

diversity and Shannon evenness showed no significance, but the Sian Ka'an had the highest mean measure for evenness (see appendix II). These data reveal a similar pattern to data presented in Table 3 for stingless bees, where dominance measures are low and evenness is high for the Sian Ka'an.

The series of ANOVA's for relative abundance of *Apis* and stingless bees showed some expected outcomes. For percent *Apis* dominance, the ANOVA was not significant, however LSD multiple comparisons showed marginal significance at the alpha .10 level ($p=.10$) for higher *Apis* abundance in Kampocolche than Santa Maria. The Sian Ka'an did not test significantly different in *Apis* dominance from either Santa Maria or Kampocolche. Percent abundance of all *Meliponinae* bees showed no significance, but when the species *Trigona fulviventris* was pulled out of the mix and treated separately, the picture changed. Not surprisingly, the ANOVA of *T. fulviventris* abundance was highly significant ($p<.001$). Post hoc multiple comparisons tests revealed the abundance of *T. fulviventris* was significantly lower in the Sian Ka'an than in Santa Maria ($p=.001$) and lower in the Sian Ka'an than Kampocolche ($P<.001$). When looking at the percent abundance of all stingless bee species minus *T. fulviventris*, the tests of between subject effects reveal marginal significance ($P=.06$). Post hoc multiple comparisons tests reveal that relative abundance of all other stingless bee species without *T. fulviventris* is significantly higher in the Sian Ka'an than in Santa Maria ($P= .03$) and marginally higher in the Sian Ka'an than in Kampocolche ($P= .07$) (see appendix III).

Competitive interactions

One of the most astounding findings of my field research was the discovery of new competitive behavior between *Apis mellifera* and stingless bees. All literature to date confirms that *Apis mellifera* bees do not show active aggression against other bees at flowers, but are insolent toward

aggression from *Trigona* species (Roubik, 1978, 1982, 1991). It has always been assumed that competition between *Apis* bees and other bees was strictly exploitation competition, meaning *Apis* bees found more efficient ways to exploit shared resources. Territorial behavior which reduces the exploitation efficiency of another species is defined as interference competition and often involves physical interactions. Interference competition may evolve under conditions where exploitation competition becomes severe (Gotelli, 2001). It seems that this is what might be happening here, and would indicate that exploitation competition is indeed becoming severe. In my total of 23 formal observation hours, I observed 5 competitive interactions between *Apis* and *Trigona* bees in which the *Apis* bee was the aggressor. It was very clear that these interactions were much more than bees incidentally bumping into each other. Interactions were brief, and usually lasted only seconds. The physical contact involved a brief hit by the aggressor at high speed that can be best described as "dive bombing." It was difficult to tell if mandibles were involved or if the bee was just using the force of its body and speed to hit and intimidate other bees. The *Trigona* bees would leave the flower they were visiting after being attacked in this way by the *Apis* bee, but usually returned to foraging after the interaction.

These interactions were observed at the following flowering species: *Croton sp. 1* (one observation of competition), *Croton sp. 2* (two observations of competition at the same location) and *Gymnopodium floribundum* (two observations at two different locations). Coincidentally, all of these species are generalist, small radial and colorless flowers which tend to attract a variety of visitors. In all cases, the "victim" was of the species *Trigona fulviventris*. At the four observation points where this competition was observed, only in one location were *Apis* bees outnumbered. At this observation point, (*Croton sp.2*) *Apis* bees were outnumbered by *T. fulviventris* by 80%, and I witnessed two aggressive attacks by *Apis* bees in a 20 minute period. At two of the other points (*Croton sp. 1* and *G. floribundium*), *Apis* bees dominated *T. fulviventris*

by more than half, and at the last point (*G. floribundium*) the two species were in exactly equal abundance. It is also notable that all of these points were in Kampocolche. I observed no such interactions at flowers in either the Sian Ka'an or Santa Maria.

I also observed bees competing at a water source in the Sian Ka'an. This was during the height of the dry season, in April, when competition for water would likely be most extreme. I observed three species of bees competing at a leaking water hose which had created a small puddle of about one meter in diameter. The three species present were *Apis mellifera, Trigona fuscipennis* (the dominant stingless bee species in the Sian Ka'an), and *Melipona beecheii.* The *M. beecheii* were coming and going from some domesticated hives that was only dozen meters away. The exact location of the hives of the competing *Trigona fuscipennis* and *Apis mellifera* bees were unknown, but it was clear that the *T. fuscipennis* bees were coming and going from the Northeast, into a patch of thick forest, and the *Apis* bees seemed to be coming and going from the South, making me believe that each of the three species of bees utilizing this site shared the same home colonies. I watched this source for several periods of about 20 minutes each over three days time, at different times of the day, totaling 2 ½ hours of observation time at this site, and wrote down all my observations. What I saw was quite remarkable. Each of the three species dominated its own area of the puddle, however the *Melipona* were always on the very outer edge of the puddle, where most of the water was already absorbed in the soil, and there were usually only a few individuals of *Melipona*, where there were numerous *Apis* and *Trigona* bees. The *Trigona* and *Apis* bees consistently dominated areas in the center of the puddle, where there was lots of fresh water from the leak. The *Trigona* were regularly aggressive toward *Apis* bees which wandered into their territory, and also toward any *Melipona* that came near - attacking with mandibles and occasionally gripping the offending bee with their bodies and briefly struggling. The *Apis* bees were mostly indigent toward the attacks, but the *Melipona* would retreat. What was more

striking, however, was the behavior of the *Apis* bees. Overall, they were less aggressive than the *Trigona*, but I observed one instance of an *Apis* bee attacking a *Melipona* that got too close, and two incidents of *Apis* bees attacking the *Trigona*. In these interactions, however, unlike the attacks at flowers which were only brief, were more intense. The *Apis* bee would actually tackle and grip the offending bee and hold them for a moments time, until the other bee struggled free, or the *Apis* bee would let go after a few seconds. The attacks were severe enough that one of the *Trigona* bees attacked took a while to get over it, stumbling around on the ground for about eight to ten seconds before it could fly again.

Discussion

It is clear that, overall, this is a species poor assemblage of bees. This is evidenced by low Shannon index results, plus much of the data fits the geometric series. Finding a fit to the geometric series is common in early succession, stressful conditions and species poor assemblages (Magurran, 1988). Literature supports the fact that the Yucatan is a species poor area for bees (Ayala et al., 1993). There are only approximately 90 known species of bees in the region and 15 of those are stingless bees, where in some tropical lowland forests there can be as many as 70 stingless bee species in an area of only 50 sq km (Roubik, 1992). The fact that the data fit the niche pre-emption hypothesis or come close to fitting it, even in an intact ecosystem (the Sian Ka'an), suggests that conditions overall are stressful for bees.

As discussed in chapter III, many studies have tried to find evidence that the Africanized bee is displacing other bees. It is difficult to find substantial proof that this is occurring. How do we know for sure that the Africanized honeybee is to blame for the displacement of *Melipona beecheii* and other species, and that it is not due to other environmental factors? Local people seem to think that the Africanized bee is to blame, and although studies have shown that

exploitation competition seems to be occurring between *Apis* and stingless bees (Roubik, 1978, 1982), science has been unable to show population level effects that are directly related to the invasion of the Africanized honeybee (Roubik and Wolda, 2001). However, the discovery of physically aggressive interference competition on the part of *Apis mellifera* against *Trigona* species and *Melipona beecheii* is a significant finding suggesting that exploitation competition is becoming severe enough that *Apis* bees are changing their behavior in order to compete better with other dominant species. I discussed this phenomenon with a technician of the Secretario de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación (SAGARPA, the agricultural secretary), Victoriano Quinones Chac, who has worked with beekeepers in the region for years. He indicated that he had begun to note this competitive behavior initiated by *Apis* bees very recently, and had not noticed it before the year 2001. Other long-time regional bee researchers (David W. Roubik, Rogel G. Villanueva, Wilberto Colli-Ucan) also indicate that this behavior is new.

This means that over in the past recent years, competition has been escalating to a point that bees are evolving new behavior patterns to adapt, and those bees which have not been able to adapt are instead displaced. *Trigona* bees are known to be aggressive foragers and have been known to physically attack other bees at flowers. This could be part of the reason for their success in competing with the *Apis* bee, while the more passive *Melipona* has not been able to compete. The water competition observation made clear what I has suspected, that the *Trigona* bees are coping with competition from the Africanized honeybees, but the *Melipona* are too passive to compete successfully.

How does disturbance fit into the equation? My data suggests that competition at flowers may be more intense in the more disturbed environment of Kampocolche, where I observed the most

competitive interactions at flowers. Species distribution patterns indicate greater dominance by *Apis mellifera* in a disturbed environment as well as heavier competition. In an already species poor, stressful environment, it appears that increased disturbance leads to decreased richness and evenness of bee species, so that those species which are less adept at interference or exploitation competition become increasingly rare, while those that excel become increasingly dominant. Although *Apis mellifera* is dominant in the protected area (Sian Ka'an) and overall bee numbers are lowest, evenness and richness of stingless bee species are still higher in this intact ecosystem. It is clear that the relative abundance of stingless bees other than *T. fulviventris* is higher in the Sian Ka'an. Stingless bees are clearly most diverse in the Sian Ka'an, and I encountered species there that I did not see in either Santa Maria or Kampocolche, including *Melipona beecheii* and *Scaptotrigona pectoralis*. In the moderately disturbed area (Santa Maria), *Apis mellifera* and *Trigona fulviventris* were still the dominant species, and stingless bee diversity and evenness was still lower than the protected area; however, diversity overall was significantly higher, due to a larger diversity of other bee species, such as *Anthophoridae* and *Halcitidae* bees. Overall, it can be concluded that for all bee species, Santa Maria seems to have the highest diversity and lowest dominance of the three areas, where for stingless bees alone, the Sian Ka'an seems to be the most diverse with the highest evenness.

Based on the evidence presented in this study, it is fair to conclude that the driving forces behind the decline in *Melipona beecheii* and other stingless bees are attributable to both competition from the Africanized honeybee and habitat destruction. The stingless bee species are variably affected. Most of the *Trigona* species, especially *Trigona fulviventris,* seem to be coping well with these pressures. However, numerous other stingless bee species, including *Melipona beecheii*, now have population levels that are so low they were barely detected by my sampling, and four stingless bee species which are known to be found in the region were completely absent

from my sample altogether (see appendix VII). The observations of my informants in the social portion of this research were unfortunately substantiated by the ecological study - the *xunan kab* are now very difficult to find.

Chapter VI: Conclusions and Recommendations for Management

As discussed in chapter 1, ecosystem management requires integration of ecological and socio-economic knowledge to understand the forces that drive land-use decisions. Economic forces, along with other social forces and changes in the bee fauna, have driven changes in beekeeping practice in Quintana Roo and have all but destroyed traditional beekeeping. I have shown how the introduction of exotic commercial species, followed by the "surprise" introduction of a more aggressive commercial species by human error, have effected the ecology of bees. I have also shown how human induced habitat disturbance is effecting the abundance patterns of bees. Finally, I have shown how the social and ecological changes have begun to cause changes in Mayan culture, and possibly could change the pollination ecology of the region. To date, there does not appear to have been much social learning about these processes. The existing science on *Melipona beecheii* decline, some of it reported for the first time here, has not been incorporated into new policies by governments. Existing social and ecological research provides an important baseline to begin to launch new government and civil society programs to try and restore earlier ecosystem processes and potentially lucrative new commercial opportunities, based on a traditional practice. The better integration of research findings into management strategies would allow adaptive management processes to begin in the region. As we have seen, adaptive management allows for resilience in the face of uncertainty by adjusting management and policy decisions in accordance with the results of scientifically based policy and management experiments. In this case, adaptive management will be essential if we expect to make changes on a regional scale through carefully designed development interventions with small groups of indigenous beekeepers. The only way scientists and managers will know if the management plan is effective, and the only way to protect against surprise elements which may hinder the success of the project, is through careful monitoring of bee populations over the next years in conjunction

with programs to build and re-establish stingless beekeeping practice and control Africanization as much as possible with re-queening domesticated colonies and destruction or capture of feral colonies. It will also be important to be actively involved in other land management programs focused on sustainable use of forest resources, since habitat destruction is a key factor for bee populations.

The best management plan for the *Melipona beecheii* would thus have two goals – to restore populations of the bees by reproducing the colonies, and to bring economic benefits to the communities. In this way, management of *Melipona* becomes a kind of restoration ecology in which we can restore populations of a native pollinator species while benefiting local people. It is important to focus on first obtaining and subsequently multiplying the colonies one or more times before harvesting, which means delaying the harvest until the beekeeper has several strong colonies. Harvest then needs to be done at a sustainable level; if the colony produces two kilos a year, one kilo a year or less should be harvested and the colony should be left with its pollen stores and its cerumen[11]. Using box hives instead of hollow logs is a good option for making management of these bees easier, it provides an easier access to the hive than the traditional hollow logs and makes both harvest and hive splitting easier. There is a desperate need for better management practices as we have seen, especially in the younger generation. Technical assistance is essential for re-introducing lost management practices to younger generation. Older individuals who have a whole lifetime of experience with these bees are still struggling, and could benefit from learning new practices and techniques of hive splitting and use of box hives.

[11] Cerumen is the material these bees make and use to store their honey in, it is a combination of wax and propolis. It is good to leave the broken pieces of cerumen behind to make it easier for the bees to rebuild their pots.

The stingless bees will still have to compete with Africanized bees, but with proper care and management, coupled with a program to combat Africanization through re-queening domestic Africanized colonies with European queens, their competitive chances can be improved. Re-queening may be only partly effective, since feral colonies of Africanized honeybees will continue to interbreed, but it is one way to begin to control the problem. Some feral colonies can be captured, domesticated and interbred with European bees, or else captured and destroyed, but it should be recognized that capturing feral colonies is a labor intensive activity since wild hives are often difficult to find and can be tricky to capture. An adaptive management approach, with producers, civil society organizations, and government agencies working together, will allow for the effectiveness to be monitored.

It has been demonstrated that new social capital can be constructed in relatively short periods of time, with the help of appropriate and respectful outside interventions (Krishna, 2000). Although we may never see the return of stingless beekeeping to the way it was before, outside programs can help to organize the existing stingless beekeepers of the region into cooperatives and to recruit new individuals, especially given the market potential for stingless bee honey. In this way, some semblance of social capital can be re-built around stingless beekeeping. However it is important to realize that the original social capital structure was based largely on religious traditions, many of which have lost influence, and not on market forces. Structuring a new formula for social capital focused on selling honey for profit will be very different. When market is the driving force behind keeping stingless bees, rather than religion, the temptation to exploit the bees in an unsustainable way will be greater. Certainly organizations and networks driven by market forces have been successfully formed around *Apis* beekeeping. However *Apis* bees are much less fragile and definitely not endangered, so that mistakes such as over harvesting or mismanaging *Apis* colonies are not detrimental. There is much less room for these sorts of

mistakes in stingless beekeeping. The knowledge of colony division and pest management must be re-introduced through technical assistance, and organizing beekeepers can allow for knowledge to be shared more readily.

We have seen that the honey of stingless bees goes for a very high price at local markets, as mentioned before, but international markets could be opened to this unique honey with its remarkable history. This is not a type of honey that should be sold in mass quantities for people to put on pancakes or as an ingredient in foods because of its high price and low quantities, and also because mass harvesting of this honey could be the final blow for this species. Large markets are not appropriate or necessary for this kind of honey. However it would fit nicely into a niche market such as the natural food and medicine market, just as other bee products such as pollen and propolis can now be found in health food stores that were almost unheard of ten years ago. Even though it will not be a mass market product, with a nice bottle, label, and tag which tells its story to consumers ("...used by the ancient Maya for healing and ritual..."), it could easily find a niche market in the natural and holistic food and health markets in the United States and Europe. One notable obstacle to this is the fact that because the honey has a slightly higher water content, it ferments easier than regular honey. The honey would need to reach the market fresh and be sold fresh, perhaps even be refrigerated, to avoid fermentation before it gets to the customer in the States or Europe. Before getting discouraged about the difficulties of introducing a new product to international markets, it is important to remember that this is still honey – it is not new, it is just a different kind of honey that may be appealing to people interested in natural foods and ecologically sound products. Along with the single source honeys, organic honeys, and wildflower honeys, people can enjoy Mayan stingless bee honey. The experiences in marketing stingless bee honey in southern Campeche that were mentioned earlier shows that these markets exist.

Whether or not international markets are opened, local demand does exist. Local markets can also be expanded and improved. Occasionally the honey is sold at the stands in the public market in Carrillo Puerto. Opening a store or market stand in Carrillo Puerto and other local cities especially dedicated to *Melipona* honey and/or other bee products could be one possibility. Individuals who have sold their honey to middlemen have gotten a significantly lower price for it than what is sells for in the stands, as low as 60 pesos a kilo when it sells for 600 a kilo, so selling directly to the market is just as important for this honey as for regular honey.

The conceptual model created earlier in chapter IV examined the driving forces behind the decrease in stingless beekeeping. We can now introduce into that conceptual model the proposed actions discussed above and see how they fit into the picture (see figure 17). The four main actions include: 1) opening more markets for stingless bee honey, which will help encourage more people to keep stingless bees as the Maya culture moves farther into the market economy; 2) organizing stingless beekeepers, which will facilitate a re-structuring of social capital; 3) technical assistance, which will help correct some of the major management problems especially among the younger generation, and 4) re-queening with European queens and capturing feral colonies to help control the problem of Africanization, which will ease the stress on native pollinators and facilitate management of exiting apiaries.

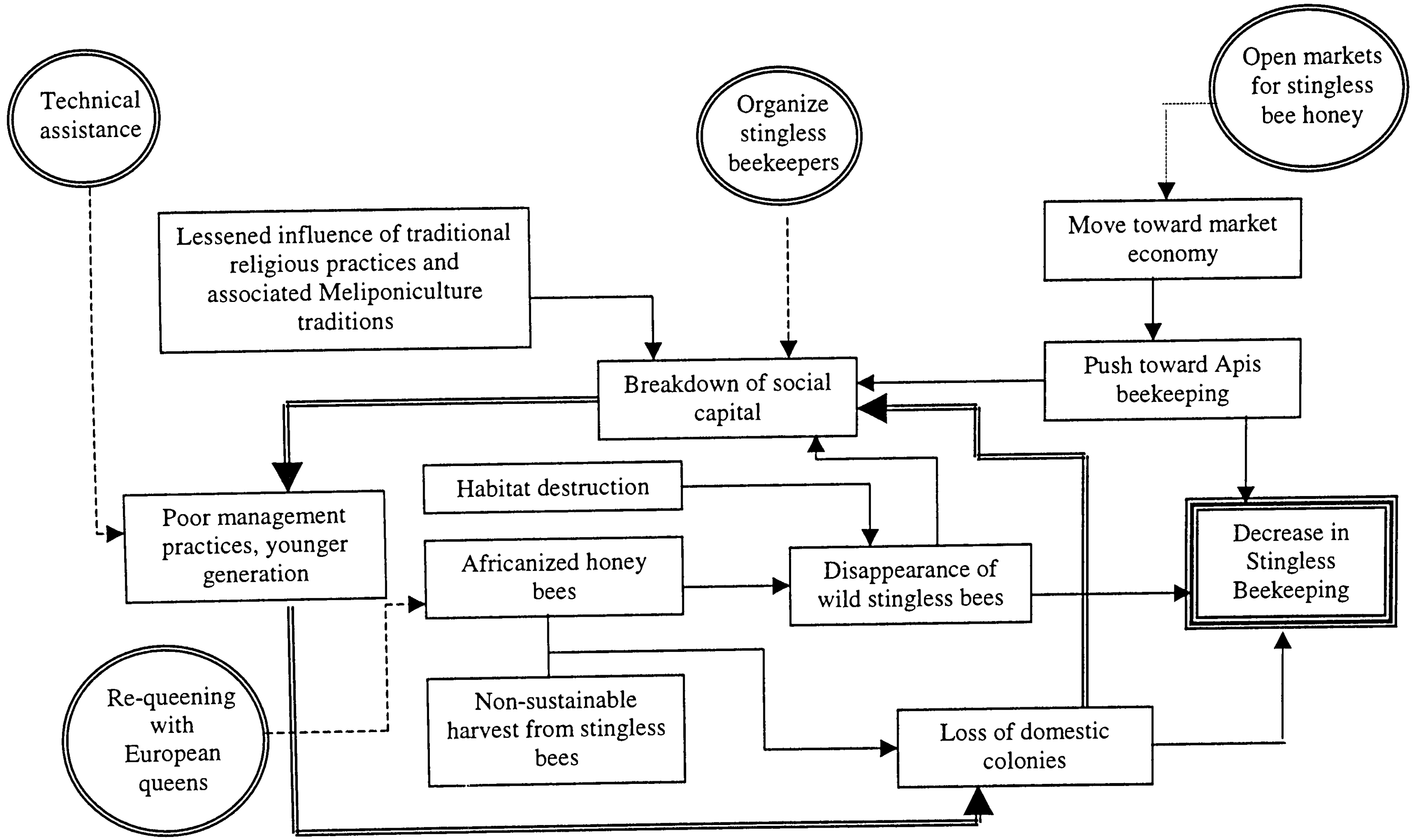


Figure 17: Conceptual Model: Management Plan Action

Continued research on this topic should focus on monitoring populations of different bee species, examining changes after another five to ten year period. Further studies should look at other variables which may be effecting bee populations such as use of chemical pesticides and fertilizers, and how these factors may be influencing floral visitation and abundances of different types of bees and other pollinators. The new competitive behavior discovered in this study needs to be further examined in the field and monitored to determine if competition is getting more intense at floral resources.

The fate of the forest is linked directly to the fate of its pollinators. In a tropical forest where 90% of plant species are dependent on insect or animal pollinators to reproduce, the seriousness of a change in pollinator makeup cannot be understated. The fate of the forest is also linked directly to the decisions of the people who live there. Every land use decision has a benefit and a consequence. Traditional beekeeping in the Yucatan is one of the few land use activities where the benefits can far outweigh any consequences, and in fact the benefits of beekeeping are both economical and environmental. Furthermore, once traditional knowledge about natural resource management is gone, it is difficult or sometimes impossible to restore. However, the traditional knowledge about keeping stingless bees has not disappeared just yet, and neither have the stingless bees. There still exists a chance to restore traditional practices and populations of the Mayas' most beloved bee, though the window of opportunity is fast closing.

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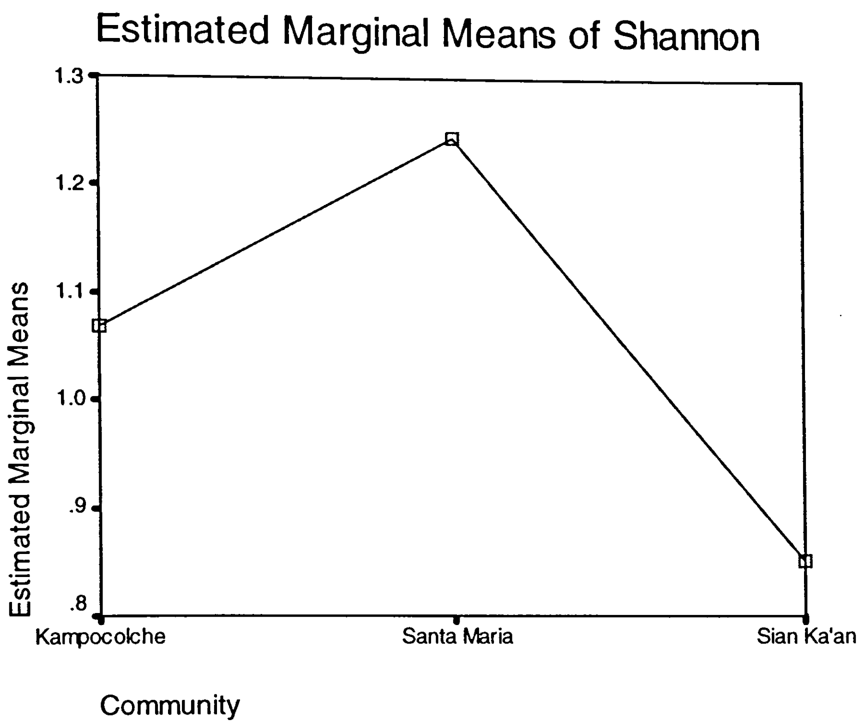
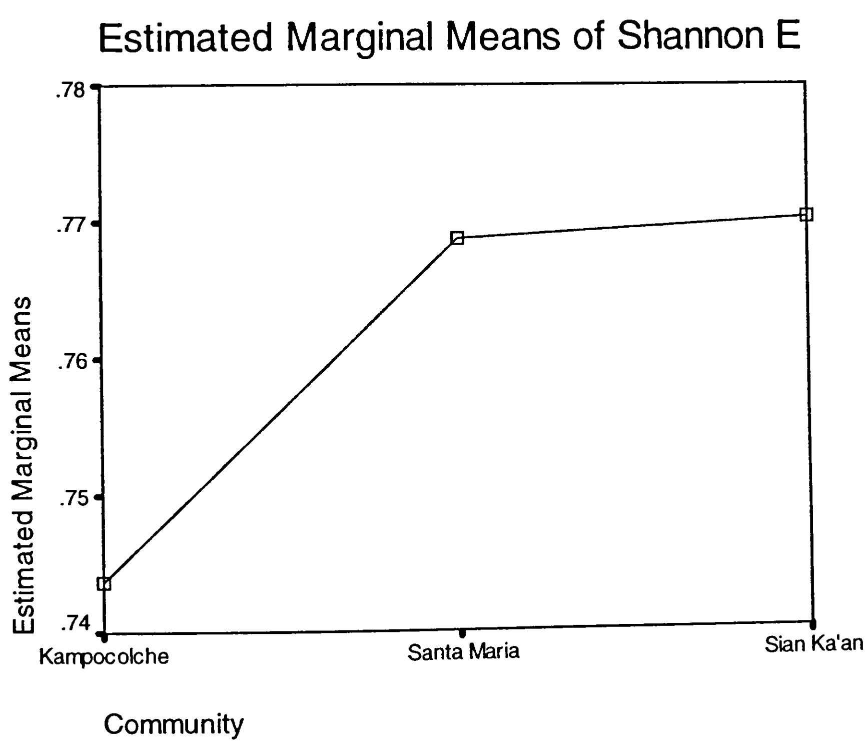
APPENDICES

APPENDIX I:

Estimated marginal means, results from one-way ANOVAs for diversity indices for all bees


Estimated Marginal Means of Shannon
Estimated Marginal Means
1.3
1.2
1.1
1.0
.9
.8
Kampocolche
Santa Maria
Sian Ka'an
Community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Estimated Marginal Means
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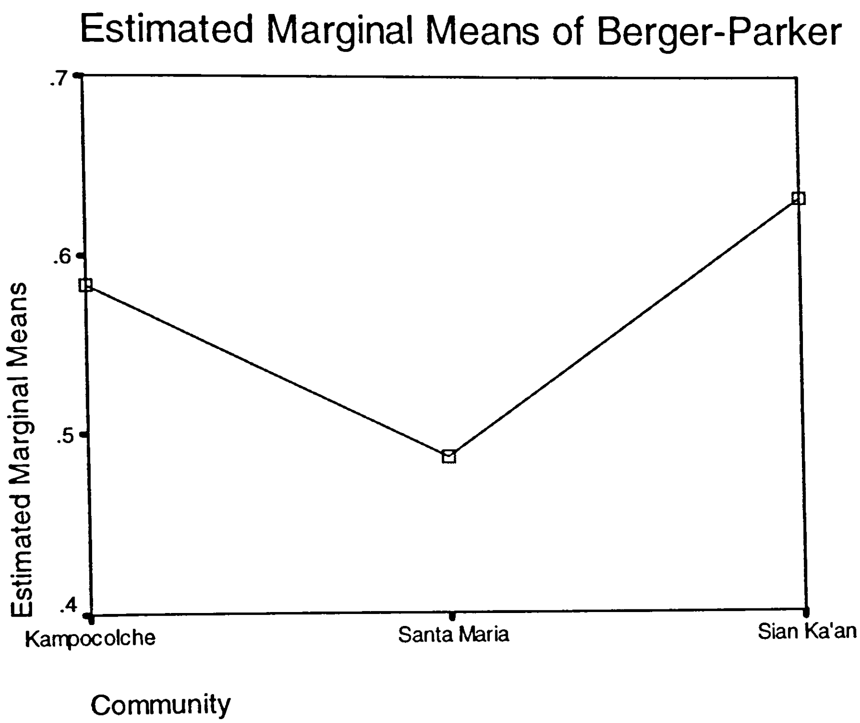
.77
.76
.75
.74
Kampocolche
Santa Maria
Sian Ka'an
Community

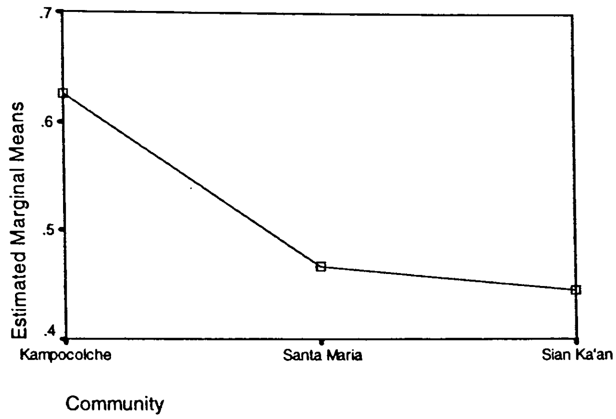


Estimated Marginal Means of Berger-Parker
Estimated Marginal Means
.7
.6
.5
.4
Kampocolche
Santa Maria
Sian Ka'an
Community

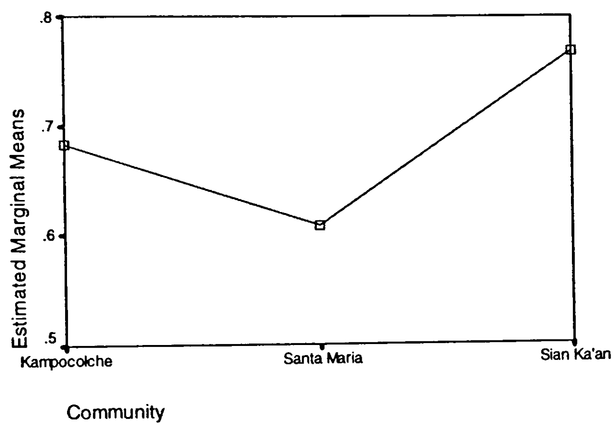
APPENDIX II:

Estimated Marginal Means, results of one-way ANOVAs for diversity indices of stingless bees only

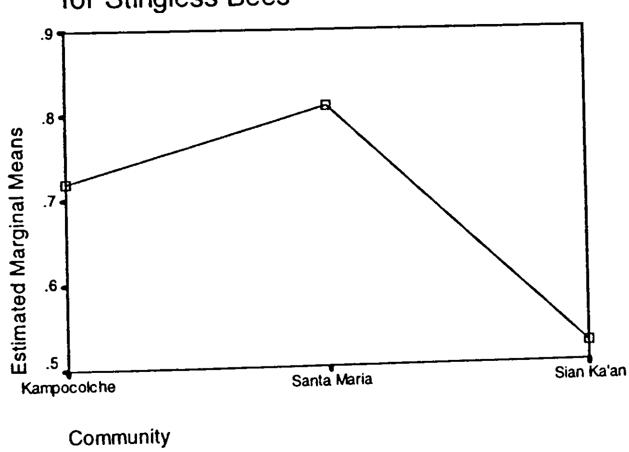
Estimated Marginal Means of Shannon for Stingless Bees



Estimated Marginal Means of Shannon E for Stingless Bees



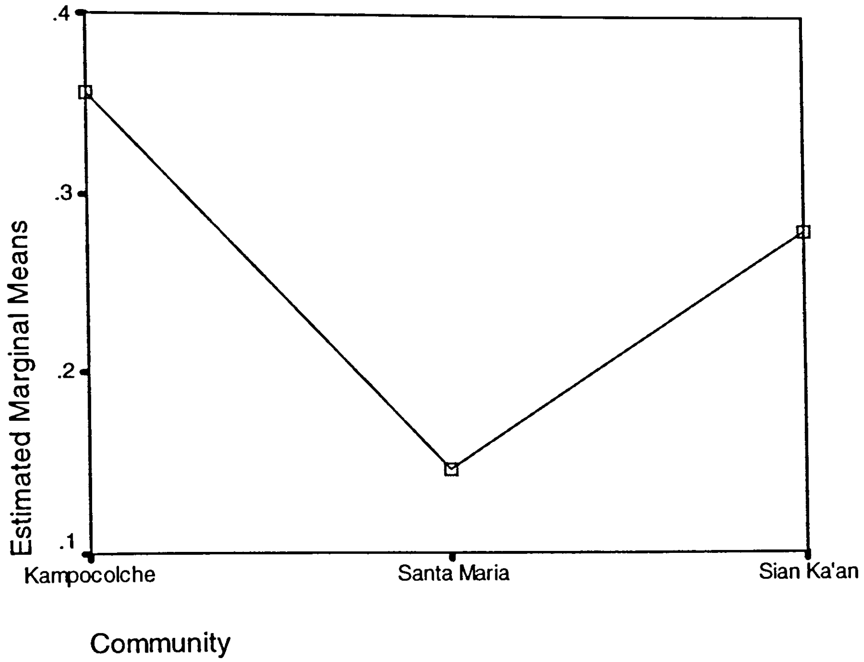
Estimated Marginal Means of Berger-Parker for Stingless Bees



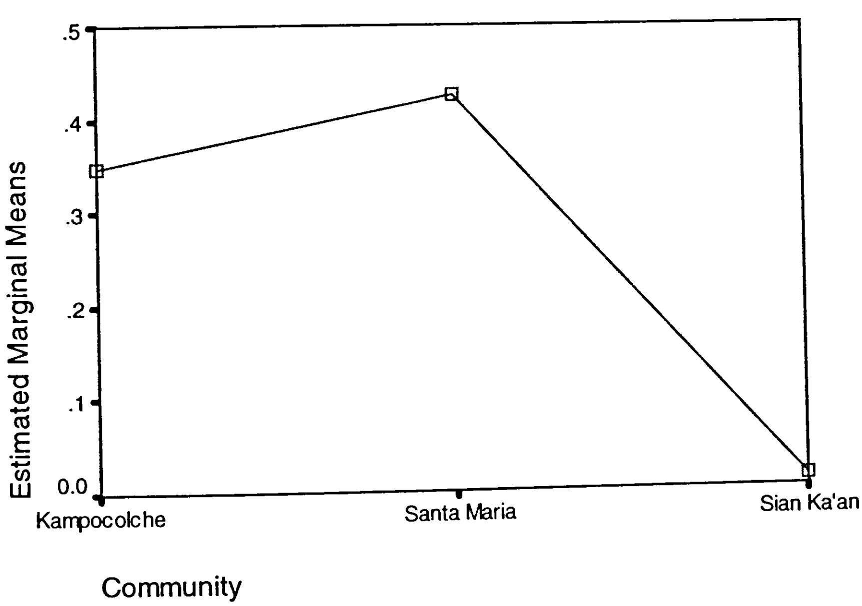
APPENDIX III:

Estimated Marginal Means, results of one-way ANOVAs for percent abundance of *Apis* and Meliponinae bees

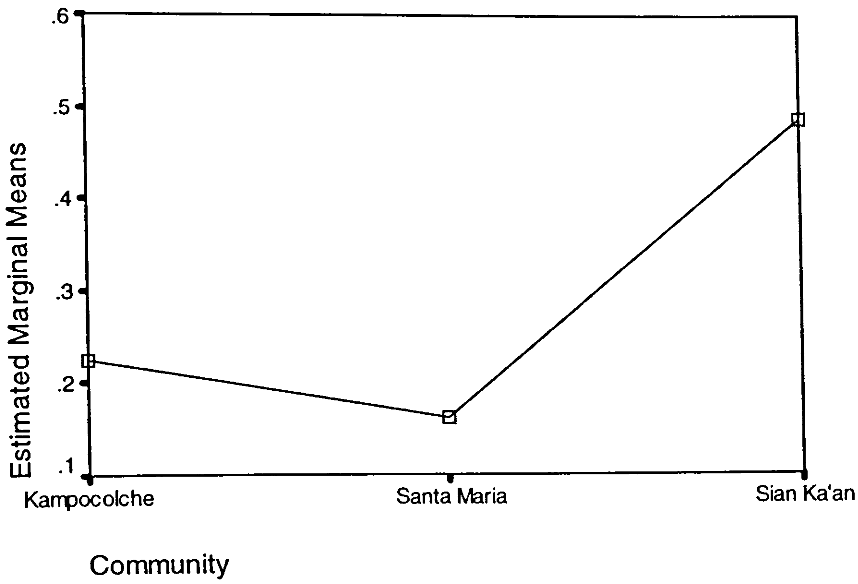
Estimated Marginal Means of Apis dominance



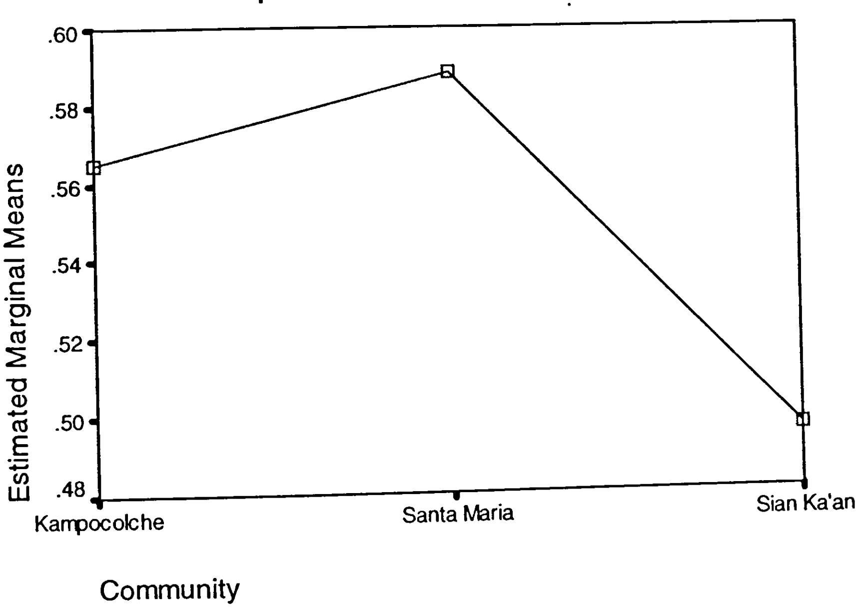
Estimated Marginal Means of T.Fulviventris abundance



Estimated Marginal Means of Meliponinae abundance minus T. Fulviventris

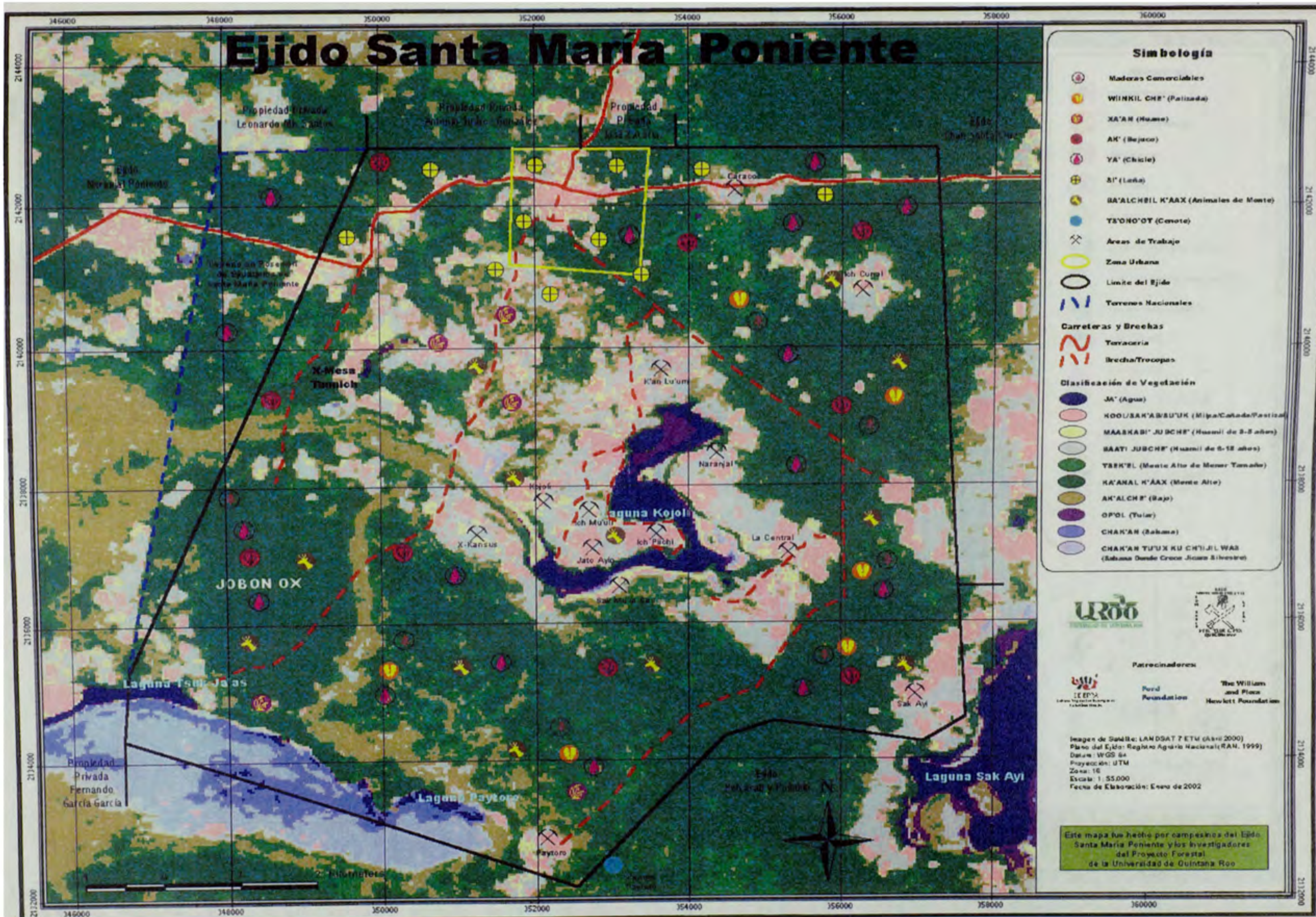


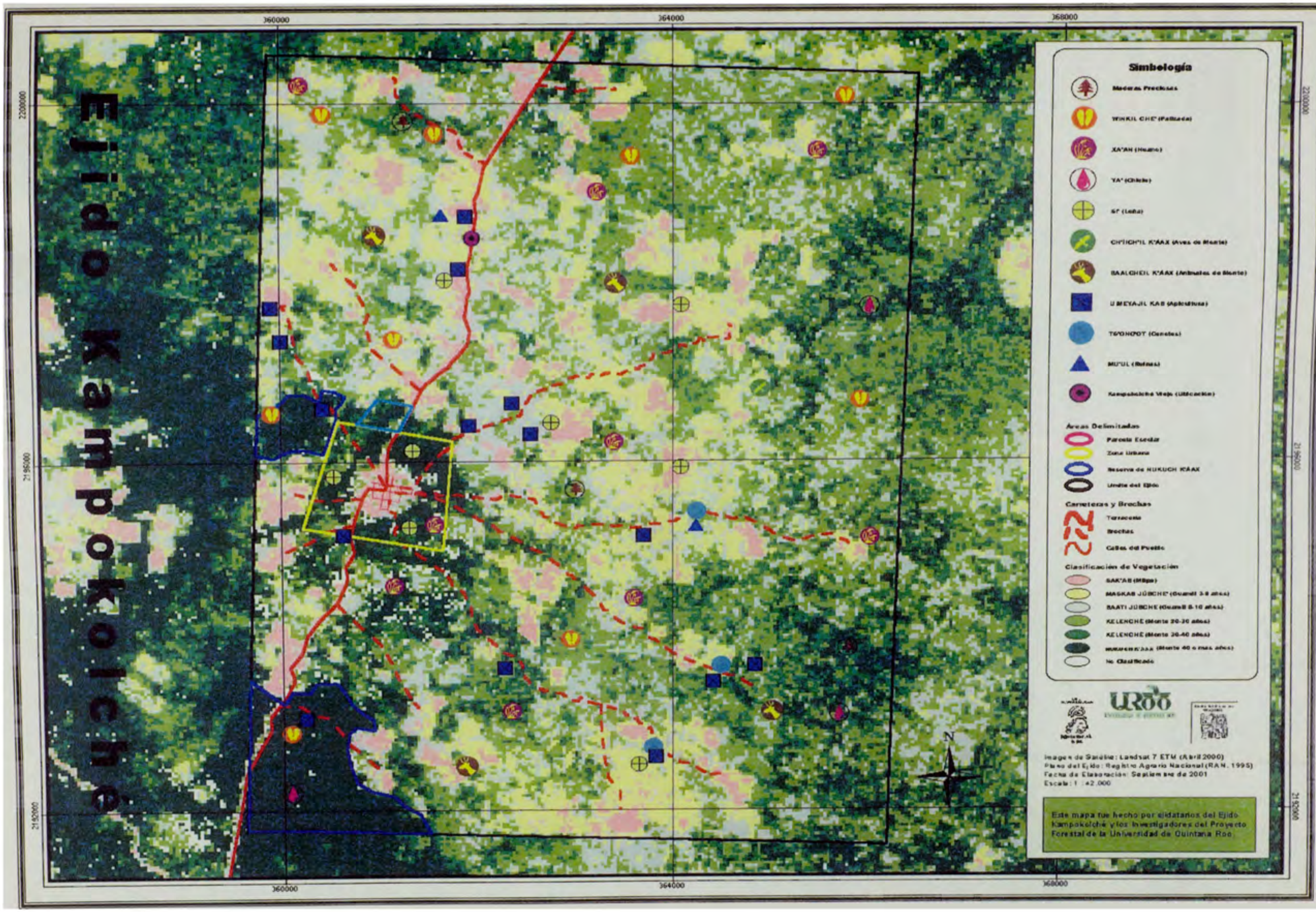
Estimated Marginal Means of Abundance of all Meliponinae With T Fulviventris



APPENDIX IV:

Maps of Kampocolche and Santa Maria, showing difference in forest cover and land uses.


Ejido Santa María Poniente
Simbología
Maderas Comerciables
WIINKIL CHE' (Palizada)
XA'AN (Huano)
AK' (Bejuco)
YA' (Chicle)
SI' (Leña)
BA'ALCHEIL K'AAX (Animales de Monte)
TS'ONO'OT (Cenote)
Areas de Trabajo
Zona Urbana
Limite del Ejido
Terrenos Nacionales
Carreteras y Brechas
Terraceria
Brecha/Trocopas
Clasificación de Vegetación
JA' (Agua)
MAASKABI' JU BCHE' (Huamil de 3-5 años)
SAATI JUBCHE' (Huamil de 6-18 años)
TSEK'EL (Monte Alto de Menor Tamaño)
KA'ANAL K'AAX (Monte Alto)
AK'ALCHE' (Bajo)
OP'OL (Tular)
CHAK'AN (Sabana)
CHAK'AN TU'UX KU CH'IJIL WAS
Patrocinadores:
Ford Foundation
The William and Flora Hewlett Foundation
Imagen de Satélite: LANDSAT 7 ETM (Abril 2000)
Plano del Ejido: Registro Agrario Nacional(RAN, 1999)
Datum: WGS 84
Proyección: UTM
Zona: 16
Escala: 1: 55,000
Fecha de Elaboración: Enero de 2002
Este mapa fue hecho por campesinos del Ejido Santa Maria Poniente y los investigadores del Proyecto Forestal de la Universidad de Quintana Roo
JOBON OX
X-Mesa Tumich
Laguna Kojoli
Laguna Sak Ayi
Laguna Tsik Ja'as
Laguna Paytoro
Propiedad Privada Fernando García García
Propiedad Privada Leonardo Mk Santos
X-Kansus
K'an Lu'um
Naranjal
La Central
Jato Ayo
Sak Ayi
Paytoro
Caraco
N


Ejido Kampokolché
Simbología
Maderas Preciosas
WINKIL CHE' (Palizada)
XA'AN (Huano)
YA' (Chicle)
CH'ICH'IL K'AAX (Aves de Monte)
BAALCHEIL K'AAX (Animales de Monte)
MU'UL (Ruinas)
Areas Delimitadas
Parcela Escolar
Zona Urbana
Reserva de HUKUCH K'AAX
Límite del Ejido
Carreteras y Brechas
Terracería
Brechas
Calles del Pueblo
Clasificación de Vegetación
SAK'AB (Milpa)
No Clasificado
Imagen de Satélite: Landsat 7 ETM (Abril 2000)
Plano del Ejido: Registro Agrario Nacional (RAN, 1995)
Fecha de Elaboración: Septiembre de 2001
Escala: 1 : 42,000
Este mapa fue hecho por ejidatarios del Ejido Kampokolché y los investigadores del Proyecto Forestal de la Universidad de Quintana Roo.
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360000
364000
368000
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2196000
2192000

APPENDIX V:

List of plant species sampled

Common name (Maya)	Scientific Name	Family	Number sampled
Mangle chaparro	*Avicennia germinans (L.) L.*	*Verbenaceae*	1
Tsurutok	*Bauhinia divaricata L.*	*Leguminosae*	1
Pukte	*Bucida buceras L.*	*Combretaceae*	1
Chakah	*Bursera simaruba (L.) Sarg.*	*Burseraceae*	1
	Byrsonima bucidifolia Standl.	*Malpighiaceae*	3
Kitamche	*Caesalpinia gaumeri Greenm.*	*Leguminosae*	1
	Cecropia peltata	*Cecropiaceae*	2
	Cirsium mexicanum DC.	*Compositae*	1
Chu'um	*Cochlospermum vitifolium (Willd.) Spreng*	*Cochlospermaceae*	3
Su'su-yuk	*Croton sp. 1*	*Euphorbiaceae*	2
Chilar	*Croton sp. 2*	*Euphorbiaceae*	1
Beec, Roble	*Ehretia tinifolia L.*	*Boraginaceae*	1
	Eupatorium pycnocephalum Less.	*Compositae*	3
Tsitsilche	*Gymnopodium floribundum Rolfe*	*Polygonaceae*	10
	Ipomoea anisomeres B. L. Rob. & Bartlett.	*Convolvulaceae*	1
Tsiminche	*Lonchocarpus hondurensis Benth.*	*Leguminosae*	1
	Lysiloma latisiliquum (L.) Bentrh.	*Leguminosae*	4
Nance	*Malpighia glabra*	*Malpighiaceae*	4
Toplan shish	*Melanthera aspera (Jacq.) Small*	*Compositae*	2
Chechem	*Metopium brownei (Jacq.) Urb.*	*Anacardiaceae*	9
Habbin	*Piscidia piscipula (L.) Sarg.*	*Leguminosae*	5
	Pluchea odorata (L.) Cass.	*Compositae*	1
	Pouteria reticulata (Engel) Eyma ssp. reticulata	*Sapotaceae*	1
Tzitzil-ya	*Sideroxylon salicifolium* (L.) Lam.	*Sapotaceae*	2
Guaya	*Talisia olivaeformis (Kunth) Radlk.*	*Sapindaceae*	1
Tabentun	*Turbina corymbosa (L.) Raf.*	*Convolvulaceae*	1
	Vigna elegans (Piper) Maréchal Mascherpa & Stainier	*Leguminosae*	1
Yash-nic	*Vitex gaumeri Greenm.*	*Verbenaceae*	5
On'no-ak	*Vitis vitifolia*	*Vitaceae*	1

APPENDIX VI

Percentage of bee types by plant family

Plant Family	N	A. Mellifera (%)	Meliponinae (%)	Other Bees (%)
Leguminosae	13	5.1	21.6	28.8
Convolvulaceae	1	0.0	4.7	3.7
Euphorbiaceae	3	7.3	4.5	1.9
Compositae	7	18.4	2.4	14.0
Vitaceae	1	2.7	0.0	0.0
Polygonaceae	10	38.7	17.8	5.6
Sapotaceae	3	5.4	2.0	0.0
Combretaceae	1	0.3	0.0	1.9
Anacardiaceae	9	3.0	18.2	1.4
Burseraceae	1	0.0	0.8	0.0
Malpighiaceae	7	0.0	6.2	35.3
Sapindaceae	1	0.3	3.2	0.4
Verbenaceae	6	12.0	8.4	5.1
Boraginaceae	1	0.0	1.3	0.4
Cecropiaceae	2	6.3	0.7	0.0
Cochlospermaceae	3	0.3	8.0	1.4
Total	69	100	100	100

APPENDIX VII

List of Stingless Bee Species and Total Count, with *Apis mellifera*, Overall and by Community

TOTAL –ALL COMMUNITIES

Species Name	Count
Apis mellifera	337
Trigona fulviventris	290
Trigona fuscipennis/ T. corvina (morpho group)	129
Trigona (cephalotrigona) capitata	45
Plebia jatiformis/ P. frontalis/ P. minima (morpho group)	37
Trigona (Friesoemelitta) nigra	35
Scaptotrigona pectoralis	22
Trigonisca buyssoni	5
Melipona beecheii	3
Trigona nigerrima	0
Nannotrigona testaceicornis	0
Partamona sp.	0
Melipona yucatanica	0

KAMPOCOLCHE

Species Name	Count
Apis mellifera	192
Trigona fulviventris	169
Trigona fuscipennis/ T. corvina (morpho group)	49
Plebia jatiformis/ P. frontalis/ P. minima (morpho group)	22
Trigona (Friesoemelitta) nigra	16
Trigona (cephalotrigona) capitata	4
Trigonisca buyssoni	2
Scaptotrigona pectoralis	0
Melipona beecheii	0
Trigona nigerrima	0
Nannotrigona testaceicornis	0
Partamona sp.	0
Melipona yucatanica	0

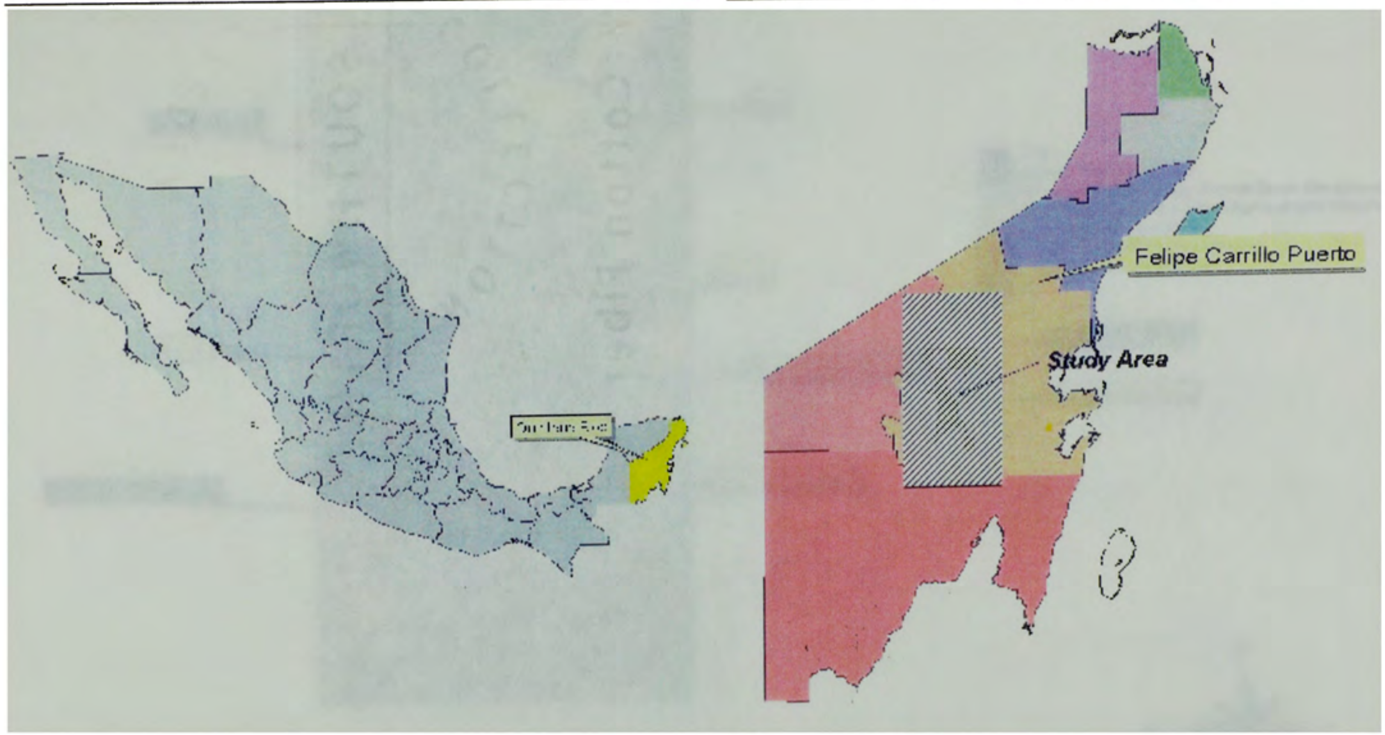
SANTA MARIA	
Species Name	Count
Trigona fulviventris	119
Apis mellifera	90
Trigona fuscipennis/ T. corvina (morpho group)	45
Trigona (cephalotrigona) capitata	39
Plebia jatiformis/ P. frontalis/ P. minima (morpho group)	6
Trigona (Friesoemelitta) nigra	3
Trigonisca buyssoni	3
Scaptotrigona pectoralis	0
Melipona beecheii	0
Trigona nigerrima	0
Nannotrigona testaceicornis	0
Partamona sp.	0
Melipona yucatanica	0

THE SIAN KA'AN	
Species Name	Count
Apis Mellifera	55
Trigona fuscipennis/ T. corvina (morpho group)	35
Scaptotrigona pectoralis	22
Trigona (Friesoemelitta) nigra	16
Plebia jatiformis/ P. frontalis/ P. minima (morpho group)	9
Melipona beecheii	3
Trigona (cephalotrigona) capitata	2
Trigona fulviventris	2
Trigonisca buyssoni	0
Trigona nigerrima	0
Nannotrigona testaceicornis	0
Partamona sp.	0
Melipona yucatanica	0

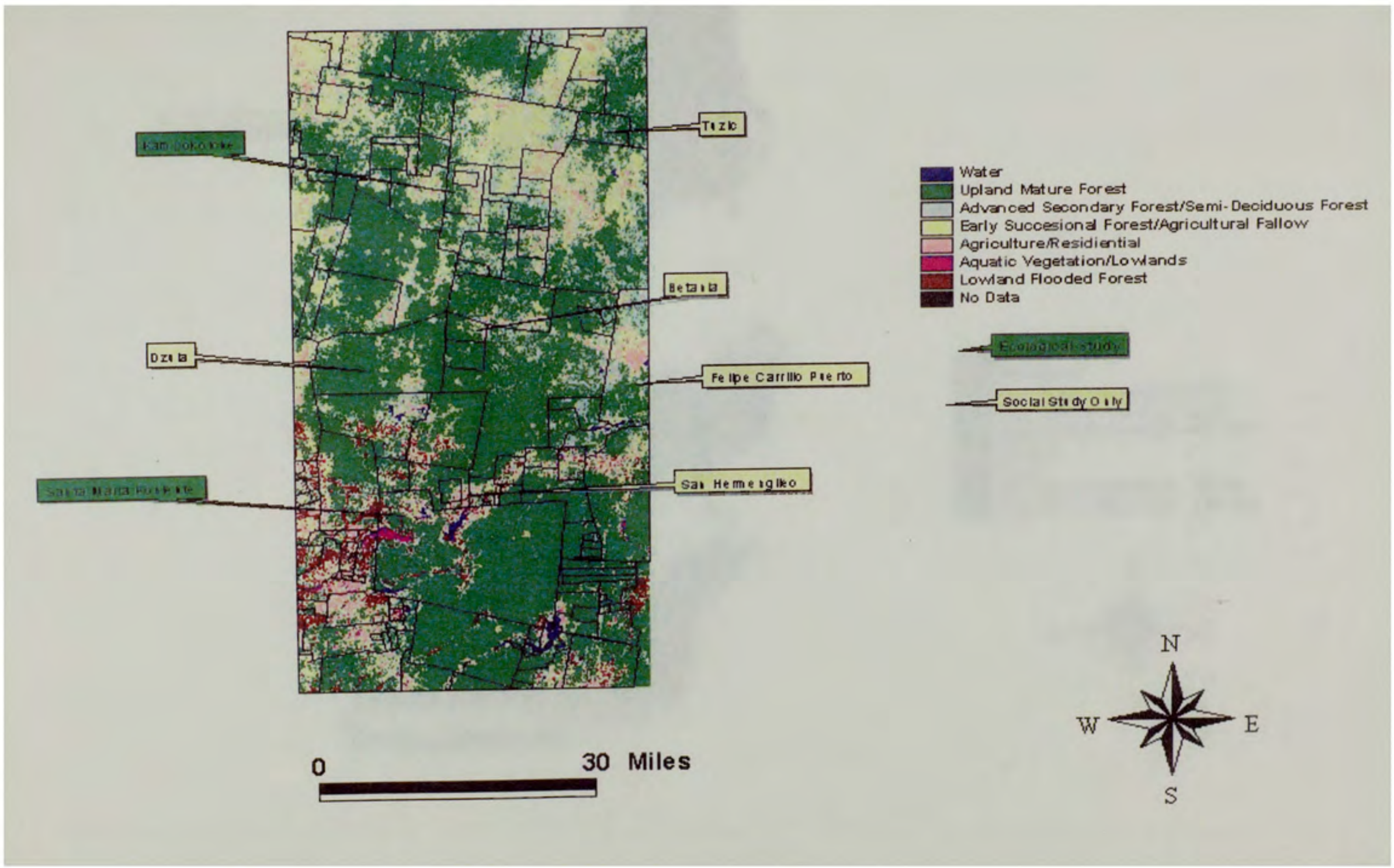
APPENDIX VIII:

Maps of the Study Area

STUDY AREA
Felipe Carrillo Puerto, Quintana Roo
Mexico



Ejidos of Central Quintana Roo: Research Communities



The Sian Ka'an Biosphere Reserve