UNIVERSITY OF CAPE COAST

NESTING ECOLOGY OF STINGLESS BEES WITHIN THREE LANDSCAPES IN THE NORTHERN PART OF THE VOLTA REGION OF GHANA

FERDINAND TORNYIE

2013

UNIVERSITY OF CAPE COAST

NESTING ECOLOGY OF STINGLESS BEES WITHIN THREE LANDSCAPES IN THE NORTHERN PART OF THE VOLTA REGION OF GHANA

BY

FERDINAND TORNYIE

THESIS SUBMITTED TO THE DEPARTMENT OF ENTOMOLOGY AND WILDLIFE OF THE SCHOOL OF BIOLOGICAL SCIENCES, UNIVERSITY OF CAPE COAST IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE AWARD OF MASTER OF PHILOSOPHY DEGREE IN ENTOMOLOGY

APRIL 2013

DECLARATION

Candidate's Declaration

I hereby declare that this thesis is the result of my own original work and that no part of it has been presented for another degree in this university or elsewhere.

Candidate' Signature:..... Date:....

Name: Ferdinand Tornyie

Supervisors' Declaration

We hereby declare that the preparation and presentation of the thesis were supervised in accordance with the guidelines on supervision of thesis laid down by the University of Cape Coast.

Principal Supervisor's Signature:..... Date:....

Name: Dr. Peter Kofi Kwapong

Co-Supervisor's Signature: Date: Date:

Name: Dr. Rofela Combey

ABSTRACT

This research was carried out to investigate the nesting ecology of stingless bees in three selected landscapes in the northern part of the Volta Region of Ghana, from June 2011 to February 2012. The study focused on three stingless bee species Meliponula bocandei (Spinola), Meliponula ferruginea (Lepeletier) and Dactylurina staudingeri (Gribodo). Using eight transects (500 X 40 m) in each landscape, number of nests, nesting heights, diameter at breast heights (DBH) of nest trees and potential nest trees were sampled at three sites namely Koru, Abotoase and Kyabobo. Out of a total of 93 stingless bee nests found, M. ferruginea recorded the highest (50) compared to M. bocandei (33) and D. staudingeri (10). Nest density for the three sites was estimated to be 1.9 nests/ha (\approx 2 nests/ha). *M. ferruginea* was the only species that nested in old termite mounds (17 nests) and in the ground (1 nest). The bees did not show preference for particular tree species they nest in. The two Meliponula bee species were found nesting in trees with DBH \geq 15 cm. Landscape characteristics appeared to have some effects on the nesting ecology of stingless bees. Koru, which recorded larger trees had the highest nest density. Less suitable nesting trees in Abotoase influenced *M. ferruginea* to nest more in old termite mounds than trees. Extraction of potential nesting trees due Agricultural activities and wild honey hunting are threats to stingless bee colonies in Koru and Abotoase. Lack of more suitable nesting trees could account for lower stingless bee nests in Kyabobo National Park.

ACKNOWLEDGMENTS

I wish to express my profound gratitude to Dr. Peter Kwapong, my principal supervisor, who supported me in the entire work. I also wish to thank Dr. Rofela Combey, School of Biological Sciences, University of Cape Coast, for guiding me through this work as my co-supervisor. I am very thankful to my family especially my dad, Mr. Raphael Kujo Tornyie and Richmond Sosu who supported me financially and emotionally throughout my work. I wish to also thank very much the Wildlife Division of Forestry Commission for allowing me to use the Kyabobo National Park for my research. The park manager Mr. Ammed Ankyie and the entire staff of Kyabobo National Park are worth mentioning for their hospitality and assistance during my research there. I cannot forget Mr. David Amedozi and his family for their warm gesture and assistance at Koru. Thanks to my family for all their support during my survey especially at Abotoase. Mr. Percy Danquah assisted me in the identification of the specimens and I wish to thank him so much. I wish to also thank Mr. Francis Otoo of School of Biological Science herbarium for the assistance in plant identification. Thanks to Mr. Samuel Acheampong, Department of Molecular Biology and Biotechnology for his immense contribution during data analysis. To all the farmers and hunters, at all my study sites, I say thank you for your support throughout the studies. Thanks to Mr. Kwame Amede (Abotoase), Wisdom Abotsi (Abotoase), Augustine (Nkwanta) and all others who were very helpful in my research.

DEDICATION

To the Tornyie Family of Mafi-Adidome

TABLE OF CONTENTS

Content

Page

DECLARATION	ii
ABSTRACT	iii
ACKNOWLEDGEMENTS	iv
DEDICATION	V
TABLE OF CONTENTS	vi
LIST OF TABLES	ix
LIST OF FIGURES	X
LIST OF PLATES	xi
LIST OF ACRONYMS	xiii
CHAPTER ONE: INTRODUCTION	1
Background to the study	1
Statement of problem	4
Research aim	6
Research objectives	6
Justification of the study	6
Definition of terms	7
Organisation of thesis	7
CHAPTER TWO: REVIEW OF RELATED LITERATURE	9
Overview	9
Stingless bees	9
Taxonomy and phylogeny of stingless bees	10
Stingless bees and their geographical distribution	12
Differences between honeybee (Apis) and stingless bees (Meliponini)	12

Reproductive biology of stingless bees	14
Communication and foraging in stingless bees	16
Nesting biology and behaviour of stingless bees	17
Nest defense in stingless bees	19
Protection of the outer nest by stingless bees	21
Stingless bees defense materials	22
Maintenance behaviour of stingless bees in their nest	24
Stingless beekeeping and livelihood	27
Importance of stingless as pollinators	30
Issue of declining pollinator populations	35
Effects of climate change on bee populations	39
Stingless bees and forest destruction	40
Bees and land uses	43
CHAPTER THREE: METHODOLOGY	50
Overview	50
Study area	50
Selection of experimental areas	50
Area one: Koru forest	52
Area two: Abotoase	52
Area three: Kyabobo National Park	52
Data collection	56
Statistical analysis	64
CHAPTER FOUR: RESULTS	66

Overview	66
Diversity of stingless bees species in the three areas	66
Nesting behaviourbehavior	66
Nesting density and nest tree characteristics	71
Tree species and potential nest trees species in which stingless bees nest	76
CHAPTER FIVE: DISCUSSION	84
Overview	84
Stingless bees nest survey and nesting sites for the three study areas	84
Nest and potential nest tree survey at Koru	89
Nest and potential nest tree survey at Abotoase	91
Nest and potential nest tree survey at Kyabobo	94
CHAPTER SIX: SUMMARY, CONCLUSIONS AND	
RECOMMENDATIONS	96
Overview	96
Summary	96
Conclusions	97
Recommendations	97
REFERENCES	99
APPENDIX	131

LIST OF TABLES

Table	Page
1. Differences between stingless bees and Apis (honeybees)) 13

2.	Nest density and potential nest tree density for the three	
	sampled areas	73
3.	Mean DBH of nest trees and nest height for Meliponula	
	bocandei and Meliponula ferruginea for the three areas	73
4.	Mean DBH of nest trees and nest height at the three	
	sampled areas (Koru, Abotoase and Kyabobo)	73
5.	Relative percentage of nests found in some specific DBH	
	ranges of nest trees	74
6	a. Nest tree species and number of nests found in them at	
	Koru	77
ł	o. Potential nest tree species and their population at Koru	78
7	a. Nest tree species and number of nests found in them at	
	Abotoase	80
ł	b. Potential nest tree species and their population at	
	Abotoase	81
8	a. Tree species and number of nests found in them at	
	Kyabobo	82
	b. Potential nest tree species and their population at	
	Kyabobo	82

LIST OF FIGURES

Figures	Page
1. Map of northern Volta Region showing the research areas	51

2. Relative nest abundance of three stingless bee species (Meliponula bocandei, Meliponula ferruginea 67 and Dactylurina staudingeri) at the three sampled areas (Koru, Abotoase and Kyabobo) 3. Number of nests found in trees, old termite mounds and in the ground for Meliponula ferruginea at Koru, Abotoase and 68 Kyabobo 4. Relative abundance of nests of the three stingless bee species 68 at the three sites (Koru, Abotoase and Kyabobo) 5 a. Number of nests found in trees of various DBH for 74 Meliponula bocandei across the three study areas b. Number of nests found in trees of various DBH for 75 Meliponula ferruginea across the three study areas 6 a. Number of nests found in trees of various heights for 75 Meliponula bocandei across the three study areas b. Number of nests found in trees of various height for 76 Meliponula ferruginea across the three study areas

LIST OF PLATES

Plates	Pages
1 a. Lumber extracted from the forest in Koru	53

b. A stream flowing through the forest at Koru	54
2 a. Degraded portions of the forest showing savanna	
grassland and farmlands at Abotoase	54
b. Forest burnt by wild fire at Abotoase	55
3 a. A low-lying forest with smaller trees Kyabobo	
National Park	55
b. Montane forest higher up the slopes of Kyabobo	
National Park	56
4. Stingless bees nest search team searching and	
documenting for nest presence	57
5. Flagging tapes on trees showing a transect boundary	58
6. Collecting stingless bees with a long sweep net	60
7. Working on stingless bees in the laboratory	61
8. Insect box containing stingless bee species	61
9. Measuring nesting height using calibrated wooden pole	62
10. Measuring diameter at breast height (DBH) of a tree in	
which stingless bee nest was found	63

11 a. Meliponula ferruginea in a tree trunk showing the	
entrance	69
b. Meliponula bocandei nest in a tree trunk showing the	
entrance	69

12. Meliponula ferruginea nest in an old termite mound	70
13. Entrance hole of Meliponula ferruginea nest in the	
ground showing the entrance	70
14. A logged tree as a result of wild hunting of stingless bee	
honey	91

LIST OF ACRONYMS

ANOVA	Analysis of Variance
DBH	Diameter at breast height
FAO	Food and Agriculture Organization

CHAPTER ONE

INTRODUCTION

Background to the study

Stingless bees (Hymenoptera, Apidae, Meliponini) are a group of small- to medium-sized bees with vestigial (non-functional) stings. They belong to the Meliponinae, one of three subfamilies of the family Apidae and occur in recurrent colonies where they store honey, pollen, propolis and royal jelly. Social organization in stingless bees is highly developed and can be comparable to that of honeybees (Sakagami, 1982). There are several hundreds of species existing worldwide, which vary considerably in colour, body and colony size (Roubik, 1992a; Michener, 2000).

Stingless bees can be found in the tropical and subtropical parts of the world where they occur sympatrically with the honeybees (Kajobe, 2007). They are said to have developed before the continents drifted apart from each other and thus the explanation for their presence in all tropical parts of the world (Food and Agriculture Organization [FAO], 2009). It is estimated that 400 to 500 different species of stingless bees are known, but new species are identified every year. Approximate numbers of species so far identified are 50 in Africa, 300 species in the Americas, 60 in Asia, 10 in Australia and 4 in Madagascar (FAO, 2009). The tribe Meliponini represents the largest biomass of bees within tropical rain forests (Roubik, 1993). The different species are diverse in size ranging from two millimeters (e.g. the tiny sweat bees) to stingless bees slightly bigger than the European honeybee. The number of bees a colony can contain ranges from some

few hundred to more than a hundred thousand bees; however, this differs from species to species (FAO, 2009).

Stingless bees are known to be important pollinators in tropical rainforests (Eltz, Brühl, Imiyabir & Linsenmair, 2003) and good candidates for providing pollination services in agricultural ecosystems thereby increasing yield and food security (Heard, 1999; Slaa, Chaves, Malagodi-Braga & Hofstede, 2006). They have also been shown to be important pollinators of non-crop species in natural habitats (Kato, 1996) thereby improving biodiversity of plants which serves as food for other animals (FAO, 2007). Their hive products; honey (for food and medicine), propolis (for medicine) and wax, all serve as sources of income for local communities (FAO, 2009; Kwapong, Aidoo, Combey & Karikari, 2010).

Stingless bees often need large pre-existing cavities to refuge their heavily populated colonies. Greater part of species depends on already existing tree holes; on the other hand, some occupy other substrata such as deserted ant and termite nests, underground cavities, rock cavities and cracks in walls (Camargo, 1970; Darchen, 1972; Hubell & Johnson, 1977; Roubik, 1989). Their dependants on pre-existing cavities have made them to be confronted with inadequate nesting sites (Hubbell & Johnson, 1977) as result of the various land uses which deprive them of nesting sites and nests. Apart from availability of suitable nesting cavities, physical factors such as temperature may also influence the preference of nesting sites by different species because they show limited and varying nest thermoregulation capacities (Darchen, 1972). Their preference to choose a cavity for nesting is also likely related to both the colony population and the species' body size (Hubbell & Johnson, 1977).

Some previous research has shown that stingless bee richness and abundance may be affected by a variety of local forest structures and conditions and overall habitat diversity, or local forest disturbance history (Salmah, Inoue & Sakagami, 1990; Eltz, Carsten, Der Kaars & Linsenmair, 2002; Eltz, 2004; Samejima, Marfaizal, Teruyoshi & Tohru, 2004). A study carried out in Sabah, Malaysian Borneo found that 91.5% of stingless bee nests were built in living trees, and at least 34% of nest trees were large enough to be harvested (Eltz et al., 2003). This makes them very vulnerable to deforestation and habitat fragmentation as these processes lessen the nest sites and food plants of the bees. Comparatively, little attention has been given to these threatened but valuable bees (Macharia, Suresh & Eliud, 2010).

In Africa, some studies have been done on the taxonomy, biology and domestication of stingless bees, however little is known about their behaviour, impact of various forest exploitation and land use on their nesting ecology. Recent studies by Kwapong et al. (2010) recorded 9 species in Ghana with the northern Volta Region habouring the most diverse and abundant colonies. This research intends to investigate the nesting ecology of stingless bees within three landscapes in the northern part of the Volta Region of Ghana.

Statement of problem

Despite ongoing concerns and controversy over a putative 'global pollination crisis' (Ghazoul, 2005; Steffan-Dewenter, Potts & Packer, 2005), there is little information on the response of bees, the most important group of pollinators, to the ongoing global changes. Land-use changes including deforestation have potential major impacts on bee communities (Allen-Wardell et al., 1998; Kearns, Inouye & Waser, 1998; Kremen, Williams & Thorp, 2002; Klein et al., 2007; Kremen et al., 2007) however, only few studies have examined the impact human induced land cover changes have had on stingless bees. Kerr and Kerr (1999) asserts that in the state of Sao Paulo-Brazil, deforestation for agriculture since 1500s resulted in 6% of pre-European contact forest and 5% of original *Meliponinae* species remaining.

Eltz et al. (2003) and Samejima et al. (2004), while studying the forests of Borneo, in Malaysia, observed that most bee nests occurred in trees of the forest at the climax stage, having diameter at breast-height larger than 50cm nevertheless these trees are the targets of logging industries. Stingless bee colonies find it difficult to disperse more than few hundred meters due to three reasons. Firstly, stingless bee queens have a highly developed abdomen that prohibits flight and perennial life (Roubik, 1987). Secondly, due to the continual parental relationship between mother and daughter colony and thirdly, the task of the workers providing a new nest before colony division (Michener, 1979). Thus, as people colonize forested regions for agriculture, felling of trees containing nest, later robbing of honey by human and subsequent burning of the area easily kill colonies (Kerr & Kerr, 1999).

The scarcity of studies on bees and land-use change is particularly marked in tropical systems. Studies exist from subtropical areas (Aizen & Feinsinger, 1994) and in tropical areas on specific bee groups, especially the euglossines (Powell & Powell, 1987; Becker, Moure & Peralta, 1991; Tonhasca, Blackmer & Albuquerque, 2002). Eltz et al. (2002) researched on nesting and nest trees of stingless bees with implications for forest management. Kojobe and Roubik (2006) also worked on colony abundance and predation by Apes and humans. Brosi, Daily, Tiffany, Federico & Guillermo (2008) studied effect of habitat fragmentation on bees considering the whole bee communities in tropical habitats. Nevertheless, very little has been done on nesting ecology of stingless bees from different landscape perspective to know the various influences they have on them.

The Volta region is one of the important habitats for stingless bees in Ghana (Kwapong et al., 2010) but is under threat from human activities such as logging, firewood harvesting, wild honey hunting and setting of wild bush fires. The most disquieting part is the practice of wild honey hunters who log down trees just to harvest honey and thereby exposing their colonies to dangers of destruction. There is therefore the need to conduct detailed studies on stingless bee nesting ecology and how nest populations are influenced by land use practices within various landscapes.

Research aim

This research is aimed at investigating the nesting ecology of stingless bees within three different landscapes in the northern part of the Volta Region of Ghana.

Research objectives

The following objectives were developed for the study of the nesting ecology of stingless bees in three landscapes in Volta Region of Ghana:

- 1. Surveying stingless bee nests in the three landscapes.
- 2. Surveying for other alternative nesting sites (e.g. deserted ant and termite nests, underground cavities, rock crevices)
- 3. Determining the tree species the bees nest in
- 4. Determining the characteristic of nesting trees (morphological characteristics)
- 5. Determining the density (population/unit area) of potential trees the bees can nest in.

Justification of the study

Stingless bees represent one of the most diversified components of the natural Apoidea fauna of pollinators in the tropics (Venturieri, 2009). They use diverse kinds of substrates and inhabit varied habitats. Some species are typical for some natural hollows and other artificial cavities. Landscape alteration of where this group of bee nests have an important impact on the natural composition of its community structure and nest density (Venturieri, 2009). Bees are the most effective pollinators of crops and natural flora and are reported to pollinate over

70 percent of the world's cultivated crops (Kenmore & Krell, 1998). Despite the potential impact of pollinator limitation on fruit set in agriculture and natural systems, the problem appears to have received less critical experimental and theoretical attention (Johnson & Bond, 1997).

In Australia, stingless bees are used by beekeepers for crop pollination (Heard, 2000). Malagodi-Braga et al. (2000) reviewed the use of stingless bees in crop pollination, and showed their efficiency in strawbery pollination. Despite the importance of these bees, people cut down all kinds of trees without considering which organisms are been deprived of their home. These calls for proper land use policies and education to take care of pollinators. This will lead to Stingless beekeeping (Meliponiculture); a unique ecosystem friendly agrological practice with the potential for environmental amelioration and generation of supplementary income to resource poor farmers around forests (Macharia et al., 2010). This research is therefore timely and very useful to facilitate education and awareness creation on stingless bees, promotion of Meliponiculture, their use for pollination, and education for their conservation.

Definition of terms

In this study, the following key terms are defined as follows:

Nest: A structure or place made or chosen by stingless bees for shelter and laying eggs.

Colony: Group of bees living in organised groups (normally, made up of one queen, few drones and many workers).

Nesting sites: Any substrate or place where a coloney of bees live/nest.

Nest tree: A trees that have a bee colony nesting in it.

Nesting height: Height (from the ground) at which a stingless bee nest entrance is found on a tree trunk.

Potential nest trees: Trees with diameter at breast height 15cm and above capable of providing suitable cavity for stingless bees to nest.

Organisation of thesis

The thesis is organized into six main chapters and each of the chapters has specific sub-topics that are discussed. Chapter One is basically an introductory chapter to the research. Sub-topics discussed under this chapter include the background to the study, including previous studies on the topic, problem statement, research aim, research objectives, justification/significance of the study, operational definition of terms and organisation of the thesis. Chapter Two includes a review of relevant literature on what stingless bees are, classification, geographical distribution and their biology. It goes on to examine the nesting behaviour of stingless bees and their importance to the environment and human livelihood. Finally, the chapter reviews literature on the problems they face in their environment as a result of human activities. Chapter Three outlines the research methodology employed in the study. Sub-headings here include the study area, study design, sampling procedures/techniques, data collection and instrument, fieldwork, data processing and analysis. Chapter Four has to do with the presentation of results. Chapter Five deals with discussions of the results. Chapter Six, deals with the presentation of main findings from the study and conclusions. Recommendations are also made in this chapter.

CHAPTER TWO

REVIEW OF RELATED LITERATURE

Overview

This chapter reviews relevant literature on stingless bees classification, geographical distribution and biology. It goes on to examine the nesting behaviour of stingless bees and their importance to the environment and human livelihood. Finally, the chapter reviews literature on the problems they face in their environment as a result of human activities and further examines the conceptual framework that guided the study in Volta Region.

Stingless bees

Stingless bees are highly social bees which live in colonies of thousands of individuals (Michener, 1990) and have vestigial stings (Heard, 1999). They are of African origin and very adapted to the tropical climatic areas of the world (Eardley, 2004). Stingless bees diverged since the Cretaceous era and have 50 times more species than *Apis*, and are both distinctive and diverse (Roubik, 2006). About one third of the human diet in tropical countries is derived from insect-pollinated plants (Wilms, Imperatriz-Fonseca & Engels, 1996) and Stingless bees represent one of the most diversified components of the natural Apoidea fauna of pollinators in the tropics. On the population level, some species are known to use floral resources from more than a hundred plant taxa over the course of several seasons in a given habitat (Wilms et al., 1996; Heard, 1999).

They are very useful bees which are managed worldwide for pollination services as an alternative to *Apis mellifera* which is declining in recent time due to threat from diseases and pests such as varroa mites (Ingram & Samways, 1996). Stingless bees store honey, propolis and other hive products that are both useful as food and medicine (Krell, 1996). Indigenous knowledge surveys done on stingless bees by Karikari and Kwapong (2007) in Ghana shows that local people are familiar with their nesting behaviour and forage resources (both wild plants and agricultural crops). Local names have been assigned to the various stingless bee species based on their behaviour. They also harvest honey from wild colonies and use them for food and medicine. Stingless bees nest in deserted termite and ant nests, cavities in rocks, in cavities in the ground, within dead and living tree cavities and cracks in mud walls (Kwapong et al., 2010). Thus, landscape alteration where this group of bees nest, has an important impact on the natural composition of its community structure (Roubik, 2006).

Taxonomy and phylogeny of stingless bees

Stingless bees belong to the family Apidae and tribe *Meliponini* and are classified into five genera: Melipona, Trigona, Meliponula, Dactylurina and Lestrimelitta (Michener, 2000; Sakagami, 1982). The classification of stingless bees has been presented differently by different authors (Sakagami, 1982). Wille (1979) was the first to recognize common characters of the African Meliponini, regarding the African group as the ancestral and placing them into five genera. Camargo and Pedro (1992) brought out the major division of African Meliponini genera and that of non-African. African taxa show outstanding external

similarities to that from the Americas (Michener, 2007). They show reduced wing venation, presence of a penicillum (a brush of long stiff setae on the anterior apical outer margin of the hind tibia), and the reduction of the sting apparatus in the females supports the monophyly of Meliponini. Presence of a hind tibial corbicula (pollen basket) is shared with other corbiculate bees, including Euglossini (Michener, 1990).

The relationship of Meliponines to the other corbiculate tribes has been contentious, as the available morphological evidence argues for Apini as the sister group (Roig-Alsina & Michener, 1993; Schultz, Engel & Ascher , 2001), while accumulating molecular evidence points to Bombini as most closely related (Cameron & Mardulyn, 2001; Lockhart & Cameron, 2001; Cameron, 2003; Cameron & Mardulyn, 2003; Thompson & Oldroyd, 2004). There may have been considerable extinction of corbiculate lineages (Engel, 2001); perhaps further obscuring morphological and behavioural transitions between the extant tribes. Morphological diversity among meliponines has led some authors to recognize many supra-specific groups at the generic level (Moure, 1961, 1971; Silveira, Melo & Almeida, 2002; Camargo & Pedro, 2003).

The African *Dactylurina* resembles the *Trigona*; African *Plebeina* resembles *Plebeia*, *Liotrigona* resembles *Trigonisca* and African *Meliponula* resembles *Melipona*. The African genera and the several group of stingless bees from other continents appeared to exhibit parallel evolution with members of the group's have acquired similar characteristics independently, though coming from related ancestral lineage (Wille, 1979). For instance, Wille (1983) concluded that

numerous names would be meaningful only for a minority of entomologists, whereas Sakagami (1982) found it convenient to use the multiplicity of names in his review of meliponine biology. In the largest meliponine genus, *Trigona* workers share a morphological synapomorphy in which the keirotrichia (a dense field of minute, blunt setae) is restricted to a median longitudinal band on the inner hind tibia, and in cross-section the hind tibia forms a broad, raised median ridge (Michener, 1990). This has been utilized for placing more than 120 species into ten subgenera (Michener, 2000) from the Indo-Malay/Australasian and Neotropical Regions. The first cladistic phylogeny of Meliponini by Michener (1990) based on an analysis of 17 morphological characters, recovered *Melipona* as sister group to the remaining taxa, whereas *Trigona* encompassed species from both the Neotropical and the Indo-Malay/Australasian regions.

Stingless bees and their geographical distribution

Stingless bees have populated tropical earth for over 65 million years, longer than *Apis*, the stinging honeybees (Camargo & Pedro, 1992; Michener, 2000). Various species have their preferred habitats and climatic conditions. Some species are present in the rain forest, savanna and also transitions between forest and savanna vegetation zones (Kwapong et al., 2010).

Differences between honeybees (Apis) and stingless bees (Meliponini)

Honeybees and stingless bees share many similar characteristics, remarkably in the honey production and in their social life styles. These characters sometimes make it difficult for some people to differentiate between the honey bees and stingless bees (Otis, 1997). Stingless bees also differ from Apis in many biologically significant ways (table 1) (Peters, Queller, Imperatriz-Fonesca, Roubik & Strassmann, 1999).

Table 1: Differences between stingless bees and Apis (honeybees)

Stingless bees	Apis
Lack stings (vestigial sting)	Possess stings
Females (workers) mate once (single	Females mate more than once
matting)	(multiple matting)
Do not use water to cool their nest	Use water to cool their nest
Build pots; a mixture of wax, propolis,	They use pure wax to build their
resin and gums (thus, they do not use	combs
pure wax to build their nest) to store	
their resources and lay eggs	
Cannot freely swarm to reproduce	Can freely swarm to reproduce
(instead must first make new domiciles)	
Generally smaller in size than Apis	Generally bigger in size than
	stingless bees
Colonies generally make less honey	Colonies make more honey than
compared to Apis	stingless bees
Males do not have membranous	Males have membranous
endophallus	endophallus
Reduced wing venation	Stretched wing venation
Many more species (374species)	Apis have fewer species (11 species)

Table 1 continued

Lack effective thermo-regulation	Possess effective thermo-regulatory
properties	properties

Source: Peters, Queller, Imperatriz-Fonesca, Roubik & Strassmann (1999).

Reproductive biology of stingless bees

The life cycle of the stingless bees is different from that of the honeybees. In stingless bees, there can be two or more queens laying eggs in the same nest. New queens are produced regularly, but most of them are killed and never allowed to produce eggs. Some queens may remain imprisoned in special cells as reserves. Replacement of the egg-laying queen does not happen every year, and some queens may live for 3-7 years. The queen lays eggs in a special way. First, a completed cell is half filled with honey and pollen by the workers. Then one or more workers lay an egg in the cell and the queen is encouraged to come near. Then the queen eats the worker egg from the cell and lays her own egg instead, and then proceeds to another cell. One or more workers close the cell by bending the upper collar of the cell against the centre. The cell is closed until the adult bee emerges. This is called the mass provisioning system and differs from the situation in honeybees where the honeybee larvae are fed continuously as they develop (FAO, 2009).

Stingless bee queens can provide 10-100 cells with eggs a day, depending on the species. When the fully developed bee leaves the brood cell, the cell is torn down, and the material is reused for building new cells. Fertile eggs from the queens develop into worker bees and queens. Drones come from unfertilized eggs from the queen, or from egg laying workers. It sometimes happens that an egg laying worker bee lays an egg into a cell already containing a queen's egg. The male egg develops into a larva more rapidly than the female egg. The male larva then punctures the queen's egg before it hatches, and is able to eat all the food in the cell. After 10 to 15 days, the drones leave their parent colony forever. Where they go is not known (FAO, 2009).

Stingless bees multiply themselves by swarming. When a colony has reached a certain size and a usable new nest place is found, some worker bees will start transporting building materials to the new place. More and more bees will fly to the new nest over the next few days, and in the end, a queen from the old nest will transfer to the new nest and begin producing eggs there. Now a new colony has been established, and little by little, the flying between the two colonies will stop. In most species, mating between a new queen and drones takes place outside the nest (FAO, 2009).

The relative numbers and positions of colonies within an area have perforce shaped the evolution of stingless bees. Virgin queens accompany swarms of workers to new nest sites, and males wait there in anticipation (Nogueira-Neto, 1997; Velthuis, Koedam & Imperatriz-Fonseca, 2005) clearly indicating the queen odors is dispersed from the nest. Afterwards, the new queen flies out for a single mating, pursued by hundreds of males (Peters et al., 1999; Palmer, Oldroyd, Quezada-Euán, Paxton & May-Itza, 2002). The queen may be killed, or indeed, several queens are killed by predators (Michener, 1961; Paxton, Bego, Shah & Mateus, 2003) on such mating attempts. Therefore, reproductive biology of stingless bees includes the connection for food and potential new virgin queens between the mother and daughter colony. The relationship has been documented to last up to six months (Wille & Orozco, 1975; Sakagami, Inoue, Yamane & Salmah, 1983; Drumond, Bego & Melo, 1995). The mean 'nearest neighbour' distance between conspecific colonies nesting in nature may be on the order of 50 to a few hundred meters (Hubbell & Johnson, 1977; Breed, McGlynn, Sanctuary, Stocker & Cruz, 1999; Samejima Marfaizal, Teruyoshi & Tohru, 2004).

Communication and foraging in stingless bees

Stingless bees are connected with tropical and subtropical forest areas. Here navigation by means of the sun, as used by honeybees, is not as easy as in open habitats. Stingless bees use different ways of communicating to each other the way to food sources. There are three main methods, depending on the different species (FAO, 2009).

One method is that the scout bee returns and makes a special sound in the nest that gets other bees to fly out and search for the flowers at random. Another method is that the scout bee lays out an odour trail by marking stones and plants on the route with a special scent. Inside the colony, she makes a sound and a zigzag dance. When leaving the nest again, she leads a group of recruits to the source by following the trail. The third method is like the second, but instead of the odour trail, the scout bee guides a group of recruits by means of a pheromone emitted during her flight back to the flowers (FAO, 2009). The communication systems of the stingless bees are three dimensional, and indicate how high in the

forest the nectar and pollen sources are and by this way, stingless bees are well adapted for tropical forests (FAO, 2009).

Nesting biology and behaviour of stingless bees

Many stingless bees have evolved a wide range of nesting and feeding behaviours that allow them to share habitats and to occur in high densities. Some species of stingless bees are nest parasites, some groups use several types of substrates for nesting (Roubik, 2006), but most species use existing cavities in living trees to build their nests (Eltz et al., 2003). However, one species of stingless bee (Dactylurina staudingeri) build its own exposed nest in the form of a ball attached to a stem or branches of a tree (Kwapong et al., 2010). The genus Melipona; the most numerous among the stingless bees (Silveira et al., 2002) and most of the species of Trigona usually build their nests in hollow tree trunks or branches, and some in cavities in the ground or empty mice or parrot nests. Other species live in ants or termites' nests. Nests can sometimes be found in cavities in buildings, cavities in unused panel doors of buildings accessed by cracks and key holes (FAO, 2009; Kwapong et al., 2010). The various species prefer different cavity dimensions and most species have characteristic nesting sites. For example, the nests of Trigona fulviventris most often are found at the foot of a tree. In other species, the selection of nest sites is more variable. The entrance of the nest is most often very small, so that it can be protected against other bees, phorid flies, parasitic wasps, small hive beetles and ants (FAO, 2009; Kwapong et al., 2010).

The nest is a notable point of bee activity, making it a spectacular example of animal architecture. This makes nesting biology a highly visible aspect of stingless bee behaviour (Michener, 1974). Colonies are active every day and therefore have sustained impact among the biota (Roubik, 1989; Hansell, 1993). The individual species are recognizable from nest entrances and often their particular site, however variety exists. Inside the nest, there are different shapes and arrangements of brood cells and food storage 'pots'. Honey and pollen are stored in separate 'pots'. Stored nectar or ripened honey are in nest cavity extremes (for storage during heavy flowering periods), while pollen and some honey surround the brood area (Sakagami, Roubik & Zucchi, 1993).

Stingless bee pots can be from five to 40 millimeters high. In some species the honey pots and pollen pots are segregated, in others they are intermixed. In a few species, the honey pots are oval and the pollen pots appear like stalactites hanging over the brood cells (FAO, 2009). One robber bee genera Lestrimelitta and *Cleptotrigona* collect and then store some mixed honey and brood provisions (Sakagami et al., 1993). The brood cells are spherical to ovoid, while food storage containers are small to large spheres, or are egg-shaped, or even conical or cylindrical. Often pots are pressed together in odd conglomerates, as are the brood cells, ranging from individual cells on pillars, to sheets of orderly cells on combs, separated by the pillars. Some few species build brood cells in piles in a special brood chamber, and one African stingless bee, Dactylurina staudingeri, builds vertical double-sided combs. The brood chamber is surrounded by a protective wall made with wax and propolis (the involucrum). The whole nest, or the ends (if placed in a hollow trunk) is enclosed in the bitume, a special material made by a mixture of resin, wax and various amounts of other materials like mud, oil, paint,

and sometimes, animal faeces making it looks dark like hard propolis (FAO, 2009).

Some resins used by meliponines were found to contain small seeds from fruit of plants (an example is *Coussapoa asperifolia*; Cecropiaceae) (Garcia, Oliveira & Campos, 1992) and also seeds such as those embedded in the mud and resin bitume block of Melipona. Such seeds were previously confused (Roubik, 1989) with Vismia (Clusiaceae). *Trigona carbonaria* collects resin with the seeds of *Eucalyptus torelliana* (Wallace & Trueman, 1995). The importance of seeds in nest construction is unclear, but the seeds of both plants (*Coussapoa* is a hemiepiphyte) germinate on the outside of the bee nests (Roubik, 2006).

Nest defense in stingless bees

Many animals including ants, small hive beetles, spiders, toads, lizards, birds, monkeys and man have been recorded predating on stingless bees (Kwapong et al., 2010). The site and architecture of stingless bee colonial nests represent compromises between nesting material, nest location and a combative versus cryptic colony profile. Many species are tremendously aggressive and attack while biting, applying sticky resin carried in the mandibles or on hind legs. Among 'fire bees', *Oxytrigona*, and a few others (reportedly *Melipona rufiventris* in Bolivia, Stierlin), caustic secretions, containing formic acid in the former, are applied (Michener, 2000). Bees of this nature emit disagreeable odours from mandibular gland secretions and seem to take special care to fly into the hair, ears, eyes or mouth, and emit distressing sounds. Moreover, colonies that appear well

protected, settled within several centimeters of living tree trunk and having a small nest entrance, can be either aggressive or timid (Roubik, 2006).

Defending bees normally come from the entrance area and nests have suitable architectural features to allow their aggregated presence there. Defensive strategies include alarm chemicals of mandibular gland origin, released in the air within and outside the nest (Smith & Roubik, 1983; Roubik, 1989; Wittmann, Radtke, Zeil, Lubke & Francke, 1990). Hovering defenders then exit in force, face the nest entrance, and engage in aerial fights with non-nest mates, or directly attack larger animals, which retreat with a cloud of defending bees surrounding the head. Very few species, for example *Tetragonisca angustula* (Latreille) and *Tetragona* clavipes (Fabricius), regularly maintain hovering defenders outside the nest. Hovering 'guard' bees may defend against the robbing bee, genus Lestrimelitta Friese (Wittmann et al., 1990), or against raiding individuals from other meliponine colonies (Sakagami et al., 1993).

Aggregations allow pooled defense against large predators. Direct molestation, rather than the release of alarm pheromone dispersed in the air, evokes multi-colony attack in *Partamona peckolti* (Roubik, 1983a). Numerous species of this genus are defensive (Camargo & Pedro, 2003). Group defense occurs among small meliponines such as *Hypotrigona* (Roubik, 2006; Michener, 1959) and *Tetragonisca weyrauchi*, but not Asian *Tetragonula* or *Heterotrigona* (Starr & Sakagami, 1987) or *Scaura tenuis* (Kerr, Sakagami, Zucchi, Portugal-Araújo & Camargo, 1967), which form aggregations.

Protection of the outer nest by stingless bees

The simplest stingless bee nest entrance protrudes slightly from the base of the entrance hole. Nest entrances are not only related to defense and foraging (Biesmeijer, Giurfa, Koedam, Potts, Joel & Dafni, 2005), but to physio-chemical regulation. A small or unornamented nest entrance is cryptic and is usually the only passage to a relatively small number of potentially defensive adult bees. The narrow tube can be closed with resin or cerumen, or coated outside with droplets of fresh resin where invaders like ants may be halted (Wittmann, 1989; Camargo, 1984). Larger species, for example Melipona, Cephalotrigona and Scaptotrigona also build long and/or wide internal nest entrance tubes, where foragers, ventilating bees or defenders are positioned. In addition, the inside alcove of the nest entrance of Partamona (Camargo & Pedro, 2003), often holds decoys of empty storage pots or brood which may confuse and discourage predators who probe, such as long-tongued anteaters, Tamandua. A few Partamona, such as P. *pearsoni* and *P. peckolti* also have the brood chamber blocked to all entry, save through a secondary entry 'bottleneck' (Camargo & Pedro, 2003).

There are completely or partly exposed nests built on stems or hard substrates by aggressive *Trigona*, *Tetragonula*, *Tetragonisca*, *Partamona*, *Paratrigona* and *Plebeia*. Many unaggressive species, including those within most of the above mentioned genera, nest in living trees, but those with exposed nests have an outer nest shell that is delicate, and workers immediately flood from the exterior of a broken nest envelope, then bite. Biting behaviour in defense against vertebrates has no direct relation to bee size. *Tetragonula fuscobalteata* is among the most aggressive and also the smallest native stingless bees in South Eesten Asia. Aggressive colonies can be aggregated in a single palm branch, whereas stem-nesting colonies, ostensibly the same species, are unaggressive (Sakagami, Inoue, Yamane & Salmah, 1983).

Tiny *Plebeia minima* build a nest on spiny palms (*Bactris* and *Astrocaryum*), sometimes in small aggregations, and the workers have strong biting responses to molestation (Roubik, 1983a). A noteworthy meliponine defensive structure is the 'scutellum nest' of Neotropical *Trigona*. This hard and thick barrier is made by exposed-nesting *Trigona* (Nogueira-Neto, 1962), by hypogeous *T. fulviventris* (Roubik, 1983a), and is an ample protective shield (Wille, 1983). Nogueira-Neto (1962) noted the scutellum is made up largely of bee faeces. The scutellum of *Trigona corvina*, is often surrounded by a few thin batumen covers, layers outside of the scutellum are easily broken by predator attack, thus function to permit release of many defending bees from throughout the nest surface. In similar nests, *T. spinipes* opens holes in the outer nest shell in response to temperature and ventilation needs (Zucchi & Sakagami, 1972; Sakagami, 1982), thus the thin shell may have more than one function.

Stingless bees defense materials

The primary activity of non-foraging bees near their nest entrances is prevention of entry by small insects, including parasites, and for the deposit of fresh resin on external entrance tubes, which may deter ants. The chemistry and choice of nest resins useful as repellants of natural enemies has not been studied, although the antibacterial properties of resins are well known (Lokvam &
Braddock, 1999; Langenheim, 2003). *Symphonia globulifera* (Clusiaceae) provides a steady resin source that is mined daily and defended by several nest mates of *Trigona fulviventris* (Roubik, 2006). Resinous materials deposited by female Centris on terminal nest cells are used by individuals or small groups of aggressive *Trigona fuscipennis* and *T. muzoensis* Panama (Roubik, 2006).

Resin sources are generally wounded trees, and they often have several species visit them, including bee predators, some of which are stingless bee mimics (Roubik, 1989). Nesting cavities with extensive sprays of resin droplets, for several centimeters from an entrance, can be found on stems with nesting colonies of African *Meliponula ferruginea*, Neotropical *Trigonisca* and Asian *Geniotrigona thoracica*, among others. The use of resin to immobilize large beetles within the nest has been well documented (Nogueira-Neto, 1997). Resin is usually placed on predators' hair, and it is applied to objects near the nest entrance. In *Melipona panamica* and other *Melipona*, hardened balls of resin are loosely cemented by the entrance; when needed, the spheres may be rolled into place, cemented together with resin and thus close the entrance to invaders (Roubik, 2006); spheres tend to accumulate in older nests at their bases. Honey has been recorded as a defense material employed by tiny *Hypotrigona braunsi* in Africa (Portugal-Araújo, 1958; Michener, 1959).

Few stingless bees make a defensive wall of enough thickness to permit use of nest cavities that have large openings; these are *Melipona*, *Cephalotrigona* and *Meliponula bocandei* (Portugal-Araújo, 1955; Roubik, 1983a). As mentioned above, *Melipona* use small stones. Colony batumen, separating the inner nest from the outer environment, may be built to a thickness of 10 cm with the stone, mud and resin mix made by *Melipona*. Workers of *Melipona* are, apparently, unique in the behaviour of surveying the outside of both nest and hive for sharp edges, openings or other irregularities, then depositing material on them (Roubik, 2006).

Maintenance behaviour of stingless bees in their nest

Fanning during night or day should be influenced by colony honey production (Nogueira- Neto, 1948). The fact that stingless bees use nectars that average about 65% water, then convert this to honey of 30% water (Roubik, 1989; Roubik, Yanega, Buchmann & Inouye, 1995) means that moisture must be removed from the nest cavity. The large batumen plates having many air channels, made by *Melipona* and some *Plebeia* (Nogueira-Neto, 1948; Roubik, 1979, Roubik, 2006) seem ideal for the purpose of water loss. However, as mentioned above, CO₂ loss may also be significant and other nest entrance features involving surface area and openings determine available fanning positions for bees. Worker bees often carry water and dumped from the nest entrance area, sometimes leaving wet marks near the nesting cavities. Apart from this, latrines are maintained within nests, where several symbionts live (Roubik, 2006).

Drainage outlets are maintained in the nests of subterranean stingless bees, such as *Meliponula* and *Plebeina*, and in tree-nesting species including *Trigona* and *Tetragona*, plus exclusively ground-nesting *Geotrigona* (Portugal-Araújo, 1955; Sakagami, 1982; Camargo & Wittmann, 1989; Camargo & Roubik, 1991; Camargo & Moure, 1996). The nesting cavities are not constructed by the bees but are often left by failed colonies in the Neotropics or termites in Africa, and are modified so that water can be ejected. Nesting by some subterranean colonies takes place just above a soil horizon of very well drained material thus nest drainage from rain or water from ripening of honey should pose no special problem (Camargo & Wittmann, 1989). The insulation provided by wood and resin, earth, stone, or other nest substrates, make it unlikely that colonies overheat, provided nests are not in full sunlight and not too many bees engage in fanning during extremely high ambient temperatures (Roubik & Peralta, 1983).

As demonstrated by Moritz and Crewe (1988) tidal air flow may cause hot external air to enter the nest. Compared to resin, wax is much more rigid and four times stronger; especially at temperatures higher than 35°C, (Hepburn & Kurstjens, 1984) yet stingless bee cerumen has a higher melting temperature (Buchwald, Greenberg & Breed, 2005). Small *Hypotrigona, Trigonisca, Schwarzula* and *Plebeia* use very little resin, using almost pure wax (Sakagami, 1982; Blomquist, Roubik & Buchmann, 1985; Drumond et al., 1995; Camargo & Pedro, 2002). Such an adaptive response by small stingless bees nesting in slender stems and exposed to high temperatures would be expected from the thermal conditions. Also loose nest element architecture and large cavities, allows adult movement as heat sources. Daily dynamics of air temperature have not been measured among the outer nest batumen layers in the large, exposed nests, although temperature measurements (Zucchi & Sakagami, 1972;Wille & Orozco, 1975; Roubik & Peralta, 1983) and direct observation of incoming foragers reveal no use of water droplets to cool nests (Moritz & Crewe, 1988; Engels, Rosenkranz & Engels, 1995; Nogueira-Neto, 1997). When water is collected by workers, it is likely to be used for honey dilution (Roubik & Peralta 1983).

Nest repairs incorporate available nesting material. Workers do essentially all the work, even though males occasionally perform superficially similar (i.e. irregular) maintenance activity (Velthuis et al., 2005). Workers make wax that is secreted from dorsal glands, but some queens or males also make a small quantity; the wax is first placed on a wax deposit in the nest (Cruz-Landim, 1967; Michener, 1974; Sakagami, 1982; Koedam, Jungnickel, Tentschert, Jones & Morgan, 2002). Cerumen, the product of plant resin mixed with wax and employed exclusively by meliponines, remains soft for an extended time and is more pliable than beeswax – that of Apis mellifera (Hepburn & Kurstjens, 1984). In addition to being used for constructing nest forms, cerumen may be taken to make an emergency repair of natural enemy damage. Cerumen is normally made freshly to construct brood cells, involucrum, nest entrance tubes, or storage pots. These may be in several positions near the nest entrance and brood cells; workers mix the materials with their mandibles (Michener, 1974; Sakagami, 1982). In response to drastic nest alteration, such as opening of the nest, bees respond by seeking and collecting more resin and, in genera such as Plebeia, Melipona, Cephalotrigona, and Partamona, mud is deposited directly on the edges of the opening (always interspersed with resin), which is then gradually closed, by working toward the middle. When a nest is severely damaged, colonies cannot fly with their queen to a new nesting site, but a queen deprived of food did fly to an empty hive box in *T. laeviceps* in Sumatra (Inoue, Sakagami, Samah & Nukrnal, 1984).

Melipona are keenly interested in returning to a damaged nest and collecting resin from resin deposits, and also cerumen and honey, as do many stingless bee genera. Bees eject water, as explained above, but are far more regularly seen ejecting a bolus of trash, carried in the mandibles. This activity may occur daylong, or primarily in the afternoon. A few genera, like *Lestrimelitta*, *Hypotrigona* and *Trigonisca* (Roubik, 2006) drop the bolus from the nest entrance, while most, like *Melipona*, fly to drop trash meters from the nest (Kerr & Kerr, 1999). Trash balls are mainly meconia (larva defecations) on cell bases. Adult defecations in the nest are gathered at small latrines which most are consumed by mutualist organisms. The cerumen coat is immediately removed from a newly spun pupae cocoon (Michener, 1974).

Stingless beekeeping and livelihood

People's capacity to make a livelihood, and their resilience to negative change, is shaped by their livelihood strategies. These strategies are the combination of people's activities and the choices they make in order to achieve their livelihood goals. They depend on the opportunities and access individuals, households and communities have to exploit different levels and combinations of assets, and are probably the major influence on people's choice of Livelihood Strategy (FAO, 2009).

When beekeeping forms part of people's livelihood strategies there are various possible outcomes. Some of these outcomes will include income and material goods, but also non-material outcomes such as well-being and contentment. In terms of beekeeping, the least visible livelihood outcome is the pollination of flowering plants, both wild and cultivated: this is an outcome impossible to quantify. Honey is a traditional medicine or food in nearly all societies and whether sold in a simple way at village level or packaged more sophisticatedly, honey generates income and can create livelihoods for several sectors within a society (FAO, 2009). Beeswax is also a valuable product from beekeeping, although in some places its value is not appreciated. Industrialized countries are net importers of beeswax, and the supply comes from developing countries (FAO, 2009).

The beekeepers and other people in a community can create further assets by using honey and beeswax to make secondary products, such as candles, beauty creams or beer. Selling a secondary product brings a far better return for the producer than selling the raw commodity. Bees also generate other products such as pollen (bee bread- very rich in protein, vitamins and minerals), propolis (proven to be effective against many health disorders, natural antibiotic that is effective in healing wounds and infections in the body, Ulcers, skin infections and rashes) that can in some situations be harvested, marketed and made into secondary products: all of this work effectively strengthening people's livelihoods (FAO, 2009; Kwapong et al., 2010).

Another crucial livelihood outcome is where, through strengthening people's livelihoods, beekeeping has managed to help a family become less vulnerable, strengthening their ability to look into the future, and reducing the chance that they will slip into poverty if a member of the family becomes ill or if a season is bad for farming or other activities. In addition to their financial value, honey and beeswax have many cultural values and form part of ceremonies for birth, marriages, funerals, Christmas and other religious celebrations in many societies. Beekeepers are generally respected for their craft. All of these aspects are livelihood outcomes from the activity of beekeeping.

While some may be difficult or impossible to quantify, they are real outcomes that strengthen people's livelihoods and therefore should be acknowledged by a beekeeping intervention. In Tanzania national beekeeping programme, considering the prevailing costs and profit margins, an ordinary beekeeper keeping an average of 150 local-style beehives can earn more than US\$200 a year (FAO, 2009).

Roughly, 80 percent of Africans rely on traditional medicine to some extent. Bee products are also widely used in Africa's traditional healthcare system. The nutritional and medicinal benefits of honey and other bee products may also lead to an increase in their demand. Honey, as a source of energy, has been advocated in the diets of people living with HIV/AIDS (FAO, 2004). Though traditional medicines definitely cannot replace the antiretrovirals, traditional medicines do however, effectively treat opportunistic infections (e.g. candidiasis; herpes simplex, and zoster) and symptoms (i.e. appetite loss, nausea, fever, diarrhea and coughing) associated with HIV/AIDS (FAO, 2004).

At the present time, quite a number of papers on the use of rational hive boxes for the keeping of stingless bees is available, and hive management is fairly simple for certain species (Maeta, Tezuka, Nadano & Suzuki, 1992; Amano, Nemoto & Heard, 2000). Stingless bees rearing became a very popular activity among beekeepers in some countries such as Brazil and Australia. In this case, stingless bees are very useful for the facility of keeping, breeding, observing, and understanding ecological rules. A market for nests of stingless bees arose, and as a consequence breeding techniques are developed (Nogueira-Neto, 1997).

Kwapong et al. (2010) have been researching into stingless bees domestication, their use to improve crop yield as well as their development for hive product in Ghana. Apart from the benefit we get from their hive products, stingless bees also have aesthetic values; such as making artifacts of them for example jewellery, key holders, T-shirts and other souvenir which can bring happiness, income and relieve to mankind. Curiosities surrounding these bees; that they do not sting, the fact that its hive products having medicinal properties and the global movement around ecology, nature and conservation create a market for nature observers. This then offers great opportunities for tourism to generate income for local communities (Kwapong et al., 2010). Also due to it friendly nature many people are interested in keeping them (Heard, 1999) making stingless beekeeping a potential business for poverty alleviation.

Importance of stingless bees as pollinators

Tropical trees and crops are mostly self-incompatible and generally dependent on animal-mediated pollination for seed production (Bawa, 1974, 1990). Disturbances that impact animal vectors of pollen transfer may therefore affect the reproductive output of tropical trees. Pollination processes can be disrupted by declining pollinator abundance (Rathcke, 2000), changes in resource availability (Jennersten, 1988), the spatial distribution of floral resources (Ghazoul, Liston & Boyle, 1998), or competitive exclusion from floral resources by inefficient pollinating species (Huryn, 1997).

Pollinators provide an essential ecosystem service that contributes to the maintenance of biodiversity and ensures the survival of plant species including crop plants. Two types of pollinators occur in nature. These include abiotic pollinators such as wind, water and gravity, and biotic pollinators such as insects, birds and various mammals. It has been estimated that over three quarters of the world's crops and over 80% of all flowering plants depend on animal pollinators, especially bees (Kenmore & Krell, 1998; FAO, 2007). Many plants have evolved intricate relationships with many insect pollinators, without which they would not reproduce and/or maintain their genetic diversity (Daily et al., 1997).

In natural ecosystem, insect pollinate more than 50% of tropical forest and thus they play a major role in maintaining and conserving biodiversity. In agricultural ecosystem, many agricultural crops are dependent on insects for their pollination, and assisted pollination may have to be done when natural pollination is insufficient in order to reduce potential yield loss (Klein et al., 2007). On a global scale, the total annual value of insect pollination services has been estimated at USD 217 billion (Helmholtz Association of German Research Centres [HAGRC], 2008).

The role of the Apoidea in pollination is even more noticeable when we consider the trees that constitute the canopy and the middle stratum. These trees not only comprise almost all species exploited by the timber industry, but they are also auto-incompatible, which means they need vectors to transfer pollen from one tree to another, sometimes over great distances (Bawa, Bullock, Perry & Coville, 1985; Bawa, 1990; Renner & Feil, 1993; Kress & Beach, 1994). Vertebrates, such as birds, bats and other non-flying mammals can be pollen vectors (Faegri & Van Der Pijl, 1979; Pesson & Louveaux, 1984; Proctor, Yeo & Lack, 1996); however most animal-pollinated plants depend on invertebrates for pollination (Kress & Beach, 1994). Among the group of invertebrate pollinators, bees play a major role as far as pollination is concern (Janzen, 1967; Frankie, 1975; Bawa et al., 1985; Frankie, Opler & Bawa, 1976, 1983, 1990; Bawa, 1990; Momose, Yumoto, Nagamitsu & Kato, 1998).

Observations of flower visits and analyses of pollen diets have indicated that stingless bees utilize a wide variety of plant species (Heithaus, 1979; Roubik, Moreno, Vergara & Wittmann, 1986; Wilms & Wiechers, 1997). Stingless bees (*Meliponini*) are good candidates in commercial pollination due to their diversity (Rindfleisch, 1980; Roubik, 1995b; Heard, 1999; Sommeijer & Ruijter, 2000) and their ability to form perennial colonies from which they forage year-round. Several hundred species exist worldwide, which differ significantly in colony size (from a few dozen to tens of thousands of individuals), body size (from 2 to 14 mm; compare to 12 mm for honeybees), and foraging strategy (some species recruit nest mates to high quality food sources, like honeybees, whereas others forage mainly individually, like bumble bees) (Roubik, 1992b; Michener, 2000; Slaa, 2003; Slaa, Wassenberg & Biesmeijer, 2003; Biesmeijer & Slaa, 2004;

Nieh, 2004). These inter-specific differences permit for selection of the most suitable stingless bees for a given crop species and crop breeding system in greenhouse and open field (Roubik, 1989).

There are other numbers of biological features that make stingless bees strong candidates for commercial pollination services. Stingless bees are true generalists, collecting nectar and pollen from a vast array of plants (Heithaus, 1979; Roubik, 1989; Ramalho, Kleinert-Giovannini & Imperatriz-Fonseca, 1990; Biesmeijer et al., 2005). A single species can collect floral rewards from up to 100 plant species on a yearly basis (Heithaus, 1979; Cortopassi-Laurino, 1982). However, individuals tend to specialize on a single floral species for a certain amount of time, a behavioural trait commonly referred to as flower constancy (Slaa, 2003; Slaa et al., 2003). Flower constancy leads to assortative mating of the visited plants and therefore to more efficient pollination (Thomson, 1983; Campbell & Motten, 1985). Stingless bees waste less pollen due to selective transfer within a species, and less non-specific pollen reaches the stigma, preventing pollen competition and stigma clogging (Waser, 1983). The fact that stingless bees are generalists at the colony level but specialists at the individual level makes them theoretically good pollinators. Certainly, stingless bees are considered vital pollinators of the native flora in tropical and subtropical parts of the world, and they have been found to contribute to the pollination of many crops and wild plants (Heard, 1999).

Although stingless bees naturally only occur in the tropics and subtropics, they have also been successfully exported and maintained indoors in colder climates, using temperature controlled rooms and/or hives for instance Utrecht University, The Netherlands; Japan manage these bees (Maeta et al., 1992; Amano et al., 2000).

Besides the fact that many species of stingless bees can be managed in hives, several other features make this group very ample for pollination services. First, colonies don't die after reproducing, unlike other bees such as *Bombus*, and colonies are naturally long-lived (Slaa, 2006). This makes it relatively easy to keep Individual hives for long periods of time (up to 60 years: Murillo, 1984). Second, they lack a functional sting, which makes them especially suitable for pollination of crops that are cultivated in inhabited areas and in enclosures such as cages and greenhouses. In Costa Rica, for example, many seed producing companies grow ornamental plants in large netted, insect proof, cages. They have a high demand for pollinators, but because all honeybees are Africanised, and hence more defensive, honeybees are hardly used for pollination in such enclosures. In such cases, stingless bees might provide a solution (Slaa et al., 2006). Third, many stingless bee species have proven to forage well in enclosed areas and under adequate climatological conditions they forage year-round. This makes them especially suitable for offseason production of crops in green houses (Heard, 1999). Most species of stingless bees have a foraging range smaller than that of the honeybee, which may enhance foraging efficiency in confined spaces (Visscher & Seeley, 1982; Seeley, 1985; Kakutani, Inoue, Tezuka & Maeta, 1993). Fourth, because most stingless bees cannot survive cold winters, there is little risk of invasion when importing stingless bees to temperate climates (Heard,

1999). Heard (1999) noted however that some species do live where it occasionally freezes, and combined with global warming these species might become feral when introduced outside the tropics of Capricorn and Cancer. Besides, they suffer from fewer diseases, pests and parasites than the honeybee (Nogueira-Neto, 1997), which simplifies colony management.

Though not all species can be used for commercial pollination (e.g. obligate parasites of other stingless bees, species with restrictive nesting habitats, extremely defensive behaviour or destructive use of flowers), several species are good candidates as commercial pollinators because they can easily be kept in hives, have sufficient numbers of workers per hive and are non-aggressive (Roubik, 1995; Heard, 1999). The diversity of the group indicates that they may be of use to pollinate a wide range of crops and ornamental plants.

Issue of declining pollinator populations

In recent years there is a world-wide decline in pollinator populations and diversity. The factors causing this decline could be the decline in the habitat, with the accompanying decrease in their food (nectar and pollen) supplies as a result of decline in pristine areas, land use changes, increase in monoculture-dominated agriculture, and negative impacts of modern agricultural interventions, e.g. use of chemical fertilizers and pesticides (Verma & Partap, 1993; Partap & Partap, 1997; Partap & Partap, 2002). Earlier, farmers used to grow a variety of crops, which bloomed during different months of the year and provided food and shelter for a number of natural insect pollinators and hence the pollination problem never existed. Monocropping also requires pesticide use to control various pests and

diseases. Thus, it does not only reduce the diversity of food sources of pollinator but also led to the killing of many pollinators due to pesticides. The insecticides have contributed to the extermination of both the diversity and abundance of pollinating insects. Changes in climate might also be affecting insect numbers (Partap & Partap, 2002). Many wild bees, including stingless bees, depend on trees for nesting, and deforestation significantly reduces their numbers (Slaa, 2003). Even selective logging may severely affect stingless bee populations, especially when the larger trees that are preferred for nesting are harvested (Eltz et al., 2002; Samejima et al., 2004). Simple management measures to increase bee abundance and diversity include preservation of natural forests and forest fragments, increasing the availability of nesting sites, and minimizing the use of pesticides including herbicides (Kearns & Inouye, 1997; Klein, Steffan-Dewenter & Tscharntke, 2003b).

The decline in pollinator population and diversity presents a serious threat to agricultural production and conservation and maintenance of biodiversity in many parts of the world. One indicator of the decline in natural insect pollinators is decreasing crop yields and quality despite necessary agronomic inputs. Examples can be found in Himachal Pradesh in northwest India, northern Pakistan and parts of China where despite all agronomic inputs, production and quality of fruit crops, such as apples, almonds, cherries and pears, is declining. Extreme negative impact of declining pollinator populations can be seen in other areas, for example in northern Pakistan where both farmers and institutions have failed to understand the importance of managed pollination. Disappointed with the very low yields and quality of apples as a result of poor pollination several farmers in Azad Jammu and Kashmir of Pakistan have chopped off their apple trees (Partap et al., 2001).

In the case of coffee (Coffea arabica), one of the most valuable export commodities from developing countries, yields on a farm in Costa Rica were 20% higher in areas near forest than in areas away from forests. The economic value of the forest in terms of pollination services was estimated to be \$60 000 for one Costa Rican farm, per year. This value is of at least the same order as major competing land uses, which illustrates the economic benefit of forest conservation in agricultural landscapes (Ricketts, Daily, Ehrlich & Michener, 2004). Similar results were found in Indonesia where fruit set was negatively correlated with forest distance (Klein, Steffan-Dewenter & Tscharntke, 2003a), and in Brazil where coffee plantations near forest fragments had an increase of 15% in production that could be related to pollination services (Marco & Coelho, 2004). Fruit set in the self-sterile lowland coffee species C. canephora was found to linearly decrease with distance from the forest (Klein et al., 2003b). Proper information to farmers about the role of wild bees as pollinators and the pollination services of forests can play a major role in the conservation of wild bees and their natural nesting habitat of tropical forests (Heard, 1999).

Some species of stingless bees, especially from the genus *Trigona*, have dented mandibles and are known to damage fruits, leaves and sometimes even flower buds (Wille, 1961). Some farmers consider these species as pests and try to eliminate the easily recognizable exposed nests, without knowing that they are losing valuable pollinators. Wille, Orozco and Raabe (1983) report that one Costa Rican family with a chayote orchard took one year to eliminate all *Trigona* nests known in their area because they believed these bees ate the tendrils and young leaves. After eliminating all nests, production decreased dramatically from previously high quantities of fruits to no yield at all (Wille et al., 1983).

One implication of the decline in the pollinator populations as well as diversity is that it has created the need for managed pollination in order to maintain crop yields and quality. In fact, farmers engaged in cash crop farming in those areas where pollinator populations have declined are forced to manage pollination of their crops through different ways. For example, farmers in Himachal Pradesh in northwest India are using honeybees for pollination of their apples, while those in Maoxian county in Hengduan mountains of China are pollinating their crops, e.g. apples and pears, through hand pollination using human beings as pollinators (beekeepers do not rent their honeybee colonies for pollination of these crops because farmers make excessive use of pesticides even during flowering season). Hand pollination is an interesting method of pollinating crops and provides employment and income generating opportunities to many people during apple flowering season. But at the same time it is an expensive, time-consuming and highly unsustainable proposition of crop pollination owing to the increased labour scarcity and costs. Moreover, a large part of farmers' income is used in managing pollination of their crops (Ricketts et al., 2004; Klein et al., 2003a; Marco & Coelho, 2004).

Effects of climate change on bee populations

Invertebrates are particularly sensitive to abiotic conditions (Chown & Nicolson, 2004). Global climate change is projected to have many direct and indirect impacts on invertebrate population dynamics including changes in population size, phenology, feeding rates, and species' distributions (Bale, 2002). In turn, these alterations to invertebrates will undoubtedly have cascading effects on the many ecosystem services that invertebrates provide. However, changes to ecosystem services mediated through climate-driven alterations of invertebrate populations have not received the attention that they merit (Bale, 2002).

In social insects, foraging activity and thus pollination are induced by climatic conditions (Roubik, 1987). It has become increasingly important to obtain baseline data on the relationship between climate and the foraging activity of keystone species such as stingless bees; one of the most important native Neotropical pollinators (Heard, 1999). Roubik (1987) found out that, flight activity is well correlated with foraging activity and has been generally used to measure foraging activity by several investigators, thereby providing useful information for comparisons. The flight activities of social insects are influenced by several factors particularly meteorological conditions. The influence of weather on the flight activity of Meliponini bees (Michener, 2000) has been studied and seasonal variations have been found in flight activity and weather variables especially temperature and luminosity (Kleinert-Giovanini & Imperatriz-Fornseca, 1986; Heard, 1999).

Declining numbers of bees could be affecting pollination by disrupting the synchronised timing of flower opening and bee emergence from hibernation. Wild lily was examined in the rocky mountains of Colorado; one of the longest-term studies of pollination ever done for 17-year. It revealed a progressive decline in pollination over the years, with particularly noteworthy pollination deficits early in the season (Cornell University, 2011, December 12).

Stingless bees and forest destruction

Cavity in trees are important structural features of natural forest, and a wide range of vertebrates and invertebrates depend on them for varying purposes, e.g. nesting and roosting (Lindenmayer, Cunningham & Donnelly,1997; Newton, 1994; Oldroyd, Lawler & crozier, 1994). The population of cavity dwelling animals could be directly affected through mortality resulting from felling of trees and indirectly, as a result of decreased availability of suitable cavities (Eltz et al., 2003). Most research focus on measuring or estimating indirect effect on population of forest animals whiles direct effect of cavity-dwelling animals has received much less attention, presumably because of difficulties quantifying logging-induced mortality in relatively mobile taxa. Nevertheless direct effect could have considerable impact on populations of long-lived organisms with low fecundity (Eltz et al., 2003). For example in one study of over 200 nests in Uganda, nest predators (primarily tool-using chimpanzees and humans) most affected colonies in trees at under seven meters height (Kajobe & Roubik, 2006).

Stingless bees are eusocial insects (Sakagami, 1982) thus after insemination marking the start of egg laying, the queen's abdomen becomes enlarged (physogastric), which implies that she will not be able to fly anymore and will stay in the same colony as long as she lives. Their colonies are also perennial, and occupy the same cavity through various generations. Obviously, the continuous removal of trees with a diameter larger than 50 cm will, over the medium to long run, negatively affect the density of stingless bee's nests. The resulting lower density has a recurrent effect on the reproductive biology of many tree species and the decline of pollinator populations will result in a reduced seed set (Venturieri, 2009).

Stingless bees use several types of substrates for nesting (Roubik, 2006), but most species use existing cavities in living trees to build their nests (Eltz et al., 2003). The genus *Melipona* is the most numerous among the stingless bees (Silveira et al., 2002). They also include the biggest and the heaviest individuals; therefore, they are the most adapted to flying long distances in their search for food (up to 2000 m) (Roubik & Aluja, 1983; Van Nieuwstadt & Iraheta, 1996; Araujo, Costa, Chaud-Netto & Fowler, 2004). Eltz et al. (2003) and Samejima et al. (2004), while studying the forests of Borneo, in Malaysia, observed that most bee nests occurred in trees of the forest at the climax stage, having diameter at breast-height larger than 50 cm. These trees are exactly the kind that the timber industry look for and exploit. Eltz et al. (2003) and Samejima et al. (2004) also determined that bee species prefer certain trees to others for nesting.

The continuous commercialization of wood will in the long run jeopardize the survival of forests because of the strong reduction in nesting places of key pollinators, including stingless bees. In particular, the exploitation of trees with diameters over 50 cm will dramatically diminish the nesting possibilities of many species of stingless bees (Eltz et al., 2003; Samejima et al., 2004).

Michener (1946), for example, reported that populations of meliponine bee colonies in Old Panama City were high because of the numerous holes and cavities suitable for nesting places in the ruins. This however, obscures the fact that fewer species are found in disturbed areas, compared to natural forest (Roubik, 1983a). In the forest, unoccupied tree cavities are fairly common (Johnson & Hubbell, 1986). However, the size of the tree hole leading to the nest cavity markedly influences acceptability to bees (Roubik, 1983a).

Human disturbance may affect both tree densities and species composition, changing the density of flowering trees and phenology patterns. The relative intensity of resource limitations may change with the magnitude of flowering activity. Inoue and Sakagami (1993) indicated that stingless bees adapt to resource fluctuations by alternating between two strategies: they utilize and store huge amounts of resources during the heavy (or general) flowering season, when their populations grow rapidly, and they consume the stores and their population gradually decreases when there are few flowering trees. Appanah (1993) and Sakai et al. (1999) have also reported population growth in stingless bees in response to flowering activity. Although decreases in the species richness and population density of stingless bees proportional to the intensity of human disturbance have been reported (Inoue & Roubik 1990; Lee, Navjot &Thomas, 2001), the mechanisms responsible for these declines in the stingless bee community are still unclear. While conserving biodiversity may be perceived as a goal in itself, poorer people depend on the goods and services that biodiversity provides. Therefore, ecosystem changes are probably unavoidable unless the local community draws benefits of biodiversity maintenance. The losses of forest cover, increased fragmentation and conversion of primary forest to plantation and even to farmlands are due to economic pressures that may be difficult to avoid. Promoting the sustainable use of commercial insects such as stingless bees can reduce the pressure exerted on rainforests in Africa (FAO, 2009). Conservation of stingless bees may also be affected by the commercial use of stingless bee colonies for pollination services. Provided that colonies for such services are mainly obtained from breeding programmes, instead of taken from nature, commercial use of stingless bees do not have to have a negative impact on the feral population, and may actually contribute to their conservation (FAO, 2009).

Bees and land uses

Understanding the scale at which habitat influences species richness in ecosystems is central to ecology (Wettstein & Schmid, 1999) as both patch and landscape factors may contribute to the diversity of resident taxa (Collinge, Prudic, & Oliver, 2003; Fleishman, Ray, Sjögren-Gulve, Boggs & Murphy, 2002; Graham & Blake, 2001; Lowe & Bolger, 2002; Noss, 1990; Soderstrom, Svensson, Vessby & Glimskar, 2001; Wettstein & Schmid, 1999). Patch-level factors include patch area and shape, natural and anthropogenic disturbances (e.g. flooding, fire, logging, and livestock grazing), vegetation structure and composition. Landscape- level factors include the type and quality of the surrounding matrix (e.g. urban, developed, undeveloped, and agricultural), elevation, and isolation. Due to anthropogenically mediated habitat, changes are taking place at multiple scales, science must distinguish between patch and landscape threats in order to develop effective conservation strategies. Community composition may be influenced by habitat variation from patch to landscape-scale depending on body size, home range area, and dispersal distance of the taxa of interest (Calder, 1984; Haskell, Ritchie & Olff, 2002).

Long-term changes in climate and topography influence the physical appearance of the landscape (Samways, 1989). Examining differences in community composition across biotic and abiotic gradients is a basic approach to understanding forces shaping animal community composition. Many factors can affect bee distribution. Pollen and nectar rewards attract bees to sites (Potts et al., 2004; Larsson & Franzen, 2007). Disturbance, in the form of fire (Potts, Vulliamy, Dafni, Ne'eman & Willmer, 2003a), agricultural development (Williams & Kremen, 2007) and residential development and deforestation (Russell, Sagvolden & Borgå, 2005; Winfree, Griswold & Kremen, 2007) can affect bee community composition, as can habitat structure by changing availability of nesting resources (Potts, Kevan & Boone, 2005; Cane, Terry & Frank, 2007) and by modifying the thermoregulatory environment (Cane & Tepedino, 2001).

Research on bees on landscape and patch level is important because of the following; the central ecosystem function bees provide as pollinators, concern over possible declines in bee populations, uncertainties concerning the role of

land use change on bee populations and the possible need to supplement pollination of agricultural crops done by commercial bee colonies with increased pollination by native bees (National Research Council [NRC], 2007).

In medium-term historical times, agriculture has dramatically and rapidly changed landscapes. It has contributed to heterogeneous partitioning of land surface and multiplied the number of small patches and line corridors (Samways, 1989). When a landscape is converted to agricultural use, the remaining habitats become fragmented and with this fragmentation there can be an increase in edge habitat which often increase invasive plant species (With, 2002). Previous work suggests that fragmentation may also cause declines in overall pollinator abundance (Jennersten, 1988; Goverde, Arnone & Erhardt, 2002) and native bee species richness (Steffen-Dewenter, 2002). Changes in the matrix surrounding core habitats have been shown to influence the ability of other invertebrates to traverse from one site to the next (Ricketts, 2001). The greatest concern is the loss of tropical forests, where probably more than half of all insects live. Currently, approximatly130,000 km² are lost annually (Sodhi, Koh, Brook & Ng, 2004). Evidence is accumulating that forest-to-farmland conversion has a major effect on insect assemblages, particularly the primary forest specialists (Castano-Meneses & Palacios-Vargas, 2003; Hill, Hamer, Lace & Banham, 1995; Jones et al., 2003).

Inclement weather can also have a short-term relatively instantaneous influence, causing fine tree fall, landslips, avalanches, mud deposition among others. These various influences, all have an impact on insect population levels and distribution. Inclement weather has a major but transient detrimental effect upon insect populations, both directly and indirectly by changing the landscape. Even apparently innocuous conditions, such as dew, can be inclement to small insects, but insect populations usually recover rapidly from such disturbances. In contrast, landscape disturbance by man has a major and fairly permanent effect upon overall insect population levels and distribution (Samways, 1989).

For bees, not much studies are common on effect of various land use on them (Goulson, Lye & Darvill, 2008), especially studies that evaluate the relative effect of different environmental gradients on bee community composition (Williams et al., 2010; Potts et al., 2003b; Brosi, Daily & Ehrlich, 2007; Schaffers, 2008). Brown and Albrecht (2001) researched on the effect of tropical deforestation on stingless bees of the genus Melipona in central Rondonia, Brazil. They examined the effects of forest fragment size, shape, isolation and landscape context on bee diversity, abundance and community composition. Previous work also on the effects of distance to a large forest fragment in the same area (Brosi et al., 2007) showed strong shifts in bee community composition but no differences in bee diversity or abundance with distance. Particularly, the meliponine bees, which nest primarily in tree cavities, declined markedly away from forest edges. Similarly, pollination of coffee declined with distance to forest, primarily resulting from reduced numbers of meliponine bees, in a nearby southern Costa Rican landscape (Ricketts, 2004).

Brosi et al. (2008) studied the effects of forest fragmentation on bee communities in tropical countryside and found out that adverse effects of deforestation on *Melipona* are detectable in the study area, despite the fact that significant areas of tropical forest cover remain. They found bee community resilience to land-use change, as deforested sites and small forest fragments can have a diverse component of bees. Eltz and Brühl (2001) also found out from their work (on Stingless bee population and community ecology) that the abundance and diversity of stingless bees in forests in Sabah is chiefly dependent on the local availability of food resources and only to a lesser degree on the availability of nest trees. Therefore, stingless bee communities are likely to recover from the effects of single selective logging events, provided that sufficient time is given for regeneration.

Sánchez and Aguilar (2004) working on Conservation of native trees and the indigenous bees in Costa Rica found out that, the number of stingless bee nests found in the forest plot was higher than in farm areas. On the other hand, the number of nests associated with a given tree could be positively correlated with tree diameter. The species of stingless bees and wild native plants change as a result of deforestation, nest density decrease as well as the species composition of the deforested area. They also found the forest plot containing more nests (14 nests/ha) than the grassland plot (1.6 nests/ha) with slightly higher stingless bee diversity in the forest (6 species) than in the grassland (5 species).

Nesting and nest trees of stingless bees (Apidae: Meliponini) in lowland dipterocarp forests in Sabah Malaysia was studied by Eltz et al. (2002). In their research they found out that stingless bee species seem to be quite opportunistic in their selection of nest sites and are likely to colonize any tree that offers a suitable cavity of the right size. They stated that harvesting is likely to kill bee colonies associated with the respective tree and because meliponine colonies are long-lived and have low fecundity thus, direct impact from logging may have lasting effects on bee populations.

In general, species diversity and the complex associations among species are essential for the stability of their community. Despite the enormous importance of stingless bees to man and his environment, not much attention is given to conserving these bees (Kwapong et al., 2010) with little known on how extensive habitat loss will affect species diversity and ecological processes (Lee et al., 2001). Less information is available regarding how stingless bees respond to forest disturbance imposed by human activities, although there is some indication that stingless bee abundance is greater in undisturbed, primary forests (Lee et al., 2001). These bees are faced with challenges as a result of some economic activities of man in addition to pests and diseases, impacting negatively on their survival and sustenance. Though bees as a whole show some degree of resilience to land-use change, there are taxon-specific responses (Samways, 1989). The situation calls for collaborative efforts to conserve stingless bees in order for them to sustainably provide the valuable ecosystem services (Kwapong et al., 2010).

Previous researches have looked at stingless bees' ecology at one landscape level (mostly primary and secondary forest) with little attention on agricultural and other landscapes and land patches. Little is also known about the characteristic of their nesting trees and other alternative nesting sites. Kwapong et al. (2010) as part of suggestions toward conservation of stingless bees, called for landscape management to be incorporated into town and country planning. In Ghana not much have been done on these bees especially country wide. This research looks at the nesting ecology of stingless bees in three landscapes considering their nests density, characteristics of nesting trees (tress species they nest in, nesting heights, size of nesting tree), other nesting sites apart from trees and density of potential nesting trees.

CHAPTER THREE

METHODOLOGY

Overview

This chapter describes the approach, techniques and methods that were used to select study sites, stingless bee species and analyze the data. It specifically describes the study areas, study design and sampling procedures/techniques. Others include the data collection equipments, recruitment of field assistants, fieldwork, data processing and analysis.

Study area

The fieldwork was carried out in three landscapes in the northern part of Volta Region of Ghana. These areas were chosen based on the knowledge that the forests harbour a rich stingless bees fauna. The bees are under the threat of losing nesting sites due to fast depletion of the forests as a result of illegal logging, wild bush fire and various agricultural land use practices (Kwapong et al., 2010). The study areas are within the Moist- Semi Deciduous Forest zone of Ghana (Hall & Swaine, 1981). The selected areas were Koru about 15 km from Pampawie (Kadjebi District), Tapa-Abotoase (Biokoye District) and Kyabobo National Park (Nkwanta District) (Figure 1).

Selection of experimental areas

Preliminary survey was conducted within the last two weeks in June, 2011, to ascertain the presence of stingless bees at the various areas. Four days was spent at each area to scan for the presence of these bees in the forest. Sweep net was also used to collect stingless bees on flowers in and at the edges of the forest. The collected bees were sent to the laboratory where they were identified by the help of a bee taxonomist. The areas were selected based on the presence of stingless bees and followed by other surveys.



Figure 1: Map of northern Volta Region of Ghana showing the research areas

Source: Remote Sensing and Cartographic Unit, University Cape Coast, 2012

Area one: Koru forest

Koru forest (07° 24.951' N; 000° 18.163' E 87.5 m elevation) is located about 70 km from Kadjebi town. The forest is characterized by logging activities for commercial purposes and wild honey hunting where the honey hunters cut down trees that have bee colonies before they are able to harvest the honey. There are very large trees of up to about 120 cm DBH and tall trees up to about 30 m. The forest has a small stream flowing through it but dries up getting to the later part of the dry season (March to April) every year (Plate 1a, 1b).

Area two: Abotoase

Abotoase (07° 25.615' N; 000° 21.209' E 261.2 m elevation) is in the Biokoye District, about 30 km from the District capital Nkonya Ahienkro. The area is characterized by forests patches joined up by grassland savanna and farms. The forest patches have open canopies with few trees. Bush fire is a common phenomenon (Plate 2b) at this area every dry season (December to April). These forest patches are degenerating gradually into savanna with fewer trees thus making most of the vegetation look like a woodland savanna (Plate 2a). There are also small streams found in the area.

Area three: Kyabobo National Park

The Kyabobo National Park (08°19.302' N; 000° 33.188' E 261.2 m elevation) is located about 10 km from the Nkwanta township. The forest reserve is about 360 km² covering an altitudinal range of approximately 300 m to 800 m (Ankudey, 1987). It is characterized by hilly terrain with woodland savanna at lower levels (Plate 3a) and montane forest higher up the slopes (Plate 3b). There

is a waterfall that flows into a long stream that passes through the forest. This forest was gazzeted in 1994, before then there were human settlements in it and a lot of human activities such as logging, farming, bush fire and wild honey hunting going on in the forest. It is managed by the Wildlife Division of Forestry Commission of Ghana.



Plate 1a: Lumber extracted from the forest in Koru



Plate 1b: A stream flowing through the forest at Koru

Source: Fieldwork, 2011



Plate 2a: Degraded portions of the forest showing savanna grassland and farm lands at Abotoase



Plate 2b: Forest burnt by wild fire at Abotoase



Plate 3a: A low-lying forest with smaller trees in Kyabobo National Park Source: Fieldwork, 2011



Plate 3b: Montane forest higher up the slopes of Kyabobo National Park Source: Fieldwork, 2011

Data collection

Survey of nests

The survey for stingless bee nests was conducted between July 2011 and February 2012. Field assistants, forest guides, local farmers and the indigenous honey-hunters residing near the study sites were engaged (Plate 4). The methods that were used to survey nests are similar to those of Roubik (1996), Eltz et al. (2002) and Hubbell and Johnson (1977). Eight random transects of 500 meters each were made using flagging tapes and nests scanned along them (Plate 5). Stingless bees nests were search in 40 m corridors along the transects. In all, an area of 16 hectares was covered for each area. To locate stingless bee colonies, nests were searched by visual inspection for bees in flight and nest entrance tubes on tree trunks of ≥ 15 cm diameter at breast height (DBH). Other possible nesting sites apart from trees were also searched for (e.g. ground nest, nest within cracks in rocks, nest in old ants and termite nests) and any nest found was also recorded. Sweep net was also used to collect bees on flowers and vegetation. Collected bees were killed, stored in 70% alcohol (methanol) and labeled according to the areas they were collected. The GPS of the three study areas were also noted and recorded. These bees were sent to the Department of Entomology and Wildlife insect museum- University Cape Coast, for identification.



Plate 4: Stingless bees nest search team searching and documenting for nest presence



Plate 5: Flagging tapes on trees showing a transect boundary
Diversity of stingless bees in study areas

Stingless bees were spot-identified whenever a nest was sighted using their colour, size and nest entrance of the bees. A sweep net of about 2.0 m long handle was used to collect stingless bees from nests found within reach and were killed with a killing jar containing soapy water. Colonies nesting higher up on the tree trunks or canopies were identified visually by using binoculars. Colonies nesting within the reach of six meters high were sampled by means of tying the sweep net to a strong four meter pole and used to collect bees entering their nest from foraging trips (Plate 6). Dead bees were placed in pre-labeled storage bottles containing 70 percent ethanol. These were sent to the laboratory for further laboratory work involving cleaning, pinning, labeling and identification with the help of a bee taxonomist (Plate 7 and 8).

Nest survey

Three stingless bee spicies, *Dactylurina staudingeri* (Gribodo), *Meliponula bocandei* (Spinola) *and Meliponula ferruginea* (Lepeletier) were considered in the nest survey experiment because their nests are big and easily sighted. They also depend mostly on bigger trees to nest, unlike *Hypotrigona sp* which can nest in any small cavity and may be difficult to locate.

Nest heights (the height at which the nest entrance is located above the ground) were measured using a calibrated long wooden pole of six meters. The pole was calibrated using a measuring tape and marked at every half meter interval. The pole is placed on the ground at the most elevated part of the ground around the tree and nest height read from the calibrated pole (Plate 9). Nest

heights above six meters were estimated and recorded.

Tree diameter is an important criterion for harvesting of trees by loggers. Diameters at breast height (DBH at1.37 m above the ground) of tree species that the bees nest were measured using measuring tape (Plate 10). In the case of trees with large buttresses, DBH recordings were taken just above the buttresses.



Plate 6: Collecting stingless bees with a long sweep net



Plate 7: Working on stingless bees in the laboratory Source: Fieldwork, 2011



Plate 8: Insect box containing stingless bee species



Plate 9: Measuring nesting height using calibrated wooden pole



Plate 10: Measuring diameter at breast height (DBH) of a tree in which stingless bee nest was found

Identification of trees in which stingless bees nests were located

Local names were used to identify trees in which nests were located in the field with the help of a local plant specialist (herbalist) and an experienced forestry staff. A field identification guide on forest plants of Ghana (Hawthorne & Gyakari, 2006) was also used. For certainty of identification, plant parts originating from the respective trees such as twig with leaves, slash of the bark and those with flowers and fruits were collected, labeled and sent to the University of Cape Coast School of Biological Sciences herbarium for confirmation. Photographs of the trees were also taken and used in the identification process and with the help of a plant taxonomist; identification was carried out to the family, genus and species levels.

Estimation of plant density

In order to make a good judgment of the bee's preference to the trees they nest in, the density of the tree species in the various sites was estimated. This study was done to ascertain whether the abundance of tree species influence bee preference to nest in them. To achieve this, sixteen 20 m by 20 m square areas of the forest were marked randomly at the areas. Within each 20 m by 20 m square area, all trees with DBH 15cm and above (DBH \geq 15 cm) were recorded. In all, an area of 6400 m² (0.64ha) was covered for each site. This was done at all the three study areas to establish the population density of the potential nest trees.

Statistical analysis

The nests counted in the area along the transects were transformed into nest density per area (per hectare) covered by incorporating area searched (500 m \times 40 m) (Roubik 1996; Roubik & Skelley, 2001).

Nest density = $\frac{\text{Number of nests}}{\text{Area search is (500 m x 40 m)}}$

All statistical analyzed was computed using the Minitab for windows release 14 and Ms Excel for windows 2007. The numbers of the various individual stingless bee species were pooled together according to transects and study areas. Minitab statistical software was used to compute a one-way analysis of varience (ANOVA) for differences in mean abundances of nests in the three areas, DBH and nest height for the various bee species and areas. A two-way (ANOVA) was also use to test for the significant level between the count of nests against bee species and study area. Percentages (in count of nest) of individual species of stingless bee nests were computed using Ms Excel for windows 2007 for each site and for all the three sites together. Histograms were also plotted for the population of various stingless bees species occurrence in the three sites, nesting tree heights and DBH against total number stingless bee nests found.

CHAPTER FOUR

RESULTS

Overview

This chapter presents the results of the data in line with the objectives of the study. It commences by examining the diversity of stingless bee species and their nesting sites in the three study areas. It also examines their nest densities relative to potential nesting trees as well as preferred nesting tree species. The three areas were also analyzed individually considering trees DBH, height, nest density as well as bees preferred nesting sites.

Diversity of stingless bee species in the three areas

A total of five species of stingless bees were found in the three landscapes studied. These include: two species of *Meliponula*: *Meliponula bocandei* (Spinola) and *Meliponula ferruginea* (Lepeletier), two unidentified species of *Hypotrigona* and *Dactylurina staudingeri* (Gribodo).

Nesting behaviour

The three stingless bee species considered for the purpose of this study recorded a total of 93 nests; *M. bocandei* (33), *M. ferruginea* (50) and *D. staudingeri* (10) (Figure 2). Out of the 93 nests, 76 nests were found in trees (cavity and open), 17 were found in old termite mounds and one nest (*M. ferruginea*) was found in the ground. However, all the species of stingless bees found in the old termite mounds were *M. ferruginea*. In one instance, both *M. ferruginea* and *M. bocandei* nests were found in separate cavities of the same tree.

Out of the 50 nests of *M. ferruginea* found at all the three sites, 64% was found in trees (Plate 11) and 34 % was found in old termite mounds (Plate 12) and 2% in the ground (Plate 13). However, there was no nest of *M. bocandei* found either in old termite mound or in the ground. Abotoase recorded many more *M. ferruginea* nests (14) out of which 10 were found occupying old termite mounds. At Koru the most aboundant species nest recorded was that of *M. ferruginea* (19 nests) followed by *M. bocandei* (17 nests) and *D. staudingeri* (2 nests). Abotoase, also recorded 14 nests of *M. ferruginea* being the highest compared to the other two sites, followed by *M. bocandei* (10 nests) and *D. staudingeri* (3 nests). Kyabobo recorded the highest number of *D. staudingeri* nest as compared to Koru and Abotoase (Figure 4).



Figure 2: Relative nest abundance of three stingless bee species (*Meliponula bocandei*, *Meliponula ferruginea* and *Dactylurina staudingeri*) at the three sampled areas (Koru, Abotoase and Kyabobo)



Figure 3: Number of nests found in trees, old termite mounds and in the ground for *Meliponula ferruginea* at Koru, Abotoase and Kyabobo



Figure 4: Relative nest abundance of nests of the three stingless bee species at the three sites (Koru, Abotoase and Kyabobo)



Plate 11a: Meliponula ferruginea nest in a tree trunk showing the entrance

Source: Fieldwork, 2011



Plate 11b: Meliponula bocandei in a tree trunk showing the entrance



Plate 12: *Meliponula ferruginea* nest in an old termite mound Source: Fieldwork, 2011



Plate 13: Entrance hole of *Meliponula ferruginea* nest in the ground showing the entrance

Nest density and nest tree characteristics

Nest density and potential nesting tree density were estimated and the results are as follows respectively; Koru: 2.4 nests/ha and 253.0 trees/ha; Abotoase: 1.7 nests/ha and 118.8 trees/ha and Kyabobo: 1.8 nests/ha and 348.4 trees/ha (Table 2). Density of nest trees did not directly relate to density of potential nest trees. In Kyabobo National park for instance, where the highest tree density (348.4 trees/ha) was recorded had the second highest nest density (1.8 nest/ha). Koru on the other hand had the highest nest density (2.4 nest/ha) but recorded the second highest tree density (253.0 trees/ ha).

There was a significant difference (p=0.001, df=2, F=10.23, [Appendix 1j]) in number of nests of individual stingless bee species found across the three sites. However the total number of stingless bee nests found did not differ significantly (p=0.609, df = 2, F=0.74, [Appendix 1k]) among the sites. This shows that number of nests recored for individual species at the various sites were not the same. Thus, some species occurred more than others. There was a significant difference (p=0.001, df=1, F=23.20, [Appendix 2b]) in *M. ferruginea* choice of place for nesting implying that they prefer to nests in a particular substrate i.e. in trees than in old termite mound. There was no interaction (p=0.393, df=4, F=1.04, [Appendix 2a]) between the bees species and the sites.

The diameter at breast height (DBH) of nest trees differ significantly for *M. bocandei* and *M. ferruginea* (p = 0.039, df=2, F=3.40, [Appendix 11]), thus these bee species have preference to particular tree sizes (DBH ≥ 15 cm) they nest in. There was no significant differences in nesting height for *M. bocandei* and *M.*

ferruginea (p = 0.529, df = 2, F = 0.64, [Appendix 1h]) suggesting that these bees do not have preference to height when they choose to nest in trees.

At individual landscapes (areas) level, there was no significant differences in stingless bee species respond to DBH of nesting trees (p=0.083, df=2, F=2.69, [Appendix 1a]) and nesting height (p=0.369, df=2, F=1.03, [Appendix 1e]) in Koru. Nest recoreds collected at Koru did not show stingless bees preference to trees of particular DBH and nesting height. However, at Abotoase DBH of nesting trees differ significantly among the two *Meliponula* species (p=0.002, df=2, F=10.71, [Appendix 1a]) while the nesting height showed no significant difference (p=0.165, df=2, F=2.05, [Appendix 1f]). There was a significant difference (p=0.041, df=2, F=3.80, [Appendix 1d]) in responds of bee species to DBH of nest trees with no significant difference (p=0.91, df=2, F=2.73 [Appendix 1c]) in preference of bee species to nesting heights at Kyabobo.

Trees at Koru were found to be significantly larger (mean DBH: 61.0 ± 13.5 cm, nest height: 7.7 ± 1.6 m) than those at Kyabobo (mean DBH: 41.8 ± 9.5 cm, nest height: 6.0 ± 1.7 m) and Abotoase (mean DBH: 39.1 ± 19.0 cm, nest height: 6.0 ± 1.7 m) (Table 3 & 4). *M. bocandei* nested in bigger trees (mean DBH: 51.4 ± 6.5 cm) as compared to *M. ferruginea* (mean DBH: 48.2 ± 5.9 cm). In terms of nest height, *M. bocandei* had the highest (6.5 ± 0.9 m) as compared to *M. ferruginea* (5.4 ± 1.1 m) (Table 3).

M. ferruginea had more nests (50% of the total nests) found in trees with DBH ranging from 20 - 41 cm as compared to *M. bocandei* which had 24.2% of total nests in the same DHB range (Table 5, Figure 5b). Thus, *M. ferruginea* had

more colonies nesting in smaller size trees than *M. bocandei*. Also, *M. ferruginea* had more colonies nesting at lower heights ranging from 0.1 m to 10.0 m (Figure 6a) as compared to *M. bocandei* with more colonies nesting at height from 2.1 m to 10.0 m (Figure 6b).

arcas						
	Nest	Nests density		est tree density		
Sites	Nests/ 16 hectares	Nests/ hectare	Trees/ 0.64 hectare	Trees/hectare		
Koru	38.0	2.4	162.0	253.0		
Abotoase	27.0	1.7	76.0	228.8		
Kyabobo	28.0	1.8	246.0	384.4		

 Table 2: Nest density and potential nest tree density for the three sampled areas

Source: Fieldwork, 2011

 Table 3: Mean DBH of nest trees and nest height for Meliponula bocandei

 and Meliponula ferruginea for the three areas

Stingless bee species	Mean DBH/cm	Mean nesting height/m	
M. bocandei	51.4 ± 6.5	6.5 ±0.9	
M. ferruginea	48.2 ± 5.9	5.4 ± 1.1	

Source: Fieldwork, 2011

Table 4: Mean DBH of nest trees and nest height at the three sampled areas (Koru, Abotoase and Kyabobo)

Site	Mean DBH±S.E Mean nesting heig	
Koru	61.0 ± 13.5	7.7 ± 1.6
Abotoase	39. 1 ± 19.0	4.8 ± 1.8
Kyabobo	41.8 ± 9.5	6.0 ± 1.7

	Nest percentage of	Nest percentage of
DBH (cm)	Meliponula bocandei (%)	Meliponula ferruginea (%)
20-41	24.2	50.0
42-63	57.6	40.6
64-96	18.2	9.4

Table 5: Relative percentage of nests found in some specific DBH ranges of nest trees



Figure 5a: Number of nests found in trees of various DBH for *Meliponula bocandei* across the three study areas



Figure 5b: Number of nests found in trees of various DBH for *Meliponula ferruginea* across the three study areas



Figure 6a: Number of nests found in trees of various heights for *Meliponula bocandei* across the three study areas



Figure 6b: Number of nests found in trees of various heights for *M*eliponula *ferruginea* across the three study areas

Tree species and potential nest trees species in which stingless bees nest

Nest tree species diversity was much higher at Kyabobo (17 species in 15 families) than Koru (16 species in 15 families) and Abotoase (seven species in five families). The trend was not different for potential nest tree density at Kyabobo: 45 species in 25 families, Koru: 34 species in 18 families and Abotoase: 18 species in 14 families (Table: 6a, 6b, 7a, 7b, 8a, 8b).

Koru

At Koru, stingless bees were found in sixteen (16) different tree species of fifteen (15) families. The tree species with the most nests (seven nests) was *Manikara multinersis* (family: Sapotaceae) followed by *Cola gigantean* (family:

Sterculiaceae): five nests and *Khaya grandifoliola* (family: Meliaceae): five nests (Table 6a). There were three unknown nest trees species. One hundred and sixty two potential nest trees (i.e. trees with DBH \geq 15 cm) representing thirty four (34) species in 18 families were counted in an area of 0.64 hectare (Table 2). There were seven unknown tree species. The most abundant potential nest tree species was *Cola gigantea* (40), followed by *Manikara mutinersis* (15), *Khaya senegalensis* (12) *Lannea Kerstingi* (8) and the others (Table 6b).

Table 6a: Tree species and number of nests found in them at Koru

		Frequen	cy of nest o	ccurrence	
Tree species	Family	Meliponula bucandei	Meliponula ferruginea	Dactylurina Staudingeri	Total
Annona muricata	Annonaceae	1			1
Blighia sapida	Sapindaceae		1		1
Ceiba pentandra	Malvaceae			1	1
	(Bombacaceae)				
Citrus sinensis	Rutaceae	1			1
Cola gigantea	Sterculiaceae	3	1		4
Daniellia olivera	Caesalpiniaceae	1			1
Erythrophleum	Caesalpiniaceae		2		2
worense					
Khaya	Meliaceae	2	3	1	6
grandifoliola					
Lannea kerstingii	Anacardiaceae		1		1
Lecaniodiscus	Sapindaceae	1			1
cupanioides					
Manikara	Sapotaceae	5	2		7
multinervis					
Ouratea flava	Ochnaceae	1			1
Persea americana	Lauraceae		1		1

Table 6a continued

Uapaca togoensis	Euphorbiaceae		1	1
Unknown	Unknown	1		1
Unknown	Unknown	2		2
Vitellaria			1	1
paradoxa	Sapotaceae			
Unknown	Unknown		3	3
Total				36

Source: Fieldwork, 2011

Tree species	Family	Number of tree species
Lannea kerstingii	Anacardiaceae	8
Anacardium occidentale	Anacardiaceae	1
Mangifera indica	Anacardiaceae	2
Annona muricata	Annonaceae	7
Funtumia Africana	Apocynaceae	7
Calotropis procera	Apocynaceae	2
Erythrophleum worense	Caesalpiniaceae	5
Daniellia olivera	Caesalpiniaceae	4
Erythrophleum worense	Caesalpiniaceae	1
Daniellia olivera	Caesalpiniaceae	2
Anogeissus leiocarpus	Combretaceae	5
Terminalia laxiflora	Combretaceae	1
Anogeissus leiocarpus	Combretaceae	1
Diospyros mespiliformis	Ebenaceae	2
Manihot glaziovii	Euphorbiaceae	4
Oncoba gilgiana	Flacoutiaceae	1
Tectona grandis	Lamiaceae	1
Strychnos barteri	Loganiacae	1
Ceiba pentandra	Malvaceae	4
	(Bombacaceae)	
Khaya segegalensis	Meliaceae	12
Parkia biglobosa	Mimosaceae	2
Chlorophora excels	Moraceae	1
Ficus asperifolia	Moraceae	3

Table 6b: Potential nest tree species and their population at Koru

Table 6b continued

Milicia exelsa	Moraceae	2
Crossopteryx febrifuga	Rubiaceae	2
Clausena anisata	Rutaceae	1
Citrus sinensis	Rutaceae	3
Clausena anisata	Rutaceae	2
Vitellaria paradoxa	Sapotaceae	2
Manikara multinersis	Sapotaceae	15
Cola gigantean	Sterculiaceae	40
Cola nitida	Sterculiaceae	1
Sterculia tragacantha	Sterculiaceae	1
Vitex doniana	Verbenaceae	2
Unknown	Unknown	1
Unknown	Unknown	1
Unknown	Unknown	2
Unknown	Unknown	5
Unknown	Unknown	1
Unknown	Unknown	1
Unknown	Unknown	2
Unknown	Unknown	1
Total		162

Source: Fieldwork, 2011

Abotoase

Nests were found in seven (7) tree species in five (5) families with one unknown nest tree. The highest nest tree recorded (7) was *Cola gigantea* followed by *Triplochiton scleroxylon* (3) and the others (Table 7a). Seventy six potential nest trees representing eighteen (18) species in 14 families with 5 unidentified tree species were counted in an area of 0.64 hectare. The most abundant tree species was *Cola gigantean* (16), followed by *Lannea kerstingii* (8), *Vitex doniana* (7) and the others (Table 7b).

		Frequency of nest occurrence				
Common names of trees species	Scientific name	Family	Meliponula bucandei	Meliponula ferruginea	Dactylurina Staudingeri	Total
Potrodum	Erythrophleum ivorense	Leguminosae	1			1
Odwen	Baphia nitida	Leguminosae			2	2
Wawa	Triplochiton scleroxylon	Malvaceae (sterculiaceae)	2	1		3
African mahogany	Khaya senegalensis	Meliaceae	1			1
Ekutu	Citrus sinensis	Rutaceae			1	1
Watapuo	Cola gigantea	Malvaceae (sterculiaceae)	4	3		7
Anansedodo- wa	Cola millenii	Sterculiaceae	1			1
Unknown	Unknown	Unknown	1			1
Total						17

Table 7a: Nest trees species and number of nests found in them at Abotoase

Source: Fieldwork, 2011

Kyabobo National Park

Nests were found in seventeen (17) tree species in fifteen (15) families with one unknown nest tree species. The highest nest tree (3) was *Maramthes glabra* followed by *Vitex doniana* (2), *Terminalia laxiflora* (2) and others (Table 8a). Two hundred and forty six potential trees representing forty five (45) species in 24 families were counted in an area of 0.64 hectare. The most abundant tree species was *Margaritaria discoidea* (49) followed by *Crossopteryx febrifuga* (27) Pterocarpus erinaceus (22), Vitex doniania (10), Maramthes glabra (5) and others (Table 8b).

		Number of potential
Scientific name	Tree family	nesting tree
Lannea welwitschii	Anacardiaceae	8
Mangifera indica	Anacardiaceae	2
Ficus sur	Moraceae	2
Ficus variifolia	Moraceae	4
Spathodea	Bignoniacaea	1
campanulata		
Daniellia thurifera	Leguminosae	2
Anogeissus leiocarpus	Combretaceae	5
Terminalia laxiflora	Combretaceae	1
Uapaca togoensis	Euphorbiaceae	5
Ceiba pentandra	Malvaceae(Bombacaceae)	3
Triplochiton	Malvaceae(sterculiaceae)	1
scleroxylon		
Ficus asperifolia	Moraceae	1
Ouratea flava	Ochnaceae	2
Mitragyna inermis	Rubiaceae	5
Cola gigantea	Sterculiaceae	16
Hildegradia barteri	Sterculiaceae	1
Vitex doniana	Verbenaceae	7
Unknown	Unknown	3
Unknown	Unknown	3
Unknown	Unknown	1
Unknown	Unknown	1
Unknown	Unknown	2
Total		76

Table 7b: Potential nest tree species and their population at Abotoase

		Frequen	cy of nest	occurrence	;
Tree species	Family	Meliponula bucandei	Meliponula ferruginea	Dactylurina Staudingeri	Total
Ceiba pentandra	Bombaceae			1	1
Burkea africana	Caesalpiniaceae	1			1
Cola gigantea	Sterculiaceae	1			1
Crossopteryx febrifuga	Rubiaceae		1		1
Daniellia olivera	Caesalpiniaceae			1	1
Diospyros mespiliforimis	Ebenaceae	1			1
Ficus Muscuso	Moraceae		1		1
Holarrhena floribunda	Apocyanaceae			1	1
Maramthes glabra	Chrysobalanaceae	1	2		3
Parkia biglobosa	Mimosaceae		1		1
Prosopis africana	Mimosaceae		1		1
Pterocarpus erinaceus	Papilionaceae		1		1
Quassia undulata	Simaroubaceae	1	1		2
Terminalia laxiflora	Combretaceae		2		2
Vitellaria paradoxa	Sapotaceae	1			1
Vitex doniana	Verbenaceae	1	1		2
Unknown	Unknown			1	1
Total					22

Table 8a: Tree species and number of nests found in them at Kyabobo

Source: Fieldwork, 2011

Table 8b: Potential nest tree species and their population at Kyabobo

Tree species	Family	Number of plant species
Lannea kerstingii	Anacardiaceae	7
Annona senegalensis	Annonaceae	1
Cussonia arborea	Araliaceae	1
Bombax buonopozense	Bombaceae	2
Daniellia olivera	Caesalpiniaceae	7
Detarium microcarpa	Caesalpiniaceae	3
Afzelia Africana	Caesalpiniaceae	1
Berlinia grandiflora	Caesalpiniaceae	1

Table 8b continued

_

Erythrophleum suaveolens	Caesalpiniaceae	2
Piliostigma thonningii	Caesalpiniaceae	1
Burkea Africana	Caesalpiniaceae	2
Parinari excels	Chrysobalanaceae	1
Maranthes glabra	Chrysobalanaceae	5
Terminalia laxiflora	Combretaceae	19
Combretum collinum	Combretaceae	1
Diospyros mespiliformis	Ebenaceae	1
Margaritaria discoidea	Euphorbiaceae	49
Alchornea cordifolia	Euphorbiaceae	2
Pentadesma butryaceum	Guttiferaceae	1
Hymenocardia acida	Hymenocardiaceae	11
Strychnos spinosa	Loganiaceae	1
Anthocleista nobilis	Loganiaceae	2
Khaya senegalensis	Meliaceae	2
Parkia biglobosa	Mimosaceae	5
Prosopis Africana	Mimosaceae	2
Entada abyssinica	Mimosaceae	1
Milicia excels	Moraceae	2
Ficus sur	Moraceae	3
Ficus exasperate	Moraceae	1
Lophira lanceolata	Ochnaceae	14
Pterocarpus erinaceus	Papilionaceae	22
Xiroderis stuhlmannii	Papilionaceae	1
Paropsia guineensis	Passifloraceae	2
Securidaca longependunculata	Polygonaceae	1
Tricalysia pallens	Rubiaceae	2
Nauclea latifolia	Rubiaceae	1
Crossopteryx febrifuga	Rubiaceae	27
Pancovia bijuga	Sapindaceae	1
Malacantha alnifolia	Sapindaceae	2
Vitellaria paradoxa	Sapotaceae	1
Quassia undulate	Simaroubaceae	1
Sterculia tragacantha	Sterculiaceae	10
Cola millenii	Sterculiaceae	2
Cola gigantean	Sterculiaceae	12
Vitex doniana	Verbenaceae	10
Total		246

CHAPTER FIVE

DISCUSSION

Overview

This chapter discusses the results of the data in line with the objectives of the study. It commences by discussing the results of the data on stingless bees nest density and nesting sites for bee species across the three study areas. It also examines the nest and potential nest tree survey in the three study areas.

Stingless bees nest survey and nesting sites for the three study areas

Different groups of bees show contrasting responses to land-use change, probably driven by differences in their foraging and nesting biology (Brosi et al., 2007). Environmental factors that influence density of many *Meliponini* include availability of food, nest sites and predation (Michener, 1974; Hubbell & Johnson 1977; Eltz et al., 2002 and Slaa, 2003). Bees as a whole show some degree of resilience to land-use change giving a clear value to conserving native habitat for the ecologically and economically important meliponine (Brosi et al., 2007) and other stingless bees. Stingless bees colony density in the world is typically 1-3 nests per hectare (Michener, 1946; Hubbell & Johnson, 1977; Roubik, 1983b; Eltz et al., 2003).

Eltz et al. (2003) and Samejima et al. (2004) propose two potential mechanisms to explain the effects of human disturbance on the community of stingless bees. First, the availability of nesting sites limiting the nest density and the number of foraging workers. Thus, the density of stingless bees may depend on the density of large trees. The second is the availability of food resources within their flight range. Eltz et al. (2003) and Samejima et al. (2004), while studying the forests of Borneo, in Malaysia, observed that most stingless bee nests occurred in trees of the forest at the climax stage, having trees with diameter at breast-height larger than 50 cm. Nonetheless, these trees are exactly the kind that the timber industry look for and exploit.

This study was aimed at finding out effects of various landscapes on stingless bees nesting ecology. Out of nine (9) species of stingless bees so far found in Ghana (Kwapong et al., 2010), five species have been found in the northern part of the Volta Region. The three species considered: *Meliponula bocandei* (Spinola); *Meliponula ferruginea* (Lepeletier) and *Dactylurina staudingeri* (Gribodo) recorded 93 nests for the three sites (a total area of 48 ha). Few surveys done on stingless bees nest density provided a mean estimate of approximately two colonies per hectare (Kajobe & Roubik, 2006). These current survey also showed an estimate of two nests per hectare (1.9 nest/ha), a confirmation of previous studies.

More species of *M. ferruginea* representing 50 nests were encountered as compared to *M. bocandei* (33 nests) and *D. staudingeri* (10 nests). *M. ferruginea* probably has adapted to alternative nesting sites (old termite mound and in the ground), the issue of less tree cavities had less effect on its nesting as compared to *M. bocandei*. *M. bocandei* seems to nest in higher heights in trees and so less tall trees may have limited its abundance.

It was documented by Eltz et al. (2003) and Samejima et al. (2004) in their studies in Borneo forest, in Malaysia that nests found are mostly in trees with

diameter at breast height larger than 50 cm. However, the current research found stingless bee nests in trees of DBH as small as 15 cm. The forests found at the three study sites are secondary forests which have been under pressure by human activities and so have very few large trees. Nonetheless the bees still had suitable nesting cavity in them to nest. According to Eltz et al. (2002), reduction in the number of large trees affects stingless bees by reducing the number of available nest sites. Koru which had the highest mean DBH (61.0 \pm 13.5 cm) had the highest nest density (2.4/ha) as compared to 1.8 nests/ha for Kyabobo (with mean DBH: 41.8 \pm 9.5 cm) and 1.7 nests/ha for Abotoase (with mean DBH: 39.1 \pm 19.0 cm). This implies that availability of more big trees increase the chance of stingless bees finding more suitable cavities in them for nesting.

Hubbell and Johnson (1977) and Salmah et al. (1990) suggested that differences in nest size among stingless bee species may lead to differences in the severity of nest site limitations among species. Thus minimum size threshold of nest tree cavities is also likely related to both the colony population and the species body size (Hubbell & Johnson, 1977). *M. bocandei* recorded the highest nest (17 nests) in Koru probably due to the larger trees in the forest, which created larger cavities for its large body size of individuals and large colonies size. *M. ferruginea* was the only species found nesting in termite mounds and in the ground but had more nests recorded in trees (32 nests) as compared to nests found in old termite mounds (17 nests) and in the ground (1 nest). *M. ferruginea* which is adapted to nesting in old termite mound and the ground. Old termite

mounds probably do not have uniform and large cavities enough to habour *M*. *bocandei* thus probably the reason why they were not found in termite mounds.

Generally, it was found that M. bocandei and M. ferruginea had no preference to particular tree DBHs and thus accounting for no significant difference found in DBH of nesting trees of bee species. M. bocandei had more nests in bigger trees (DBH \geq 46 cm representing 66.7% of total nests in trees) as compared to *M. ferruginea* (DBH \geq 46 cm representing 46.9% of total nest in trees). Thus, M. ferruginea had more nest in smaller trees as compared to M. bocandei. This probably suggests that M. bocandei due to its fairly larger body size and population will need bigger cavities to nest as compared to M. ferruginea, which is relatively small in body size and population. There was no significant difference in the bees preference to height at which they nest. This shows that stingless bees may be opportunistic in their selection of nesting height. It is more likely that, stingless bees will nest at any height in trees, which provide large cavities with suitable holes to the outside of the tree, which the bees will use as their nest entrance. Thus in hostile environment with human interferences, bees might nest at any height provided suitable cavities are present. Nonetheless, M. *bocandei* nested at higher height $(6.5 \pm 0.9 \text{ m})$ as compared to *M. ferruginea* (5.4 \pm 1.1 m) a situation, which may be linked to its foraging behaviour.

Eltz et al. (2002) found a positive correlation between the density of large trees and nest density. This study however did not show any direct relation between density of potential nest trees and density of stingless bee nests. Apart from availability of suitable nesting site, availability of food also limits the population density of stingless bees (Hubbell & Johnson, 1977). On the other hand, probably because there is no uniform density of suitable nesting sites like tree hollows (Samejima et al, 2004) and old termite mounds. In addition, not all trees of DBH \geq 15 cm that may be having suitable cavities for nesting. This probably makes it uncertain to directly relate the density of potential nest trees to the density of nests per hectare.

Generally, nest trees species and potential nest tree species composition were different at the various sites though few of the tree species were found in all the three sites. *Cola gigantean* was common at all the three sites, a tree which is gradually becoming a commercial tree for loggers after they have extracted almost all the commercial trees such as *Triplochiton scleroxylon* (*Wawa*) and *Milicia exelsa* (*Odum*) from the forest. *Cola gigantean* (local name: *watapou*) probably offers suitable cavity for stingless bees to nest in thus recording 11 nests for all the three sites. Therefore, the commercialization of this tree species poses a threat to stingless bee colonies, which will be losing nesting sites. Abotoase had the lowest potential nest tree density (229 trees/ha) due to agriculture activities which contributed to removal of large trees.

According to Eltz et al. (2003) and Samejima et al. (2004), stingless bee species prefer certain trees species to others for nesting. The result of this study however did not show this trend clearly. This study considered three different landscapes, which had varying tree species composition and give a better perspective for stingless bees preference to particular tree species for nesting. At the various sites, stingless bee nests were found in rather common tree species, which offered them suitable cavities. Abotoase and Koru for instance, recorded more nests in the most abundant potential nest tree species (Abotoase: 7 nests in *Cola gigantean*; the highest potential nest tree species, Koru: 7 nests found in *Manikara multinersis*; the second highest). This trend however was different in Kyabobo national park. Thus, there was no significant evidence to associate a particular tree species to stingless bees preference for nesting. It is more likely associated with the predominant potential nest tree species at the sites. These findings confirm similar observations by Roubik (1989) in which no evidence of tree species preference by cavity nesting stingless bees was found. This generally suggests that stingless bees may like to nest in common trees that provide them with a suitable nesting cavity and not necessarily showing preference for some particular tree species. Probably, suitable cavities influence stingless bees to nest in trees and some tree species may generally be good cavity providers.

Nest and potential nest tree survey at Koru

The continuous commercialization of wood and the resultant unsustainable extraction of trees posse threat to stingless bees by depriving them of nesting sites (Venturieri, 2009). The exploitation of trees with diameters 50cm and above could diminish dramatically the nesting possibilities of many stingless bee groups (Eltz et al., 2003; Samejma et al., 2004). Generally, nest surveys of stingless bees or *Apis* are made in secondary or old primary forests however, occasionally there are obviously many bee colonies in more disturbed areas (Samejma et al., 2004). Koru forest characterized by logging and wild honey hunting recorded the highest stingless bee nest density (2.4 nests/ha) as compared to Kyabobo (1.8 nests/ha)

which is a reserve. One may expect to have fewer colonies in a disturbed forest like Koru as compared to a reserve however it did not show this trend. This result is similar to a survey done by Samejima et al. (2004) which recorded more nests in a disturbed habitat than a protected forest. However, because nest sites availability for these species is not too limited, the effects may be weaker (Sánchez & Aguilar, 2004).

Eltz et al. (2002) also found a positive correlation between the density of large trees and nest density, which is a possible explanation to more nest recorded in Koru. Koru had bigger trees (mean DBH: 61. 0 ± 13.5 cm) as compared to Kyabobo (mean DBH: 41. 8 ± 9.5 cm) thus providing more suitable nesting sites for the bees. Availability of food resources (pollen and nectar rewards) also attracts bees to sites (Potts et al. 2004; Larsson & Franzen, 2007) and this could be a possible factor contributing to the increased nest density at Koru where there are teak plantations around which produce a lot of flowers.

The presence of more nests found in this disturbed landscape does not mean human disturbances do not have any effect on the nesting ecology of these bees. During the survey, many of the logged trees were as the results of wild hunting of stingless bees honey (Plate 14). These activities coupled with commercial logging endanger stingless bees by limiting their nesting sites and destroying the colonies.



Plate 14: A logged tree as a result of wild hunting of stingless bee honey Source: Fieldwork, 2011

Nest and potential nest tree survey at Abotoase

Globally, agriculture is the biggest cause of habitat destruction (Andrew, 2010). Other human activities, such as mining, clear-cut logging, trawling, and urban sprawl, also destroy or severely degrade habitats (Andrew, 2010). Habitat loss and fragmentation have been shown to dramatically alter tree communities in

tropical forests and usually exhibiting reduced species richness and diversity (Laurance, 2006) a true reflection in Abotoase.

Abotoase, characterized by farming activities, wild bush fires and logging, recorded the lowest potential nest tree density (229 trees/ha), a reflection of the lowest nest density recorded (1.7nests/ha). This result confirms a previous research by Sánchez and Aguilar (2004) which recorded more nests of stingless bees in a forest plots (14 nests) as compared to a farm area (9 nests).

Other works however suggest that certain species of bees can thrive in a fragmented landscape depending on their foraging behaviour, nest site availability (Cane, 2001; Steffen-Dewenter, 2002) and adaptation to nest substrates. The species diversity and the number of nests in a habitat type are related to the diversity of substrata available for nest building (Batista et al., 2003). Sánchez and Aguilar (2004) also stated that depleted habitat with very few trees may offer many artificial cavities. Abotoase recorded 10 nests of *M. ferruginea* in old termite mounds as against 4 nests in trees, an indication of limited suitable nesting trees (229 trees/ha).

Agricultural expansion is often enabled by using fire as a tool to clear forests, a pattern that has occurred since the rise of civilization and mostly occur in the tropics. Recurrent burning can therefore trigger a landscape-level transformation of tropical rainforests into flammable scrub and savanna (Bowman, 2010), a characteristic of Abotoase. This provides possible alternative explanation to the phenomenon of more nests of *M. ferruginea* found in old termite mounds. Brown and Albrecht (2001) drew attention to why certain species of stingless bees appear to resist deforestation better than others. In relation to fire, they hypothesized that colonies that survive tree felling and is not harmed by humans will have to resist the effects of fire, which is related to how well the colony can close itself off from the outside and resist the high heat of fire. It may be an adaptive behaviour by *M. ferruginea* to escape the annual and frequent wild fire and logging characterizing the landscape here by nesting in old termite mounds. Old termite mounds are generally free of debris that will burn so during wild fires little or no heat will be experienced. Thus in the absence of suitable trees (DBH \geq 15 cm), ground nesting and old termite mound nesting bees such as *M. ferruginea* can still thrive in this environment by nesting in termite mounds (made of clay) which are poor conductors of heat and cannot burn during bush fire outbreaks.

Nevertheless, this phenomenon (more nest of *M. ferruginea* recorded in old termite mound) gives a threat signal of the bees being desperate for nesting sites due to depletion of forest trees. This will be of a great disadvantage to solely-tree cavity nesting species like *M. bocandei* which recorded a total of 10 nests in Abotoase against 17 nests in Koru. *D. staudingeri* nests were generally low in all the three sites (Abotoase: 3 nests) a trend which may be due to their behaviour of building exposed nests. Their nests are protected from the outside only by thick bitume and gums thus fire can affect it easily by melting it. Logging can directly affect them by depriving them of substrates they should nest on or during logging, a falling tree can easily knock off a colony from unlogged tree. Due to their exposed nest structure, it is difficult to harvest their honey without destroying

their nest, making them least preferred for honey production. Nonetheless they are very good pollinators visiting almost every flowering plant in their environment.

The farmlands (with food crops) in Abotoase may have also complemented food resource from wild plants in the forest for stingless bees. This provided variety of nectar and pollen resources for the bees. This probably influences the nesting of the stingless bees. Considering the low potential nest tree density here, nonetheless it recorded a moderate number of nests (27 nests) in relation to the number of nests found at the other two sites (Koru: 38 nests and Kyabobo: 28 nests)

Nest and potential nest tree survey at Kyabobo

Increasing numbers of studies establish baseline numerical density and abundance of bee colonies in natural habitats (Kajobe & Roubik, 2006). Eltz et al. (2003) and Samejima et al. (2004), while studying the forests of Borneo, in Malaysia, observed that most bee nests occurred in trees of the forest at the peak stage. Nest density was the second highest (1.8 nests/ha) in Kyabobo National Park which had the highest potential nest tree density (384 trees/ha). A confirmation of the result of a survey done by Sánchez and Aguilar (2004) which recorded tree density and diversity much higher in the forest than in the grassland. Sánchez and Aguilar found more nests in the forest plot than the grassland plot. Eltz et al. (2003) also recorded nest densities positively correlating with the densities of trees with DBH \geq 50 cm, thus reduction in the number of large trees affects stingless bees by reducing the number of available nesting sites.
Kyabobo National Park having the highest potential nest tree density, one may expect it to have the highest nest density compared to Koru and Abotoase nonetheless, this was not the case. The possible reason for this may be due to the smaller DBH of trees in Kyabobo as compared to Koru. There were fairly more nests of *M. ferruginea* in old termite mound than trees in kyabobo (6 termite mound nests and 11 tree nests) as compared to Koru (1 termite mound nest and 17 tree nests). This trend may be due to the mixed nature of the vegetation at Kyabobo National Park: woodland savanna at lower levels and montane forest high up the slopes (Ankudey, 1987). Casual observation throughout the survey indicated that roughly more termite mounds occured in savanna- like vegetation than forest areas. This suggests that the woodland savanna provided more alternative nests site (old termite mounds) for *M. ferruginea* making it record fairly more nests as compared to Koru.

CHAPTER SIX

SUMMARY, CONCLUSIONS AND RECOMMENDATIONS Overview

This chapter presents the summary, conclusions and recommendations of the study. It summarises the major findings of the study and draws conclusions based on the results. Recommendations are then made towards sound environmental practices that will help conserve stingless bees in Ghana.

Summary

The three species considered; *Meliponula bocandei* (Spinola), *Meliponula ferruginea* (Lepeletier) and *Dactylurina staudingeri* (Gribodo) recorded a total of 93 nests in the three sites. *M. ferruginea* recorded the highest nest as compared to *M. bocandei* and *D. staudingeri*.

M. ferruginea was the only species among the three species that nested in old termite mounds and in the ground. However, there were more nests found in trees than old termite mounds. Stingless bees nest density was found to be 1.9 nests/ha (an approximation of two nests per hectare). There were more stingless bee nests in Koru than Abotoase and Kyabobo National Park due to more large trees found there.

Generally, trees size (diameter at breast height) had a positive influence on the bees choice of trees for nesting. The two *Meliponula* bee species nests were found in trees with DBH of 15 cm and above. The bees showed no preference to the height and any particular trees species they choose for nesting. Population density of potential nest trees had no direct influence on density of stingless bee nests found at the sites.

Conclusions

The landscape type did not have a significant influence on the density of stingless bees even though there were slight differences in the number of nests found at the various sites. However bigger trees influenced positively the number of nests found at the areas. Stingless bees have no preference to the height at which they nest but rather preferred to place their nest entrance at any suitable hole leading to a suitable cavity in a tree at any height.

In the absence of more suitable nest trees (trees with bigger DBH) for example, in Abotoase, *Meliponula ferruginea* still survived by nesting in old termite mounds. This adaptation probably helps it to escape wild fire and logging activities. Thus, agricultural activities, which lead to cutting down of trees and burning of the forest, influenced the bees' choice of substrates (old termite mounds, in the ground and in tree cavities) for nesting.

Recommendations

Based on the major findings and the subsequent conclusion drawn, the following recommendations are made:

 Since the African stingless bee honey is mostly collected by harvesting from feral colonies, which subsequently destroys them, stingless beekeeping (Meliponuculture) should be encouraged among local communities especially farmers. This can reduce loss of wild colonies by wild honey hunters.

- The results of this study should be used to facilitate education and awareness creation on conservation of stingless bees to save them from the destruction of their nesting sites.
- Farmers should be encouraged to leave old termite mounds in their farms without destroying them since they may provide nesting sites for stingless bees, which help in their conservation.
- 4. This study should be replicated in other ecological zones to compare the trend of their nesting behaviour.
- 5. *M. ferruginea* should further be investigated to know what influences its adaptation to nest in old termite mound and in the ground.
- A survey should be done to ascertain the economic implication of stingless bees on the livelihood of farmers and wild honey hunters around the study sites.
- A survey should be done on the forage resources of the bees (plant species stingless bees visit) especially food crops to assess their contribution to pollination.

REFERENCES

- Aizen, M. A., & Feinsinger, P. (1994). Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology*, 75, 330- 51.
- Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane J., Cox, P. A., Dalton, V., Feinsinger, P., Inouye, D., Ingram, M., Jones, C.
 E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G. P., Pavlik, B., Tepedino, V., Torchio, P. & Walker, S. (1998). The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology*, 12, 8–17.
- Amano, K., Nemoto, T., & Heard, T. (2000). What are stingless bees and why and how to use them as crop pollinators? A review Jarq-Japan Agricultural Research Quarterly, 34, 183–190.
- Andrew, F. B., & Denis, A. S. (2010). Conservation Biology for all: Habitat fragmentation and landscape change. UK: Oxford University Press, 88-108. Retrieved September 5, 2011, from http://ukcatalogue.oup.com/product/9780199554249.
- Ankudey, N. K., (1987). Preliminary reconnaissance survey of Nkwanta area in North Volta Region for a game reserve. Wildlife Division of Ghana, Accra.
- Appanah, S. (1993). Mass flowering of dipterocarp forests in a seasonal tropics. Journal of Bioscience, 18, 457–474.

- Araújo, E. D., Costa, M., Chaud-Netto, J., & Fowler, H. G. (2004). Body size and flight distance in stingless bees (Hymenoptera: Meliponini): Inference of flight range and possible ecological implications. *Brazil Journal of Biology*, 64, 563-568.
- Bale, J. S. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, 8, 1-16.
- Bartomeus, I., Ascher, J. S., Wagner, D., Danforth, B. N., Colla, S. R., Kornbluth,
 S., & Winfree, R. (2011). Climate-associated phenological advances in
 bee pollinators and bee-pollinated plants. Proceedings of the National
 Academy of Sciences, 108(51), 20645-20649.
- Batista, M. A., Ramalho, M., & Soares, A. E. E. (2003). Nesting sites and abundance of Meliponini (Hymenoptera: Apidae) in heterogeneous habitats of the Atlantic rain forest, Bahia, Brazil. *Lundiana*, 4, 19–23.
- Bawa, K. S. (1990). Plant–pollinator interactions in tropical rain-forests. Annual Review of Ecology and Systematics, 21, 399–422.
- Bawa, K. S. (1974). Breeding system of tree species of a lowland tropical community. *Evolution*, 28, 85–92.
- Bawa, K. S., Bullock, S. H., Perry D. R., & Coville, R. E. (1985). Reproductive biology of tropical lowland rain forest trees: II Pollination systems. *America Journal of Botany*, 72, 346-356.
- Becker, P., Moure, J. S., & Peralta, F. J. A. (1991). More about euglossine bees in Amazonian forest fragments. *Biotropica*, 23, 586–591.

- Biesmeijer, J. C., & Slaa, E. J. (2004). Information flow and organization of stingless bee foraging. *Apidologie*, 35, 143-157.
- Biesmeijer, J. C., Giurfa, M., Koedam, D., Potts, S. G., Joel, D. M., & Dafni, A. (2005). Convergent evolution: floral guides, stingless bee nest entrances, and insectivorous pitchers. *Naturwissenschaften*, 92, 444–450.
- Blomquist, G. J., Roubik, D. W., & Buchmann, S. L. (1985). Wax chemistry of two stingless bees of the *Trigonisca* group (Apidae: Meliponinae), composition biochemistry. *Physiolog*, 82, 137–142.

Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M.,

Cochrane, M. A., Antonio, C. M., DeFries, R. S., Doyle, J. C.,

Harrison, S. P., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C.

A., Marston, J. B., Moritz, M. A., Prentice, I. C., Roos, C. I., Scott, A.

C., Swetnam, T. W., Van der Werf, G. R., & Pyne, S. J. (2009/2010). Fire in the earth system. *Science*, *324*, 481-484.

- Breed, M. D., McGlynn, T. P., Sanctuary, M. D., Stocker, E. M., & Cruz, E. (1999). Distribution and abundance of selected stingless bee colonies in a Costa Rican tropical wet forest. *Journal Tropical Ecology*, *16*, 765–777.
- Brosi, B. J., Daily, G. C., & Ehrlich, P. R. (2007). Bee community shifts with landscape context in a tropical countryside. *Ecological Applications*, 17, 418–430.
- Brosi, B. J., Daily, G. C., Tiffany, M. S., Federico, O., & Guillermo, D. (2008).
 The effects of forest fragmentation on bee communities in tropical countryside. *Journal of Applied Ecology*, 45, 773–783.

- Brown, J. C., & Albrecht, C. (2001). The effect of tropical deforestation on stingless bees of the genus Melipona (Insecta: Hymenoptera: Apidae: Meliponini) in central Rondonia, Brazil. *Journal of Biogeography*, 28, 623-634.
- Buchwald, R., Greenberg, A. R., & Breed, M. D. (2005). A biomechanical perspective on beeswax. *American Entomology*, *51*, 39–41.
- Calder, W. A. (1984). *Size, Function, and Life History*. Cambridge, MA: Harvard University Press.
- Camargo, J. M. F. (1970). Ninhose biologia de algumas species de Meliponídeos (Hymenoptera: Apidae) da região de Porto Velho, Território de Rondônia, Brasil. *Revista de Biologia Tropical*, 16, 207-239.
- Camargo, J. M. F. (1984). Notas sobre habitos de nidificação de Scaura (Scaura) latitarsis (Friese) (Hymenoptera, Apidae, Meliponinae). The Museu Paraense Emílio Goeldi, 1, 89–95.
- Camargo, J. M. F., & Moure, J. S. (1996). Meliponini neotropicais: o gênero Geotrigona Moure, 1943 (Apinae, Apidae, Hymenoptera), com especial referência à filogenia e biogeografia, Arq. Zoology São Paulo, 33, 71–161.
- Camargo, J. M. F., & Pedro, S. R. M. (1992). Systematics, phylogeny and biogeography of the Meliponinae (Hymenoptera, Apidae): a mini-review. *Apidologie*, 23, 509–522.
- Camargo, J. M. F., & Pedro, S. R. M. (2002). Mutualistic association between a tiny Amazonian stingless bee and a wax-producing scale insect. *Biotropical*, 34, 446–451.

- Camargo, J. M. F., & Pedro, S. R. M. (2003). Meliponini neotropicais: Ogênero Partamona Schwarz, 1939 (Hymenoptera, Apidae, Apinae) - bionomia e biogeografia. Revista Brasileira de Entomologia, 47(3), 311-372.
- Camargo, J. M. F., & Roubik, D. W. (1991). Systematics and bionomics of the apoid obligate necrophages: The *Trigona hypogea* group (Hymenoptera: Apidae; Meliponinae). *Biological Journal of the Linnean Society*, 44, 13–39.
- Cameron, S. A. (2003). Data from the elongation factor-1α gene corroborates the phylogenetic pattern from other genes revealing common ancestry of bumble bees and stingless bees (Hymenoptera: Apinae). III seminario Mesoamericana sobre abejas sin aguijón, Tapachula, Chiapas, Mexico, pp. 132-136.
- Cameron, S. A., & Mardulyn, P. (2001). Multiple molecular data sets suggest independent origins of highly eusocial behaviour in bees (Hymenoptera: Apinae). Systematic Biology, 50, 194 - 214.
- Cameron, S. A., & Mardulyn, P. (2003). The major opsin gene is useful for inferring higher level phylogenetic relationships of the corbiculate bees. *Molecular phylogenetics and evolution*, 28, 610-613.
- Campbell, D. R., & Motten, A. F. (1985). The mechanism of competition for pollination between two forest herbs. *Ecology*, *66*, 554 -563.
- Cane, J. H. (2001). Habitat fragmentation and native bees: a premature verdict? Conservation Ecology, 5(1), pp 3. Retrieved August 20, 2012, from http://www.consecol.org/vol5/iss1/art3.

- Cane, J. H., Minckley, R. L., Kervin, L. J., Roulston, T. H., & Williams, N. M. (2006). Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications*, 16, 632–644.
- Cane, J. H., & Tepedino, V. J. (2001). Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. *Conservation Ecology*, 5(1). Retrieved June 9, 2011, from http://www.consecol.org/vol5/iss1/art1.
- Cane, J. H., Terry, G., & Frank, D. P. (2007). Substrates and Materials Used for Nesting by North American Osmia Bees (Hymenoptera: Apiformes: Megachilidae). Annals of Entomology Society of America, 100(3), 350-358.
- Castano-Meneses, G., & Palacios-Vargas, J. G. (2003). Effects of fire and agricultural practices on Neotropical ant communities. *Biodiversity Conservation*, 12, 1913–1919.
- Chown, S. L., & Nicolson, S. W. (2004). *Insect physiological ecology: mechanisms and patterns*. New York City, NY :Oxford University Press.
- Collinge, S. K., Prudic, K. L., & Oliver, J. C. (2003). Effects of local habitat characteristics and landscape context on grassland butterfly diversity. *Conservation Biology*, 17, 178–187.
- Cornell University (2011, December 12). As climate change sets in, plants and bees keep pace. ScienceDaily, December 12. Retrieved February 13,

2013, from http://www.sciencedaily.com

/releases/2011/12/111212124601.htm.

- Cortopassi-Laurino, M. (1982). Pollen sources of the orchid bee *Euglossa* annectans Dressler (Hymenoptera: Apidae, Euglossini) analyzed from larval provisions. *Genetic and Molecular Research*, 8 (2), 546 – 556.
- Cruz-Landim, C., & Mello, M. L. S. (1967). The post-embryonic changes in Melipona quadrifasciata anthidioides Lep. (Hymenoptera: Apoidea). II.
 Development of the salivary glands system. Journal of Morphology, 123, 481–502.
- Daily, G. C., Alexander, S., Ehrlich, P. R., Goulder, L., Lubchenco, J. P., Matson,
 A., Mooney, H. A., Postel, S., Schneider, S. H., Tilman, D., & Woodwell,
 G. M. (1997). Ecosystem services: Benefits supplied to human societies
 by natural ecosystems. *Ecology*, *2*, 1-16.
- Darchen, R. (1972). Écologie de quelques trigones (*Trigona sp.*) de la Savane de Lamto (Cote d'Ivoire). *Apidologie*, *3*, 341- 367.
- David, M. J. S. B., & Brett, P. M. (2010). Conservation for all: Fire and Biodiversity. UK: Oxford University press, 163 – 179.
- Drumond, P. M., Bego, L. R., & Melo, G. A. R. (1995). Nest architecture of the stingless bee *Plebeia poecilochroa* and related considerations (Hymenoptera: Apidae, Meliponinae). *Iheringia Serie Zoologia*, 79, 39–49.

- Eardley, C. D. (2004). Taxonomic revision of the African stingless bees (Apoidea: Apidae: Apinae: Meliponini). *African Plant Protection*, *10*, 63–96.
- Eltz, T. (2004). Spatio-temporal variation of apine bee attraction to honey baits in Bornean forests. *Journal of Tropical Ecology*, 20, 317–324.
- Eltz, T., Brühl, C. A., Imiyabir, Z., & Linsenmair, K. E. (2003). Nesting and nest trees of stingless bees (Apidae: Meliponini) in lowland dipterocarp forests in Sabah, Malaysia, with implications for forest management. *Forest Ecology Manage*, 172, 301-313.
- Eltz, T., Carsten, A. S., & Linsenmair, K. E., (2002). Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. *Oecologia*, 131, 27-34.
- Engel, M. S. (2001). Monophyly and extensive extinction of advanced eusocial bees: insights from an unexpected Eocene diversity. Proceedings of the national academy of sciences of the United States of America, 98, 1661-1664.
- Engels, W., Rosenkranz, P., & Engels, E. (1995). Thermoregulation in the nest of the Neotropical stingless bee *Scaptotrigona postica* and a hypothesis on the evolution of temperature homeostasis in highly eusocial bees, Stud. Neotrop. *Fauna Environ*, 30, 193–205.
- Faegri, K. & Van der Pijl, L. (1979). *The principles of pollination ecology*, (3rd ed.). Oxford, UK: Pergamom press, pp. 244.

- Food and Agriculture Organization (2004). Nutritional guidelines for care and support for people living with HIV/AIDS. Food and Agriculture Organization, Rome.
- Food and Agriculture Organization (2007). Pollinators: Neglected biodiversity of importance to food and agriculture CGRFA- 11/07/Inf.15. FAO of United Nations, Rome.
- Food and Agriculture Organization (2009). Non-wood forest products, bees and their role in forest livelihoods. FAO of United Nations, Rome.
- Fleishman, E., Chris R., Sjögren-Gulve, P., Boggs, C., & Murphy, D. (2002). Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conservation Biology*, 16(3), 1–11.
- Frankie, G. W. (1975). Tropical Forest Phenology and Pollinator Plant Coevolution. In L. E. Gilbert, & P. H. Raven (Eds), *Coevolution of Animal and Plants*. Austin: University of Texas press, pp. 192-209.
- Frankie, G. W., Haber, W. H., Opler, P. A., & Bawa, K. S. (1983). Characteristics and organization of the large bee pollination system in the Costa Rican dry forest. In C. E. Jones, & R. J. Little (Eds.), *Handbook of Experimental Pollination Biology*. New York, NY: Scientific and Academic press, pp. 411-447.
- Frankie, G. W., Opler, P. A., & Bawa, K. S. (1976). Foraging behaviour of solitary bees: Implications for outcrossing of a Neotropical forest tree species. *Journal of Ecology*, 64, 1049-1057.

- Frankie, G. W., Vinson, S. B., Newstrom, L. E., & Barthell, J. F. (1990). Plant Phenology, Pollination Ecology, Pollination Behaviour and Conservation of Pollinators in Neotropical dry Forest. In K. S. Bawa, & M. Hadley, (Eds.), *Reproductive Ecology of Tropical Forest Plants*. Carnsforth and Paris: UNESCO and Parthenon Publishing Group, 37-47.
- Garcia, M. V. B., Oliveira, M. L., & Campos, L. A. O. (1992). Use of seeds of *Coussapoa asperifolia magnifolia* (Cecropiaceae) by stingless bees in the central Amazonian forest (Hymenoptera: Apidae: Meliponinae). *Entomologia Generalis*, 17, 255–258.
- Ghazoul, J. (2005). Buzziness as usual: Questioning the global pollination crisis. *Trends in Ecology and Evolution*, 20, 367–373.
- Ghazoul, J. K., Liston, A., & Boyle, T. J. B. (1998). Disturbance-induced densitydependent seed set in *Shorea siamensis* (Dipterocarpaceae), a tropical forest tree. *Journal of Ecology*, 86, 462–473.
- Goulson, D., Lye, G. C., & Darvill, B., (2008). Decline and conservation of bumble bees. Annual Review of Entomology, 53, 191-208.
- Goverde, M., Arnone, J. A., & Erhardt, A. (2002). Species-specific reactions to elevated CO₂ and nutrient availability in four grass species. *Basic and Applied Ecology*, *3*, 221–227.
- Graham, C. H. & Blake, J. G. (2001). Influence of patch- and landscape-level factors on bird assemblages in a fragmented tropical landscape. *Ecological Applications*, 11, 1709-1721.

- Hall, J. B., & Swaine, M. D. (1981). Geobotany. Distribution and ecology of vascular plants in a tropical rain forest: Forest vegetation in Ghana. The Hague-Boston, London: Dr.W. Junk Publishers, pp 1928.
- Hansell, M. H. (1993). The ecological impact of animal nests and burrows. *Functional Ecology*, 7, 5–12.
- Haskell, J. P, Ritchie, M. E, & Olff, H. (2002). Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature*, 418, 527–530.
- Hawthorne, W. D, & Gyakari, N. (2006). Photoguide for the forest trees of Ghana: A tree- spotter's field guide for identifying the largest trees.Oxford Forestry Institute, Department of plant Science, 236-247.
- Heard, T. A. (1999). The role of stingless bees in crop pollination. *Annual Review* of Entomology, 44, 183-206.
- Heard, T. A (2000). Could Aussie stingless bees pollinate avocado? Aussie Bee, 15, 20-21.
- Heithaus, E. R. (1979). Community structure of Neotropical flower visiting bees and wasps: Diversity and phenology. *Ecology*, *60*, 190–202.

Helmholtz Association of German Research Centres (2008, September 15).
Economic Value Of Insect Pollination Worldwide Estimated At U.S. \$217
Billion. *ScienceDaily*. Retrieved February 18, 2013, from http://www.sciencedaily.com /releases/2008/09/080915122725.htm.

Hepburn, H. R., & Kurstjens, S. P. (1984). On the strength of propolis (bee glue). *Naturwissenschaften*, *71*(11), 591-592.

- Hill, J. K., Hamer, K. C., Lace L. A. & Banham, W. M. T. (1995). Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal* of Apply Ecology, 32, 754–60.
- Hines, H. M., & Hendrix, S. D. (2005). Bumble bee (Hymenoptera: Apidae) diversity and abundance in tall grass prairie patches: effects of local and landscape floral resources. *Environmental Entomology*, 34, 1477–1484.
- Hubbell, S. P., & Johnson, L. K. (1977). Competition and nest spacing in a tropical stingless bee community. *Ecology*, 58, 949–963.
- Huryn, V. M. B. (1997). Ecological impacts of introduced honey bees. *Quarterly Review of Biology*, 72, 275–297.
- Ingram, D. S., & Samways, M. J. (1996). Application of fragmentation and variegation models to epigaeic invertebrates in South Africa. *Conservation Biology*, 10, 1353-8.
- Inoue, T., & Roubik, D. W. (1990). Kin recognition of a stingless bee, Melipona fasciata. In G. K.Veeresh, B. Mallik, & C. A. Viraktamath (Eds.), Social Insects and the Environment, pp. 517- 518.
- Inoue, T., & Sakagami, S. F. (1993). A new name of *Trigona* (Hymenoptera, Apidae). *Japanese Journal of Entomology*, *61*, pp. 769.
- Inoue, T., Sakagami, S. F., Samah, S., & Nukrnal, N. (1984). Discovery of successful absconding in the stingless bees Trigona (Tetragonula) Laeviceps. *Journal of Apicultural Research*, 23, 136-142.

- Janzen, D. H. (1967). Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution*, 21, 620-637.
- Jennersten, O. (1988). Pollination in *Dianthus deltoides* (Caryophyllaceae): Effects of habitat fragmentation on visitation and seed set. *Conservation Biology*, 2, 359–366.
- Johnson, L. K., & Hubbell, S. P. (1986). Nest tree selectivity and density of stingless bee colonies in a Panamanian forest. In A. C. Chadwick, & S. L. Sutton (Eds.), *Tropical rain forest: The Leeds symposium*. Leeds Philosophical and Literary Society, pp. 147–154.
- Johnson, S. D., & Bond, W. J. (1997). Evidence for widespread pollen limitation of fruiting success in Cape wildflowers. *Oecologia*, *109*, 530-534.
- Jones, D. T., Susilo, F. X., Bignell, D. E., Hardiwinoto, S., Gillison, A. N., & Eggleton, P. (2003). Termite assemblage collapse along a land-use intensification gradient in lowland central Sumatra, Indonesia. *Journal Apply Ecology*, 40, 380–91.
- Kajobe, R. (2007). Pollen foraging by Apis mellifera and stingless bees Meliponula bocandei and Meliponula nebulata in Bwindi Impenetrable National Park, Uganda. African Journal of Ecology, 45 (3), 265–274.
- Kajobe, R., & Roubik, D. W. (2006). Honey-making bee colony abundance and predation by apes and humans in a Uganda forest reserve. *Biotropica*, 38, 210–218.
- Kakutani, T., Inoue, T., Tezuka, T., & Maeta, Y. (1993). Pollination of strawberry by the stingless bee, *Trigona minangkabau* and the honeybee, *Apis*

mellifera an experimental study of fertilization efficiency. *Researches on Population Ecology*, *35*, 95–111.

- Karikari, A. S., & Kwapong, P. K (2007). Survey of indigenous knowledge of stingless bees (Apidae: Meliponini) in the central region of Ghana. *Journal of Ghana Science Association*, 9 (2), 132-137.
- Kato, M. (1996). Plant-pollinator interactions in the understory of a lowland mixed dipterocarp forest in Sarawak. American Journal of Botany, 83, 732–743.
- Kearns, C. A., & Inouye, D. W. (1997). Pollinators, flowering plants, and conservation biology. *Bioscience*, 47, 297-307.
- Kearns, C. A., Inouye, D. W., & Waser, N. M. (1998). Endangered mutualisms: the conservation of plant–pollinator interactions. *Annual Review of Ecology and Systematics*, 29, 83–112.
- Kenmore, P., & Krell, R. (1998). Global perspectives on pollination in agriculture and agroecosystem management. Proceedings of international workshop on the conservation and sustainable use of pollinators in agriculture, with emphasis on bees. October 7-9, Sao Paulo, Brazil.
- Kerr, A. S., & Kerr, W. E. (1999). Melipona garbage bees release their cargo according to a Gaussian distribution. Revista Brasileira de Zoologia, 59, 119–123.
- Kerr, W. E., Sakagami, S. F., Zucchi, R., Portugal-Araújo, V. D., & Camargo, J.M. F. (1967). Observações sôbre a arquitetura dos ninhos e comportamento de algumas espécies de abelhas sem ferrão das vizinhaças

de Manaus, Amazonas (Hymenoptera, Apoidea). *Atas do Simpósio Sôbre a Biota Amazônica, Zoologia, 5*, 255-309.

- Klein, A., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society of London Series B. *Biological Sciences*, 274, 303–313.
- Klein, A. M., Steffan-Dewenter, I., & Tscharntke, T. (2003a). Fruit set of highland coffee increases with the diversity of pollinating bees.Proceedings of the Royal Society of London. *Series B*, 270, 955-961.
- Klein, A. M., Steffan-Dewenter, I., & Tscharntke, T. (2003b). Pollination of *Coffea canephora* in relation to local and regional agro-forestry management. *Journal of Applied Ecology*, 40, 837-845.
- Kleinert-Giovannini, A., & Imperatriz-Fonseca, V. L. (1986). Flight activity and responses to climatic conditions of two suspecies of Melipona marginata
 Lepeletier (Apidae, Meliponinae). *Journal of Apicultural Research*, 25, 3–
 8.
- Koedam, D., Jungnickel, H., Tentschert, J., Jones, G. R., & Morgan, E. D. (2002).
 Production of wax by virgin queens of the stingless bee *Melipona bicolor* (Apidae, Meliponinae). *Insectes Soceity*, 49, 229–233.
- Krell, R. (1996). Value-added products from beekeeping fao agricultural services. Bulletin No. 124, FAO, Rome.
- Kremen, C., Williams, N. M., & Thorp, R. W. (2002). Crop pollination from native bees at risk from agricultural intensification. Proceedings of the

National Academy of Sciences of the United States of America. *PNAS*, 99, 16812–16816.

- Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Harren, B., LeBuhn, G.,
 Minckley, R., Packer, L., Potts, S. G., Roulston, T., Steffan-Dewenter, I.,
 Vazquez, D. P., Winfree, R., Adams, L., Crone, E. E., Greenlead, S. S.,
 Keitt, T. H., Klein, A. M., Regetz, J., & Ricketts, T. H. (2007).
 Pollination and other ecosystem services produced by mobile organisms:
 A conceptual framework for the effects of land-use change. *Ecology*, *10*, 299-314.
- Kremen, C., Williams, N. M., Bugg, R. L., Fay, J. P., & Thorp, R. W. (2004). The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters*, 7, 1109–1119.
- Kress, W. J., & Beach, J. H. (1994). Flowering Plant Reproductive Systems. In L.
 A. McDade, K. S. Bawa, H. A. Hespenheide, & G. S. Hartshorn (Eds), *La* Selva: Ecology and natural history of a neotropical rain forest. Chicago: Chicago University Press, pp. 142-182.
- Kwapong, P. K, Aidoo, K., Combey, R., & Karikari, A. S. (2010). Stingless bees: importance, management and utilisation. (1st ed). Accra, Ghana: Unimax Macmilland Press, pp. 5 – 36.
- Langenheim, H. J. (2003). *Plant resins. Chemistry, evolution, ecology, ethnobotany*. Portland Oregon: Timber Press, pp. 586.

- Larsen, T. H, Williams, N., & Kremen, C. (2005). Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letter*, 8, 538–547.
- Larsson, M., & Franzén, M. (2007). Estimating the population size of specialized solitary bees. *Ecological Entomology*, *33*, 232–238.
- Laurance, W. F. (2006). *Habitat destruction: death by a thousand cuts Conservation Biology for All* (pp. 73-87). Retrieved August 20, 2012, from <u>http://ukcatalogue.oup.com/product/9780199554249</u>.
- Lee, H. L., Navjot, S. S., & Thomas, E. (2001). Bee diversity along a disturbance gradient in tropical lowland forests of South-East Asia. *The Journal of Applied Ecology*, 38(1), 180-192.
- Lindenmayer, D. B, Cunningham, R. B., & Donnelly, C. F., (1997). Decay and collapse of trees with hollows in eastern Australian forest; Impacts on arboreal marsupials. *Appllied Ecology*, *7*, 625-641.
- Lockhart, P. J., & Cameron, S. A. (2001). Trees for bees. *Trends in Ecology and Evolution*, *16*, 327-355.
- Lokvam, J., & Braddock, J. F. (1999). Anti-bacterial function in the sexually dimorphic pollinator rewards of *Clusia grandiflora* (Clusiaceae). *Oecologia*, *119*, 534-540.
- Lowe, W. H., & Bolger, D. T. (2002). Local and landscape-scale predictors of salamander abundance in New Hampshire headwater streams. *Conservation Biology*, 16, 183-193.

- Macharia, J. K. (2007). Distribution of stingless bees in selected Kenyan forests:
 potential for meliponiculture enterprises. In S. K. Raina, E. Muli, E.
 Nguku, & E. Kiokoet (Eds), proceedings of development of Sericulture
 and Apiculture products for the poor in fragile ecosystems using the value
 chain approach (pp. 188–191). Nairobi, Kenya: *icipe* Science Press.
- Macharia, J. K., Suresh, K. R., & Eliud, M. M. (2010). Stingless beekeeping: An incentive for rain forest conservation in Kenya. Science and Management of Protected Areas Association, pp. 514-518.
- Maeta, Y., Tezuka, T., Nadano, H., & Suzuki, K. (1992). Utilization of the Brazilian stingless bee, *Nannotrigona testaceicornis* as a pollinator of strawberries. *Honeybee Science*, 13, 71–80.
- Malagodi-Braga, K., Peixoto-Kleinert, A. M., & Imperatriz-Fonseca, V. L., (2000). Stingless bees: Greenhouse pollination and Meliponiculture. IV Encontro sobre Abelhas Ribeirao Preto, pp. 145-50.
- Marco, P., & Coelho, F. (2004). Services performed by the ecosystem: forest remnants influence agricultural cultures' pollination and production. *Biodiversity and Conservation*, 13, 1245-1255.
- Michener, C. D. (1946). Notes on the habits of some Panamanian stingless bees (Hymenoptera, Apidae). Journal of the New York Entomological Society, 54, 179-197.
- Michener, C. D. (1959). Sibling species of *Trigona* from Angola (Hymenoptera, Apidae). *American Museum Novitates*, 1956, 1–5.

- Michener, C. D. (1961). Observations on the nests and behaviour of *Trigona* in Australia and New Guinea (Hymenoptera: Apidae). *American Museum of Novitates*, 2026, 1-45.
- Michener, C. D. (1974). *The social behaviour of the bees: a comparative study*. Cambridge, Massachusetts: Belknap Press of Harvard University Press, pp. 404.
- Michener, C. D. (1979). Biogeography of bees. Annals of the Missouri Botanical Garden, 66, 277-347.
- Michener, C. D. (1990). Classification of the Apidae (Hymenoptera). Appendix: *Trigona genalis* Friese, a hitherto unplaced New Guinea species. University of Kansas science bulletin, 54, 75-164.
- Michener, C. D. (2000). *The Bees of the World*. Baltimore, USA: Johns Hopkins University Press, pp. 914.
- Michener, C. D., (2007). *The bees of the world, second edition*. Baltimore, USA: Johns Hopkins University press, pp. 913.
- Momose, K., Yumoto, T., Nagamitsu, T., Kato, M, Nagamasu, H., Sakai, S., Rhett, D. H., Itioka, T., Abang A. H., & Inoue, T. (1998). Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia: Characteristics of the plant-pollinator community in a lowland dipterocarp forest. *America Journal of Botany*, 85(10), 1477-1501.
- Moritz, R. F. A., & Crewe, R. M. (1988). Air ventilation in nests of two African stingless bees *Trigona denoiti* and *Trigona gribodoi*. *Experientia*, 44, 1024-1027.

- Moure, J. S. (1961). A preliminary supra-specific classification of the old world meliponine bees (Hymenoptera, Apoidea). *Studia Entomologica*, 4, 181-242.
- Moure, J. S. (1971). Descrição de uma espécia de *Tetragona* do Brasil central (Hymenoptera Apidae). *Boletim da universidade federal do Paraná, Zoologia, 4*, 47-50.
- National Research Council (2007). Status of Pollinators in North America. Retrieved October 22, from

http://www.nap.edu/catalog.php?record_id=11761.

- Newton, I. (1994). The role of nest sites in limiting the number of hole-nesting birds. *Review Conservation Biology*, 70, 265-276.
- Nieh, J. C. (2004). Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini). *Apidologie*, *35*, 159-182.
- Nogueira-Neto, P. (1948). Notas bionomicas sobre meliponineos, I. Sobre ventilação dos ninhos e as constucões com ela relationadas. *Revista Brasileira De Zoologia*, 8, 465–488.
- Nogueira-Neto, P. (1962). The scutellum nest structure of *Trigona (Trigona)* spinipes Fab. (Hymenoptera: Apidae). Journal of the New York Entomological Society, 70, 239- 264.
- Nogueira-Neto, P. (1997). Vida e criação de abelhas indigenas sem ferrão. Editora Nogueirapis Sao Paulo, pp. 445.
- Noss, R.F. (1990). Indicators of monitoring biodiversity: a hierarchical approach. *Conservation Biology*, *4*, 355-364.

- Oldroyd, B. P., Lawler, S. H, crozier, R. H. (1994). Do feral honey bees (Apis mellifera) and regent parrots (*Polytelis anthropeplus*) compete for nest sites? *Australian Journal* of *Ecology*, *19*, 444-450.
- Otis, G. W. (1997). Distributions of recently recognized species of honey bees (Hymenoptera: Apidae; Apis) in Asia. Journal of the Kansas Entomological Society, 69(4), 311-333.
- Palmer, K. A., Oldroyd, B. P., Quezada-Euán, J. G., Paxton, R. J., & May-Itza,
 W. D. J. (2002). Paternity frequency and maternity of males in some stingless bee species. *Molecular Ecology*, 11, 2107-2113.
- Partap, U., & Partap, T. (1997). Managed crop pollination: The missing dimension of mountain agricultural productivity, mountain farming systems' discussion paper. *Kathmandu: ICIMOD*, *Series No. MFS* 97/1.
- Partap, U., & Partap, T. (2002). Warning signals from apple valleys of the HKH region: Productivity concerns and pollination problems. *Kathmandu: ICIMOD*, pp. 106.
- Partap, U., Partap, T., & Yonghua, H. (2001). Pollination failure in apple crop and farmers' management strategies. *Acta Horticulturae*, *561*, 225- 30.
- Paxton, R. J., Bego, L. R., Shah, M. M., & Mateus, S. (2003). Low mating frequency of queens in the stingless bee *Scaptotrigona postica* and worker paternity of males. *Behavorial Ecology Sociobiology*, 53, 174–181.
- Pesson, P., & Louveaux, J. (1984). Pollinisation et Productions Végétales. Paris: INRA, pp. 663.

- Peters, J. M., Queller, D. C., Imperatriz-Fonesca, V. L., Roubik, D. W., & Strassmann, J. E. (1999). Mate number, kin selection and social conflicts in stingless bees and honeybees. *Royal Society of London, Series B*, 266, 379-384.
- Portugal-Araújo, V. (1955). A contribution to the bionomics of Lestrimelitta cubiceps (Hymenoptera, Apidae). Journal of the Kansas Entomological Society, 31, 203–211.
- Portugal-Araújo, V. (1958). Notas sobre coloinas de meliponineos de Angola. Dusenia, 6, 97–114.
- Potts S. G., Kevan, P. G., & Boone, J. W. (2005). Conservation in pollination: collecting, surveying and monitoring. In A. Dafni, P. Kevan, & C. Husband (Eds), *Practical Pollination Biology*. Cambridge Ontario, Canada: Enviroquest press, pp. 401-434.
- Potts, S. G., Vulliamy, B., Dafni, A., Ne'eman, G., & Willmer, P. G. (2003a). Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology*, 84, 2628-2642.
- Potts, S. G., Vulliamy, B., Dafni, A., Ne'eman, G., O'Toole, C., Roberts, S., & Willmer, P. G. (2003b). Response of plant-pollinator communities following fire: changes in diversity, abundance, and reward structure. *Oikos*, *101*, 103-112.
- Potts, S. G., Vulliamy, B., Robert, S., O'Toole, C, Dafni, A., Neeman, G., & Willmer, P. G. (2005). Role of nesting resources in organising diverse bee

communities in a Mediterranean landscape. *Ecological Entomol*ogy, 30, 78–85.

- Potts, S. G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G., Willmer, P. G. (2004). Nectar resource diversity organizes flower-visitor community structure. *Entomologia Experimentalis et Applicata*, 113, 103-107.
- Powell, A. H., & Powell, G. V. N. (1987). Population-dynamics of male euglossine bees in Amazonian forest fragments. *Biotropica*, 19, 176–179.
- Proctor, M., Yeo, P., & Lack, A. (1996). The natural history of pollination., Portland: Timber Press.
- Ramalho, M., Kleinert-Giovannini, A., & Imperatriz-Fonseca, V. L. (1990). Important bee plants for stingless bees (*Melipona* and *Trigonini*) and Africanized honeybees (*Apis mellifera*) in Neotropical habitats. *Review Apidologie*, 21, 469-488.
- Rathcke, B. J. (2000). Hurricane causes resource and pollination limitation of fruit set in a bird-pollinated shrub. *Ecology*, *81*, 1951–1958.
- Rathcke, B. J., & Jules, E. (1994). Habitat fragmentation and plant-pollinator interactions. *Current Science Association*, 65, 273–278.
- Renner, S. S., & Feil, J. P. (1993). Pollinators of tropical dioecious angiosperms. *American Journal Botany*, 80, 1100-1107.
- Ricketts, T. H. (2001). The matrix matters: source effective isolation in fragmented landscapes .*The American Naturalist*, 158 (1), 87-99.

- Ricketts, T. H. (2004). Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology*, *18*, 1262–1271.
- Ricketts, T., Daily, G. C., Ehrlich, P. R., & Fay, J. (2001). Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conservation Biology*, 15, 378–388.
- Ricketts, T. H., Daily, G. C., Ehrlich, P. R., & Michener, C. D. (2004). Economic value of tropical forest to coffee production. *National Academy of Sciences of the United States of America*, 101, 12579–12582.
- Rindfleisch, J. (1980). A case for Meliponiculture in pollination. *American Bee Journal*, *120*, 468-470.
- Roig-Alsina, A, & Michener, C. D. (1993). Studies of the phylogeny and classification of long tongued bees (Hymenoptera: Apoidea). University of Kansas science bulletin, 55, 123-162.
- Roubik, D. W. (1979). Nest and colony characteristics of stingless bees from French Guiana (Hymenoptera: Apidae). Journal of the Kansas Entomological Society, 52, 443–470.
- Roubik, D. W. (1983a). Nest and colony characteristics of stingless bees from Panama. *Journal* of the *Kansas Entomological Society*, *56*, 327–355.
- Roubik, D. W. (1983b). Experimental community studies: time-series tests of competition between African and Neotropical bees. *Ecology*, 64, 971-978.
- Roubik, D. W. (1987). Notes on the biology of anthophorid bee *Tetrapedia* and the mite *Chaetodactylus panamensis* Baker, Roubik and Delfinado-Baker (Acari: Chaetodactylidae). *International Journal of Acarolog*, 13, 75-76.

- Roubik, D.W. (1989). *Ecology and natural history of tropical bees*. New York, NY: Cambridge University Press, pp. 514.
- Roubik, D. W. (1992a). Loose niches in tropical communities: why are there so few bees and so many trees? In M. D. Hunter, P. W. Price, & T. Ohgushi (Eds.), *Effects of resource distribution on animal-plant interactions*. San Diego: Academic Press, pp. 327-354.
- Roubik, D. W. (1992b). Stingless bees (Apidae: Meliponinae): a guide to
 Panamanian and Mesoamerican species and their nests. In D. Quintero &
 A., Aiello (Eds.), *Insects in Panama and Mesoamerica: Selected Studies*.
 Oxford, England: Oxford University Press, pp. 495-524.
- Roubik, D. W. (1993). Tropical pollinators in the canopy and understorey: Field data and theory for stratum 'preferences'. *Journal of Insect Behaviour*, 6, 659–673.
- Roubik, D. W. (1995). *Pollination of cultivated plants in the tropics*. FAO, Rome, Italy, pp. 197.
- Roubik, D. W. (1996). Order and chaos in tropical bee communities. In C. A. Garofalo, C. F. Martins, & I. Alves-dos-santos (Eds.), II Encontro sobre abelhas de Ribeirao Preto (pp. 122-132). Sao Paulo, Brazil.

Roubik, D. W. (2006). Stingless bee nesting biology. Apidologie, 37, 124–143.

Roubik, D. W., & Aluja, M. (1983). Flight ranges of *Melipona* and *Trigona* in tropical forest. *Journal* of the *Kansas* Entomological *Society*, 56, 217-222.

- Roubik, D. W., Moreno, J. E., Vergara, C., & Wittmann, D. (1986). Sporadic food competition with the African honeybee: Projected impact on Neotropical social bees. *Journal of Tropical Ecology*, 2, 97–111.
- Roubik, D. W., & Nieh, J. C. (1995). A stingless bee, Melipona panamica, indicates food location without using a scent trail. *Behavioural Ecology* and Sociobiology, 37, 63-70.
- Roubik, D. W., & Peralta, F. (1983). Thermodynamics in nests of two Melipona species in Brazil. *Acta Amazonica*, *13*, 453-466.
- Roubik, D. W., Yanega, D., Buchmann, S. L., & Inouye, D. W., (1995). On optimal nectar foraging by some tropical bees (Hymenoptera: Apidae).
 Apidologie, 26 (3), 197-211.
- Russell, V. A, Sagvolden, T., & Borgå, E. J. (2005). Animal models of attentiondeficit hyperactivity disorder. *Behavioural* and *Brain Functions*, *1*, pp. 9.
- Sakagami, S. F. (1982). Stingless bees. In H. R. Hermann, Social Insects (Ed.), III New York, NY: Academic Press, pp. 361-423.
- Sakagami, S. F., Inoue, T., Yamane, S., & Salmah, S. (1983). Nest architecture and colony composition of the Sumatran stingless bee, *Trigona* (*Tetragonula*) laeviceps. Kontyu, 51, 100–111.
- Sakagami, S. F., Roubik, D. W., & Zucchi, R. (1993). Ethology of the robber stingless bee, *Lestrimelitta limao* (Hymenoptera: *Apidae*). *Sociobiology*, 21, 237-277.
- Sakai, S., Mornose, K., Yumoto, T., Nagamitsu, T., Nagamasu, H., Hamid, A. A.,& Nakashizuka, T., (1999). Plant reproductive phenology over four years

including an episode of general flowering in a lowland dipterocarp forest, Sarawak Malaysia. *American. Journal of Botany*, 86, 1414-436.

- Salmah, S., Inoue, T., & Sakagami, S. F., (1990). An analysis of apid bee richness (Apidae) in central Sumatra. In S. F. Sakagami, R. Ohgushi & D. W. Roubik (Eds.), *Natural History of SocialWasps and Bees in Equatorial Sumatra*. Sapporo, Japan: Hokkaido University Press, pp. 139–174.
- Samejima, H., Marfaizal, M., Teruyoshi, N., & Tohru, N. (2004). The effects of human disturbance on a stingless bee community in a tropical rainforest. *Biological Conservation*, 120, 577–587.
- Samways, M. J. (1989). Insect conservation and the disturbance landscape. International Symposium on Agricultural Ecology and Environment, 27, (1–4), pp. 183–194.
- Sánchez, L. A., & Aguilar, I. (2004). Conservation of native trees and the indigenous bees in Costa Rica: food plants and nest tree selectivity. Proceedings of tropical beekeeping: Research and development for pollination and conservation conference, February 22-25. San José :Costa Rica, pp. 7.
- Schaeffer, S. W. (2008). Selection in heterogeneous environments maintains the gene arrangement polymorphism of *Drosophila pseudoobscura*. *Evolution*, 62, 3082-3099.
- Schultz, T. R., Engel, M. S., & Ascher J. S. (2001). Evidence for the origin of eusociality in the corbiculate bees (Hymenoptera: Apidae). *Journal of the Kansas Entomological society*, 74, 10-16.

- Seeley, T. D. (1985). Review of defensive mechanisms in social insects. In R. H. Henry (Eds.), American Scientist. New York: Praeger Publishers.
- Silveira, F. A., Melo, G. A. R., & Almeida, E. A. B. (2002). Abelhas brasileiras: sistemática e identificação. Ministério do Meio Ambiente, Fundação Araucária. Belo Horizonte, Brazil, pp. 253.
- Slaa, E. J. (2003). Foraging ecology of stingless bees: from individual behaviour to community ecology. (unpublished PhD thesis), Department of Behavioural Biology. Utrecht, Utrecht University, The Netherlands. Retrieved September 5, 2011, from

 $http://labs.biology.ucsd.edu/nieh/TeachingBee/eds_stingless.htm.$

- Slaa, E. J. (2006). Spatial nesting patterns in a Neotropical stingless bee community: do bees compete for food? Proceedings of the Netherlands Entomological Society Meeting, 17, pp. 71-78.
- Slaa, E. J., Chaves, L. A. S., Malagodi-Braga, K. S., & Hofstede, F. E. (2006). Stingless bees in applied pollination: practice and perspectives. *Apidologie*, 37, 293-315.
- Slaa, E. J, Wassenberg, J., & Biesmeijer, J. C (2003). The use of field-based social information in eusocial foragers: local enhancement among nestmates and heterospecifics in stingless bees. *Ecological Entomology*, 28, 369-379.
- Smith, B. H., & Roubik, D. W. (1983). Mandibular glands of stingless bees (Hymenoptera: Apidae): chemical analysis of their contents and biological

function in two species of Melipona. Journal of Chemical Ecology, 9, 1465–1472.

- Soderstrom, B., Svensson, B., Vessby, K., & Glimskar, A., (2001). Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodiversity and Conservation*, *10*, 1839–1863.
- Sodhi, N. S., Koh, L. P., Brook, B. W., & Ng P. K. L. (2004). Southeast Asian biodiversity: an impending disaster. *Trend Ecology and Evolution*, 19, 654–660.
- Sommeijer, M. J., & Ruijter, A. (2000). Insect pollination in greenhouses. In proceedings of specialists meeting held in Soesterberg, Netherlands Utrecht University, pp. 220.
- Starr, C. K., & Sakagami, S. F., (1987). An extraordinary concentration of stingless bees colonies in the Philippines, with notes on the nest structure (Hemenoptera: Apidae: *Trigona sp.*). *Insects Soceity*, 34, 96-107.
- Steffen-Dewenter, I. (2002). Landscape context affects trap-nesting bees, wasps, and their natural enemies. *Ecological Entomology*, 27, 631-637.
- Steffan-Dewenter, I., Klein, A. M., Alfert, T., Gaebele, V., & Tscharntke, T. (2006). Bee diversity and plant-pollinator interactions in fragmented landscapes. In N. M. Waser, & J. Ollerton (Eds.), *Specialization and* generalization in plant- pollinator interactions (pp. 387–408). Chicago: Chicago Press.

- Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., & Tscharntke, T. (2002). Scale- dependent effects of landscape context on three pollinator guilds. *Ecology*, 83, 1421–1432.
- Steffan-Dewenter, I., Potts, S. G., & Packer, L. (2005). Pollinator diversity and crop pollination services are at risk. *Trends in Ecology and Evolution*, 20, 651–652.
- Thompson, G. J., & Oldroyd, B. P. (2004). Evaluating alternative hypotheses for the origin of eusociality in corbiculate bees. *Molecular Phylogenetics and Evolution*, 33, 452-456.
- Thomson, J. A. (1983). Is continuous visual monitory necessary in visually guided locomotion? *Journal of Experimental Psychology, Human Perception and Performance*, 9, 427-443.
- Tonhasca, A., Blackmer, J. L., & Albuquerque, G. S. (2002). Abundance and diversity of euglossine bees in the fragmented landscape of the Brazilian Atlantic forest. *Biotropica*, 34, 416–422.
- Van-Nieuwstadt, M. G. L., & Iraheta, C. E. R. (1996). Relation between size and foraging range in stingless bees (Apidae, Meliponinae). *Apidologie*, 27, 219-228.
- Velthuis, H. H. W., Koedam, D., & Imperatriz-Fonseca, V. L. (2005). The males of *Melipona* and other stingless bees, and their mothers. *Apidologie*, 36, 169-185.

- Venturieri, G. C. (2009). Effect of landscape change on the structure of the stingless bee community (Hymenoptera: Apidae) in Meta. *Colombia Molecular Research*, 8(2), 684-689.
- Verma, L. R., & Partap, U. (1993). The Asian hive bee, *Apis cerana*, as a pollinator in vegetable seed production. *Kathmandu: ICIMOD*, pp. 52.
- Visscher, P. K., & Seeley, T. D. (1982). Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology*, 63, 1790-1801.
- Wallace, H. M., & Trueman, S. J. (1995). Dispersal of *Eucalyptus torelliana* seeds by the resin collecting stingless bee, *Trigona carbonaria*. *Oecologia*, 104, 12-16.
- Waser, N. M. (1983). Competition for pollination and floral character differences among sympatric plant species: a review of evidence. In C. E, Jones, & R. J. Little (Eds), *Handbook of experimental pollination biology* (pp. 277–293). New York, NY: Academic Press.
- Wettstein, W., & Schmid, B., (1999). Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. *Journal of Applied Ecology*, 36, 363–373.
- Wille, A. (1961). Evolutionary trends in the ventral nerve cord of the stingless bees (Meliponini). *Revista de Biología Tropical*, 9, 117-129.
- Wille, A. (1979). Phylogeny and relationships among the genera and subgenera of the stingless bees (Meliponinae) of the world. *Revista de biología tropical*, 27, 241-277.

- Wille, A. (1983). Biology of the stingless bees. *Annual Review of Entomology*, 28, 41–64.
- Wille, A., & Orozco, E. (1975). Observations on the founding of a new colony by *Trigona cupira*Apidae) in Costa Rica. *Revista de Biología Tropical*, 22, 253-287.
- Wille, A., Orozco, E., & Raabe, C. (1983). Polinización del chayote Sechium edule (Jacq.) Swartz en Costa Rica. Revista de Biología Tropical, 31, 145-154.
- Williams, M. J. B., & Ryan, M. G. (2001). Evaluating different soil and plant hydraulic constraints on tree function using a model and sap flow data from ponderosa pine. *Plant, Cell and Environment, 24*, 679–690.
- Williams, N. M., Crone, E. E., Roulston, T. H., Minckley, R. L., Packer, L., Potts, S. G. (2010). Ecological and life history traits predict bee species responses to environmental disturbances. *Biological Conservation*, 143, 2280–2291.
- Williams, N. M., & Kremen, C. (2007). Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications*, 17, 910-921.
- Williams, N. M., Minckley, R. L., & Silveira, F. A. (2001). Variation in native bee faunas and its implications for detecting community changes. *Conservation Ecology*, 5(7). Retrieved August 20, 2011, from hhttp://www.consecol.org/vol5/iss1/art7/i.
- Wilms, W., Imperatriz-Fonseca, V. L., & Engels, W. (1996). Resource partitioning between highly eusocial bees and possible impact of the introduced Africanized honeybee on native stingless bees in the Brazilian Atlantic rainforest. *Studies on Neotropical Fauna and Environment*, 31, 137–151.
- Wilms, W., Ramalho, M., & Wendel, L. (1997). Stingless bees and Africanized honeybees in the Mata Atlântica rainforest of Brazil. In XXXth International Apicultural congress of Apimondia. *Antuérpia*, pp. 167-170.
- Wilms, W., & Wiechers, B. (1997). Floral resource partitioning between native Melipona bees and the introduced Africanized honey bees in the Brazilian Atlantic rain forest. *Apidologie*, 28, 339–355.
- Winfree, R., Griswold, T., & Kremen, C. (2007). Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology*, 21, 213– 223.
- With, K. A. (2002). The landscape ecology of invasive spread. Conservation Biology, 16, 1192-1203.
- Wittmann, D. (1989). Nest architecture, nest site preferences and distribution of *Plebeia wittmanni* in Rio Grande do Sul, Brazil (Apidae: Meliponinae), Stud Neotropic. *Fauna Environ*, 24, 17–23.
- Wittmann, D., Radtke, R., Zeil, J., Lubke, G., & Francke, W. (1990). Robber bees (*Lestrimelitta limao*) and their host chemical and visual cues in nest defense by *Trigona (Tetragonisca) angustula* (Apidae: Meliponinae). *Journal of Chemical Ecology*, 16, 631–641.

Zucchi, R., & Sakagami, S. F. (1972). Capacidade termoreguladora em *Trigona* spinipes e em algumas outras espécies de abelhas sem ferrão (Hymenoptera: Apidae: Meliponinae). In W. E. Kerr, & R. Zucchi (Eds.), *Homenagem* (pp. 301-309). Rio Claro: UNESP.

APPENDIX

Appendix 1a: One-way ANOVA: DBH cm versus Bee species. _Koru

 Source
 DF
 SS
 MS
 F
 P

 Bee species.
 2
 2090
 1045
 2.69
 0.083

 Error
 33
 12822
 389
 389

 Total
 35
 14912
 35
 389

S = 19.71 R-Sq = 14.02% R-Sq(adj) = 8.81%

Level N Mean StDev Dactylurina 2 77.23 25.90 Meliponula bocandei 17 58.21 23.12 Meliponula ferruginea 17 47.53 15.00

 Individual 95% CIs For Mean Based on Pooled StDev

 Level
 -+-----+

 Dactylurina
 (-----*----)

 Meliponula bocandei
 (----*----)

 -+-----+
 -+-----+

 40
 60
 80
 100

Appendix 1b: One-way ANOVA: DBH cm versus Bee species _ Abotoase

 Source
 DF
 SS
 MS
 F
 P

 Bee species.
 2
 2454
 1227
 10.14
 0.002

 Error
 14
 1694
 121

 Total
 16
 4148

S = 11.00 R-Sq = 59.17% R-Sq(adj) = 53.34%

Level N Mean StDev Dactylurina 3 17.83 1.10 Meliponula bocandei 10 45.19 12.97 Meliponula ferruginea 4 54.30 7.68

Pooled StDev = 11.00

Appendix 1c: One-way ANOVA: DBH cm versus Bee species _ Kyabobo

Source DF SS MS F P Bee species. 2 971 486 3.80 0.041 Error 19 2429 128 Total 21 3400 S = 11.31 R-Sq = 28.56% R-Sq(adj) = 21.04% N Mean StDev Level 5 32.04 2.42 Dacty. Meliponula bocandei 6 50.90 9.28 Meliponula ferruginea 11 42.65 14.05 Individual 95% CIs For Mean Based on Pooled StDev Level -----+ (------) Dacty. Meliponula bocandei (------) Meliponula ferruginea (------) (-----) Meliponula ferruginea ----+-----+-----+ ----+--50 60 30 40

Appendix 1d: One-way ANOVA: DBH cm versus Bee species _ all three sites combine

 Source
 DF
 SS
 MS
 F
 P

 Bee species.
 2
 2108
 1054
 3.31
 0.042

 Error
 72
 22926
 318
 5
 5

 Total
 74
 25034
 5
 5
 5
 5

S = 17.84 R-Sq = 8.42% R-Sq(adj) = 5.88%

LevelNMeanStDevDactylurina1036.8223.94Meliponula bocandei3352.9319.03Meliponula ferruginea3246.7014.11

Pooled StDev = 17.84

Pooled StDev = 11.31

Appendix 1e: One-way ANOVA: Nesting Height m versus Bee species_Koru

 Source
 DF
 SS
 MS
 F
 P

 Bee species.
 2
 15.51
 7.75
 1.03
 0.369

 Error
 33
 248.75
 7.54
 7.54

 Total
 35
 264.26
 7.54
 7.54

S = 2.745 R-Sq = 5.87% R-Sq(adj) = 0.16%

LevelNMeanStDevDactylurina29.1000.000Meliponula bocandei176.1763.110Meliponula ferruginea176.3292.424

Individual 95% CIs For Mean Based on
Pooled StDev
Level -+++++
Dactylurina (*)
Meliponula bocandei (*)
Meliponula ferruginea (*)
_++
5.0 7.5 10.0 12.5

Pooled StDev = 2.745

Appendix 1f: One-way ANOVA: Nesting Height m versus Bee species _ Abotoase

 Source
 DF
 SS
 MS
 F
 P

 Bee species. Abot
 2
 24.34
 12.17
 2.05
 0.165

 Error
 14
 82.96
 5.93
 5.03

 Total
 16
 107.30
 5
 100

S = 2.434 R-Sq = 22.69% R-Sq(adj) = 11.64%

Level N Mean StDev Dactylurina 3 2.667 0.289 Meliponula bocandei 10 5.850 2.550 Meliponula ferruginea 4 5.675 2.844

Pooled StDev = 2.434

Appendix 1g: One-way ANOVA: Nesting Height m versus Bee species _ Kyabobo

 Source
 DF
 SS
 MS
 F
 P

 Bee species.Kyabobo
 2
 44.92
 22.46
 2.73
 0.091

 Error
 19
 156.47
 8.24

 Total
 21
 201.39

S = 2.870 R-Sq = 22.30% R-Sq(adj) = 14.13%

LevelNMeanStDevDactylurina56.3401.976Meliponula bocandei67.4673.157Meliponula ferruginea114.2093.017

Pooled StDev = 2.870

Appendix 1h: One-way ANOVA: Nesting Height m versus Bee species _ all the three sites combine

 Source
 DF
 SS
 MS
 F
 P

 Bee species.com
 2
 10.38
 5.19
 0.64
 0.529

 Error
 72
 581.45
 8.08

 Total
 74
 591.83

S = 2.842 R-Sq = 1.75% R-Sq(adj) = 0.00%

Level N Mean StDev Dactylurina 10 5.790 2.758 Meliponula bocandei 33 6.312 2.924 Meliponula ferruginea 32 5.519 2.779

Pooled StDev = 2.842 Appendix 1i: One-way ANOVA: Count of nests versus Sites

Source DF SS MS F P Sites 2 3.08 1.54 0.74 0.481 Error 69 143.79 2.08 Total 71 146.88

S = 1.444 R-Sq = 2.10% R-Sq(adj) = 0.00%

Individual 95% CIs For Mean Based on Pooled StDev Level N Mean StDev ------+-----+------+ Abotoase 24 1.125 1.154 (------*-----) Koru 24 1.583 1.840 (------*-----) Kyabobo 24 1.167 1.239 (------*------) ------+-----+-----+-----+ 1.00 1.50 2.00 2.50

Pooled StDev = 1.444

Appendix 1j: One-way ANOVA: Count of nests versus Bee species

 Source
 DF
 SS
 MS
 F
 P

 Bee species
 2
 33.58
 16.79
 10.23
 0.000

 Error
 69
 113.29
 1.64
 1.64

 Total
 71
 146.87
 1.64
 1.64

S = 1.281 R-Sq = 22.87% R-Sq(adj) = 20.63%

Pooled StDev = 1.281

Appendix 1k: One-way ANOVA: DBH cm versus Bee species.combine

Source DF SS MS F P Bee species.com 2 21499 10749 3.40 0.039 72 227403 3158 Error Total 74 248902 S = 56.20 R-Sq = 8.64% R-Sq(adj) = 6.10% N Mean StDev Level Dactylurina 10 114.60 76.17 Meliponula bocandei 33 166.21 59.76 Meliponula ferruginea 32 146.63 44.32 Individual 95% CIs For Mean Based on Pooled StDev Level ----+-----+-----+------+------+------(-----) Dactylurina Meliponula bocandei (-----*----) (-----*----) Meliponula ferruginea 90 120 150 180

Pooled StDev = 56.20

Appendix 2a: Two-way ANOVA: Count of nests versus Bee species, Sites

 Source
 DF
 SS
 MS
 F
 P

 Bee species
 2
 33.583
 16.7917
 10.23
 0.000

 Sites
 2
 3.083
 1.5417
 0.94
 0.396

 Interaction
 4
 6.833
 1.7083
 1.04
 0.393

 Error
 63
 103.375
 1.6409
 104
 104

 Total
 71
 146.875
 104
 105
 106

S = 1.281 R-Sq = 29.62% R-Sq(adj) = 20.68%

Stingless Bee Species	Site	Number of nests in trees	Number of nest in old termite mounds	Number of nests in the ground	Total number of nests
Meliponula bocandei	Koru	17	0	0	17
	Abotoase	10	0	0	10
	Kyabobo	6	0	0	6
Meliponula ferruginea	Koru	17	1	1	19
	Abotoase	4	10	0	14
	Kyabobo	11	6	0	17
Dactylurina staudingeri	Koru	2	0	0	2
	Abotoase	3	0	0	3
	Kyabobo	5	0	0	5
	Total	75	17	1	93

Appendix 3: Nesting behaviour of the three stingless bee species within various landscapes in the study sites (Koru, Abotoase and Kyabobo).

Appendix 2b:Two-way ANOVA: count of nest versus Bee species, Nesting choice

DF SS MS F P Source 2 18.431 9.2153 8.84 0.000 Bee sp Nesting choice 1 24.174 24.1736 23.20 0.000 Interaction 2 5.931 2.9653 2.85 0.061 Error 138 143.792 1.0420 Total 143 192.326

 $S = 1.021 \quad R\text{-}Sq = 25.24\% \quad R\text{-}Sq(adj) = 22.53\%$

Individual 95% CIs For Mean Based on Pooled StDev Bee sp Decty 0.20833 (-----*----) Mel Black 1.08333 (-----) (-----) Mel Brown 0.68750 --+-----+-----+------+---0.00 0.40 0.80 1.20

Nesting

_

Individual 95% CIs For Mean Based on Pooled StDev

choice	Mean	+	+	++
T.M nest	0.25000	(*)	
Tree nest	1.06944			()
	+	+	+	+
	0.00	0.35	0.70	1.05

Appendix 4: Diameter at breast height (DBH) and nesting height of nesting trees for the three sampling sites.

	Site/(nest population)	DBH of nest tree (cm)		Nesting height of tree nests (m)	
Stingless bee species		Mean	Range	Mean	Range
	Koru (17)	58.2 ± 15.0	20.0-96.0	6.2 ± 2.4	1.5-11.3
Meliponula bocandei	Abotoase (10)	45.2 ± 13.0	20.0-57.0	5.9 ± 2.6	3.0-9.5
	Kyabobo (6)	50.9 ± 9.3	40.0-61.0	7.5 ± 3.2	5.0-12.0
	Koru (19)	47.5 ± 23.1	31.0-83.0	6.3 ± 3.1	3.4-9.1
Meliponula ferruginea	Abotoase (14)	54.3 ± 7.7	43.0-60.0	5.7 ± 2.8	2.2-8.0
	Kyabobo (17)	*	*	4.2 ± 3.0	1.2-10.5
	Koru (2)	*	*	9.1 ± 0.0	9.1-9.1
Dactylurina staudingeri	Abotoase (3)	*	*	2.7 ± 0.3	2.5-3.0
	Kyabobo (5)	*	*	6.3 ± 2.0	4.5-9.7

* Tree DBH was not considered for *Dactylurina staudingeri* species (have exposed nest)

Source: Field work, 2011

	Common names for
Tree species	trees species
Afzelia Africana	Рарао
Alchornea cordifolia	Gyama
Anacardium occidentale	cashew nut
Annona muricata	abroofontunkum
Annona senegalensis	wild custard apple
Anogeissus leiocarpus	kane
Anthocleista nobilis	cabbage palm
Baphia nitida	Odwen
Berlinia grandiflora	Kwatafombaboa
Blighia sapida Akye	
Bombax buonopozense	Akata/Akonkodie
Burkea Africana	wild seringa
Calotropis procera	Giant Swallow Wort
Ceiba pentandra	Onyina
Chlorophora excels	Odum nua
Citrus sinensis	Ekutu
Clausena anisata	Horsewood
Cola gigantean	Watapuo
Cola millenii	Anansedodowa
Cola nitida	Bese
Combretum collinum	bushwillows

Appendix 5: Scientific and common name(s) of tree species

Appendix 5 continued

Crossopteryx febrifuga	Common crown-berry
Daniellia olivera	Sofo
Detarium microcarpa	Takyikyiriwa
Diospyros mespiliformis	African ebony/ Kusibiri
Entada abyssinica	tree entanda
Erythrophleum ivorense	Potrodum
Ficus asperifolia	Amangyedua/Tsatsaflala
Ficus exasperata	Nyankyerene
Ficus sur	Amangyedua
Ficus variifolia	Nyankyerene
Funtumia africana	Okae
Hildegradia barteri	Akyere-kyewewa
Holarrhena floribunda	
Hymenocardia acida	sabrakyie
Khaya grandifoliola	Kruba
Khaya senegalensis	African mahogany/Dubini
Lannea kerstingii	Kumanini
Lannea welwitschii	Kumanini
Lecaniodiscus cupanioides	Dwindwera
Lophira lanceolata	red ironwood
Malacantha alnifolia	Fafaraha

Appendix 5 continued

Mangifera indica	Mango
Manihot glaziovii	tree cassava
Manikara multinersis	Berekankum
Maramthes glabra	Afam nini
Margaritaria discoidea	Pepea
Milicia excelsa	Odum (-nua)
Mitragyna inermis	Afafali (Ewe)
Nauclea latifolia	African peach/ Kusia
Ouratea flava	Labati (Ewe)
Parinari excelsa	Afam
Parkia biglobosa	dawa-dawa
Pentadesma butryaceum	Abotoasabie
Persea americana	Avocado/ pear
Piliostigma thonningii	camel's foot (Etkin)
Prosopis africana	kiriy (Hausa)
Pterocarpus erinaceus	Hote
Quassia undulata	Hotorohotoro
Securidaca longependunculata	violet tree / krinkhout
Spathodea campanulata	Akuakuoninsuo
Sterculia tragacantha	Sofo
Strychnos barteri	Snake-wood
Strychnos spinosa	Green Monkey Orange

Appendix 5 continued

Tectona grandis	Teak
Terminalia laxiflora	Efeti (Ewe)
Terminalia laxiflora	Emire
Tricalysia pallens	Turomdua
Triplochiton scleroxylon	Wawa
Uapaca togoensis	kuntan esirem
Unknown	Wusrukortor (Twi)
Unknown	Sakramatidze (Twi)
Unknown	Kporti
Unknown	Wormatrikuo
Unknown	Openyi dua
Unknown	Aziwoe
Unknown	Ayikuti
Unknown	Wusrokortor
Unknown	Sakramatidze
Unknown	Unknown
Unknown	Egati (Ewe)
Unknown	Atindeti (Ewe)
Unknown	Sesewu
Unknown	Aziwoe (Ewe)
Vitellaria paradoxa	Shea Butter Tree
Vitex doniana	Forye /Black Plum