

THE EFFECTS OF LAND USE ON CAPE HONEY BEE (*Apis mellifera capensis*
ESCHOLTZ) NESTING DYNAMICS IN THE EASTERN CAPE, SOUTH AFRICA

By

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To Mother Earth

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Abstract of Thesis Presented to the Graduate School
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The Cape honey bee (*Apis mellifera capensis* Escholtz) is a unique subspecies of western honey bee whose workers are known to produce diploid eggs, and thus other female bees, through thelytokous parthenogenesis. It is the exclusive bee of the Cape Floristic Region and its distribution extends to thicket and succulent biomes of the Eastern Cape, South Africa, making it an important component of these unique and ancient biomes. Livestock farming in the Eastern Cape, South Africa is a common land use practice and it transforms the landscape. This has affected the biodiversity and abundance of plants and animals in the region negatively. Likewise, populations of the Cape honey bee also may suffer as a result of farming practices. Recently, farmers have been converting their farms to game reserves as ecotourist attractions for people to view charismatic animals. The goal of this research was to determine if land use habits affect Cape honey bee nesting dynamics in the Eastern Cape. Specifically, I determined how two land use practices (livestock farming and conversion to game reserves) affected Cape bee nest site selection, colony strength, and population density.

Novel and modified methodologies were used for field work and data collection on wild Cape bee colonies. Specifically, I collected data on Cape bee population density, nest selection parameters, and colony strength indices. Wild colonies were found using modified methods published on bee hunting. Furthermore, I developed an index that I used to estimate the population density of colonies in an area, though the index has yet to be validated. I used this technique to determine if land use practices affected bee population densities. This method involves counting bee lines and number of foraging bees established at a food source which may indicate the number of colonies nesting near a central location. I also investigated Cape bee nest site selection practices including nest height, nest location, entrance direction, and nest cavity volume. Finally I sampled a subset of colonies in both locations (livestock farms and reserves) to determine land use effects on various colony strength parameters including total area of comb in the colony, the volume of stored honey, pollen, and brood, adult bee population, the weight per bee, and the bee/nest cavity volume ratio.

When viewed collectively, the data indicated that land use practices affected Cape bee nesting dynamics and trends in the data suggested that colonies nesting on the reserves might be healthier and occur in greater densities than those nesting on livestock farms. Hopefully, this work will be continued as honey bee conservation, particularly in areas where they are native, is crucial to the health of agriculture and whole ecosystems.

CHAPTER 1 INTRODUCTION

The Cape Honey Bee

The Cape honey bee, *Apis mellifera capensis* Escholtz (Hymenoptera: Apidae), is a subspecies of Western honey bee whose native distribution is restricted to the Western and Eastern Cape Provinces in South Africa (Hepburn et al. 1998). Since it is the principle subject of this treatise, it will be referred to in this text as the Cape honey bee, honey bee, and/or bee. The majority of its habitat is located in the Cape Floristic Region. The rest of its distribution, that in the Eastern Cape, is located in thicket, succulent, savanna, and afromontane forest biomes. From what is known, it is the exclusive honey bee in its territory (Hepburn et al. 1998). A hybrid zone occurs on the northern boundary of its distribution where *A. m. capensis*, *A. m. scutellata*, and hybrids of the two are found (Hepburn et al. 1998) (Figure 1-1).

Cape bees are recognized as the honey bee race that exhibits a unique form of worker bee reproduction. Accomplished through thelytokous parthenogenesis whereby the polar body and nucleus of gamete cells fuse (Mortiz and Hillesheim 1985), Cape bee workers can lay diploid eggs. These worker-laid eggs develop into female “pseudoclones” of the mother.

It has been hypothesized that this particular type of thelytoky evolved in the Cape honey bee because of queen loss through a long history of predation by humans and other animals and high rates of absconding behavior (Hepburn et al. 1999; Hepburn, personal communication). If a colony becomes queenless, it can survive because its workers can produce new workers and potentially a new queen. Cape laying workers have ovaries that are more developed and have more ovarioles than those of workers of

other western honey bee subspecies (Rutner and Hesse 1981, Hepburn and Crewe 1991). Furthermore, they produce 9-ODA (9-Oxo-decenoic acid), a principle queen pheromone (Wossler 2002). In this way, they can avoid policing from other workers and maintain dominance in the nest (Moritz et al. 1999).

Because of the reproductive capacity of Cape laying workers, the Cape honey bee has become a parasite on managed *A. m. scutellata* colonies in northern parts of South Africa. This was initiated when managed Cape bee colonies were relocated to other parts of South Africa because they are more docile than *A. m. scutellata*, therefore easier for beekeepers to manage. When this occurred, beekeepers soon discovered that Cape bee workers enter *A. m. scutellata* colonies by “drifting” into those colonies, replace the *A. m. scutellata* queen (how they do this is unknown), reproduce via parthenogenesis, and exhibit dominance over *A. m. scutellata* workers (Neumann and Moritz 2002). The parasitic, reproducing workers and their offspring rarely contribute to hive maintenance (Martin et al. 2002). Infected *A. m. scutellata* colonies ultimately dwindle and die when led by Cape laying workers.

Cape honey bees are not only interesting because of their reproductive behavior but also because of the geographic region in which they inhabit. Cape bees live principally in the Cape Floristic Region (CFR), which houses the Cape Floral Kingdom, a recognized biodiversity “hotspot”. The CFR is one of only six floral kingdoms in the world, containing the highest diversity of plant species per unit area among all floral kingdoms with over 8,800 species and approximately 68% endemism (Born et al. 2007). It is ~90,000 km², with over half of it covered by fynbos (Born et al. 2007), the scrubland or heathland found in the CFR.

The natural distribution of Cape bees also includes sections of the Maputaland-Pondoland-Albany hotspot (MPA), particularly the Albany region, also known as the Albany Centre of Floristic Endemism (Victor and Dold 2003). The MPA is ~274,316 km² and extends from the eastern boundary of the CFR along the eastern coast of South Africa to eastern Swaziland and Southern Mozambique. The Albany Centre of Floristic Endemism contains many different vegetative biomes, including succulent, thicket, savanna, and forest biomes. At least 21% of the plants in the region are endemic (Mittermeier et al. 2004).

Where they are distributed naturally, Cape honey bees are important to the ecosystems they support. Cape honey bees pollinate at least 27% of the herbs, 44% of the shrubs, and 28% of the trees present in the region (Hepburn and Radloff 1998). In the dry savanna biome of Africa, which includes the MPA, honey bees in general pollinate at least 18% of the herbs, 29% of the shrubs, and 52% of the trees present (Hepburn and Radloff 1998).

Despite their importance, little is known about Cape bee natural history or its ecological importance to the CFR, thicket, and other biomes present in the region. The majority of the research involving Cape bees concerns their reproductive and parasitic habits. Furthermore, the research has been conducted on managed colonies housed in Langstroth-style hives. Few studies exist on wild populations of Cape bees. The goal of this research was to determine if land use habits affect Cape honey bee nesting dynamics in the Eastern Cape, South Africa. Specifically, I determined how two land use practices (livestock farming and conversion to game reserves) affected Cape bee nest site selection, colony strength, and population density.

Habitat loss may be a large threat to honey bee populations in Africa by transforming land for cities and agriculture (Dietemann et al. 2009). To determine and isolate land use effects, other potential effects on honey bee health have to be controlled. The Eastern Cape South Africa provides the opportunity to research honey bees that occur in their natural habitat and are free of many pests, parasites, and diseases plaguing honey bees in the United States of America and Europe (Dietemann et al. 2009, Murray et al. 2009).

Land Use

The effects of land use practices on biodiversity are well known in the fynbos, thicket, and succulent biomes where avian, arthropod, reptilian, and plant biodiversity have been affected negatively by agriculture (Fabricius and Burger 1996a, 1996b, Mangnall and Crowe 2003, Witt and Samways 2004). Furthermore, agricultural practices have been a serious threat to rare plants found in Cape lowlands (Heydenrych et al. 1999) and the Eastern Cape region (Victor and Dold 2003). Agricultural land use is one of the most common uses of land in the region, typically in the form of sheep, cattle, and goat farming.

When farming livestock, much of the natural landscape is removed to accommodate pastureland for grazing livestock, which often leads to overgrazing (Kerley et al. 1995, Mills et al. 2005) and other land quality issues. When allowed to regenerate, natural vegetation and food webs could take an unpredictable amount of time to return to pristine condition, possibly being transformed forever through extinctions (Whitmore and Sayer 1992, Novacek and Cleland 2001). Furthermore, poor land use habits may cause and/or expedite soil erosion (Le Roux et al. 2009), which can reduce the productivity of an area.

Though livestock farming is common in the Eastern Cape, farmers in the area are converting their farms to game reserves due to the economic benefits associated with ecotourism in South Africa (Langholz and Kerley 2006). These reclaimed lands can regenerate, though overgrazing can still occur as livestock is replaced with other large herbivores. However, vegetative structural diversity is greater on reserves due to the varying sizes and feeding strategies of wild herbivores (Fabricius et al. 1996a, Lechmere-Oertel et al. 2005). If managed properly, are not as destructive as large numbers of livestock (Fabricius et al. 1996b). However, some game reserves stock white rhinoceroses and giraffes which are not native to the area, elephants, which can be destructive to patchy levels of vegetation, and large numbers of other charismatic game to attract tourists (Langholz and Kereley 2006). Therefore, proper conservation and land management is important to allow the vegetation structure to regenerate.

The effects of reduced native vegetation and diminished food webs affecting an ecosystem's ecology have not been researched for wild honey bees in the Eastern Cape, South Africa. Some have proposed that honey bees are healthier in areas where there is no artificial selection of bees, lower proportion of cropland, lower use of pesticides, less beekeeping, and less developed land (Naug 2009, Vandame and Palacio 2010). Murray et al. (2009) outlined the need to study the pollination services of native bees in order to understand the ecological threats facing them. Among the topics of special concern to native pollinators are population densities of wild pollinators, resource availability, land use effects, habitat loss and fragmentation, and the potential loss of nesting resources (Dietemann et al. 2009, Murray et al. 2009). In this project, I attempted to address many of these issues for Cape honey bees.

Research Foci

Land Use Effects on Cape Bee Nesting Dynamics

Colony population density

The population density of a species can be indicative of the carrying capacity of an ecosystem for that particular species (Dempster and Pollard 1981), and therefore can be measured to compare the relative health of two or more areas. Therefore, I developed and used a tool to determine a population density index for bees nesting on livestock farms or game reserves, allowing me to roughly estimate the effects of land use on colony density per unit area. If, for example, there is a lower colony density on livestock farms, the data may indicate that the ecosystem cannot support large honey bee populations and maybe a threatened habitat (Dempster and Pollard 1981, Haynes et al. 2007, Steffan-Dewenter and Schiele 2008).

Nest site selection

The selection of a nest site is an important decision for any nesting species because of the need for safety and adequate resources (Steinhouse et al. 2005). Regarding honey bees, the selection of a nest site by a scout bee involves a thorough inspection inside and outside the potential usable cavity (Seeley 1977). Land transformation may result in a depletion of nest sites and I predict that it will be reflected by honey bee nest site selection. There are a number of ways that bees choose an optimal nest site. Seeley and Morse (1976) investigated the nest entrance height, cavity volume, and entrance direction as important parameters in honey bee nest site selection in the northeastern U.S. I will determine the same for Cape bee colonies. I also will record the nest location (building, cliff, ground, or tree) of each colony.

Colony strength parameters

If agricultural land use negatively affects honey bees and the ecosystem, I predict that colonies inhabiting agricultural areas will not have as many resources available and therefore will be weaker than colonies on reserves. To address this, I measured the adult bee population and cm² brood, honey, and pollen for each colony studied. Comparing these variables between colonies nesting on farms and reserves should allow me to determine if using land for livestock production negatively affects bee colonies.

Methodology

A final purpose of this project was the development, modification, and utilization of honey bee research methodologies that are inexpensive, uncomplicated, effective, and cause little damage to the surveyed colonies. First, I developed and utilized a new method for estimating a population density index of wild honey bee colonies by counting bee lines and numbers of foraging bees at a feeding station, which is described in Chapter 2. This technique allows the researcher to compare the population densities between two or more areas. However, the accuracy of this technique has not yet been quantified. Second, I tracked and located wild colonies in the study area through the process of “bee hunting,” the baiting of honey bees and using bee lines to locate wild colonies (Edgell 1949, Seeley and Morse 1976, Seeley et al. 1982, Seeley 1983, Visscher and Seeley 1989, Crane 1999; Seeley, personal communication). I modified existing techniques in order to effectively locate wild colonies quickly. The methodology is described in Chapter 3. Finally, in Chapter 4, I document the process of extracting comb from wild colonies and how to recapture the bee cluster.

Study Sites

Grahamstown, South Africa and its surrounding vicinity are located in the Albany region of the MPA hotspot, a region that exhibits a convergence of the Albany and CFR biomes. Even though Grahamstown and its vicinity are considered to be in the hybrid zone of the Cape honey bee and *A. m. scutellata*, it is now understood that the Cape bee is the dominant inhabitant (Cambray, personal communication; Hepburn, personal communication) (Figure 1-1). Fynbos, thicket, xeric succulent thicket, and grasslands can be found intermixed and within close proximity to each other in this area (Victor and Dold 2003).

Four reserves and four livestock farms in the Grahamstown area were used as study areas in this research (Table 1-1). Additionally, observations were made for colonies nesting in Grahamstown to determine possible urbanization effects on nest site selection. The four reserves used were Amakhala Game Reserve/Carnavron Dale (<http://www.amakhala.co.za/index.php>), Crown River Safari and Wildlife Reserve (<http://www.crownriversafari.com/>), Emlanjeni Game Reserve, and Kwandwe Game Reserve (<http://www.kwandwereserve.com/>). Each reserve contained land that was converted from cattle and other livestock farms to reserves within the preceding five to fifteen years. The four livestock farms utilized were Assegaaï Trails (<http://www.assegaaitrails.co.za/>), Brentwood, Theo Harris's and Ezra Schoonbee's cattle farms (shared borders), and Hounslow (<http://www.johndelldorpers.co.za/>). All had been livestock farms for at least 15 years, with the farmers following farming practices typical of those promoted using Best Management Practices or the equivalent. The study region is labeled in Figure 1-1.

Concluding Remarks

Though the specific goal of my research was to determine land use effects on Cape honey bee nesting dynamics, I anticipate that the data generated by my work will aid in Cape and other honey bee conservation efforts in general. The purpose of this research is to study the current health and population of honey bees in South Africa. The Cape honey bee is free from many of the complications that are being experienced by honey bees in the United States and Europe. Additionally, Cape bees possess attributes and behaviors that are unique among all other western honey bee species. Finally, Cape bees appear very important to the fynbos and thicket biomes of the CFR. Preserving the health and populations of Cape honey bees is important, not only to South Africa but also to the global honey bee community in general.

Table 1-1. Reserve and Farm study sites used in the project.

Name	Type	Dominant Vegetation Biome	Large Mammals Present
Amakhala Game Reserve/ Carnavron Dale	Reserve	Thicket, Savanna	Cheetah, Buffalo, Elephant, Giraffe Rhinoceros, Wilderbeast, Zebra, various Bovines
Crown River Safari and Wildlife Reserve	Reserve	Thicket	Zebra, various Bovines
Emlanjeni Game Reserve	Reserve	Thicket	Buffalo, Giraffe Rhinoceros, Zebra, various Bovines
Kwandwe Game Reserve	Reserve	Thicket, Fynbos, Savanna, Succulent	Cheetah, Buffalo, Elephant, Giraffe, Lion, Rhinoceros, Wilderbeast, Zebra, various Bovines
Assegaaï Trails	Farm	Thicket, Savanna	Cattle
Brentwood	Farm	Thicket, Savanna	Cattle
Hounslow	Farm	Thicket, Fynbos, Succulent	Sheep, Goat
Theo Harris/Ezra Schoonbee	Farm	Thicket, Afromontane Forest, Savanna	Cattle

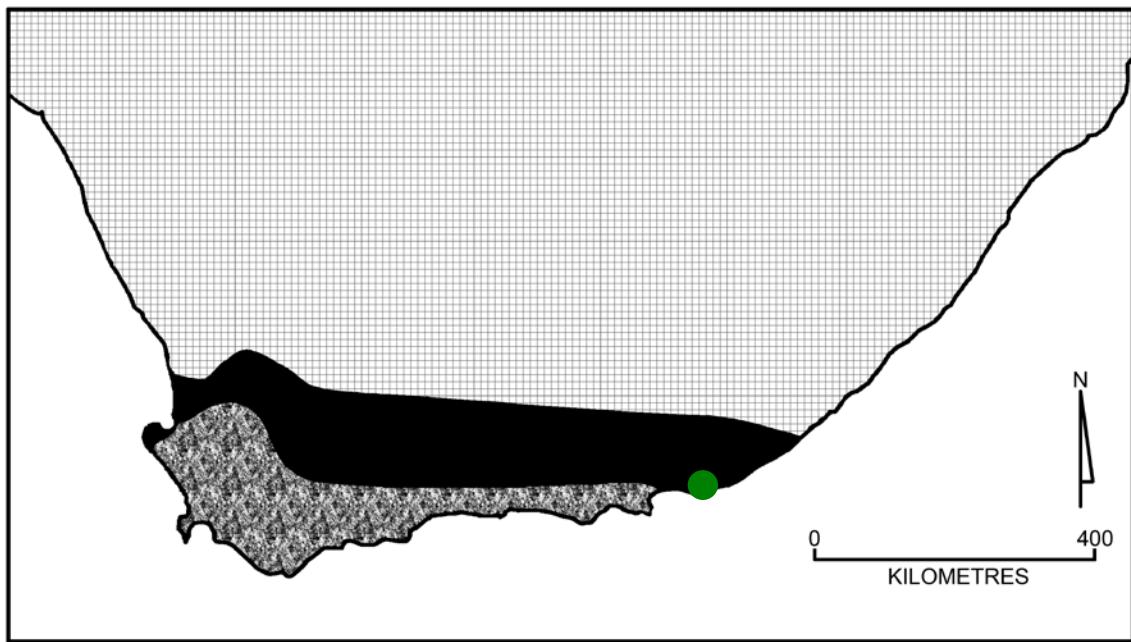


Figure 1-1. The natural distribution of the Cape honey bee in South Africa. The southern grey region represents the Cape Floristic Region and distribution of the Cape bee. The black area represents the hybrid zone between the Cape bee and *A. m. scutellata*. The hashed region represents the natural distribution of *A. m. scutellata*. The green dot represents the study region for this project. The figure is modified from Ellis (2008).

CHAPTER 2

THE EFFECTS OF LAND USE ON CAPE HONEY BEE (*Apis mellifera capensis* ESCHOLTZ) COLONY POPULATION DENSITY

Introduction

The population density (# individuals per unit area) of a particular species can indicate important information about that species and its habitat. A high density can indicate that the population of the target species and the ecosystem supporting it are healthy with the reciprocal being true as well. Regarding honey bees, a healthy ecosystem, one where plant species richness and abundance are high and many nest sites are available, should be able to support a high colony density (Steffan-Dewenter and Schiele 2008). High densities also indicate genetically diverse populations which lead to higher productivity and fitness of the colonies (Mattila and Seeley 2007). Comparing population densities of honey bee colonies between two or more areas within the same geographic region may indicate the relative health and honey bees of those areas. This information could be used to determine land use effects on honey bee populations and stress effects on honey bee colonies nesting *in vivo* and may indicate the carrying capacity and health of the ecosystem supporting their populations.

It is difficult to determine the absolute population density of small animals, especially insects. Although honey bees nest in typically sessile colonies, their nests can be difficult to locate, especially in environments where plant densities are high. Furthermore, honey bees usually nest in cavities, often elevated >2 m from the ground (Seeley and Morse 1978). Consequently, one may fail to notice bees flying into and out of a colony's entrance, especially if the bees are nesting in high trees or cliffs (Kajobe 2006). Finally, determining the population density of honey bees in an area can be time

consuming and inaccurate, requiring one to survey an area in detail and locate all nesting bee colonies.

There are some drawbacks to using published methodologies to estimate colony densities. First, DNA markers have been used to estimate population density by determining the number of drone genotypes represented in the worker population (Moritz et al. 2008). The number of drone genotypes was divided by their average distance of recruitment to a drone congregation area (2km^2) to determine the density (Moritz et al. 2008). However, the technology only can be used by those with the proper economic resources and training. Further, the population estimates were representative of previous years because the ages of the queens producing the workers were unknown. Because queens mate early in life, the method may estimate the colony density when the queen mated originally (Moritz et al. 2008).

Oldroyd et al. (1997) and Baum et al. (2005) studied colony population densities by counting all colonies inhabiting an area. This is time consuming and requires considerable manpower to locate colonies and record data. Consequently, there is a need to develop practical ways of estimating honey bee populations in the environment without counting all colonies in an area or utilizing expensive technology requiring special skills. To that end, I developed a practical and inexpensive methodology that allows one to generate an index of honey bee colony densities in many settings. I used the index to compare relative population densities of honey bees nesting on game reserves and livestock farms in the Eastern Cape, South Africa.

Livestock farming typically reduces the diversity and abundance of plants through land clearing practices of farmers and overgrazing by livestock (Kerley et al. 1995, Mills

et al. 2005). Not only does this reduce the resources available to honey bees, but it also may reduce the number of potential nest sites for honey bees (Steffan-Dewenter and Schiele 2008). Therefore, agricultural land use practices may reduce an area's carrying capacity for honey bee populations, thus leading me to predict that there would be fewer honey bee colonies per unit area on livestock farms than on reserves. Because honey bees are important for the maintenance of plant communities through the pollination services they provide, the index I developed may be used to estimate honey bee populations and compare the relative health and carrying capacities in habitats managed with different land use tactics.

Methods and Materials

Feeding Stations

Ten feeding stations were used to attract foraging honey bees (Figure 2-1). The stations consisted of a 2 m tall iron rod angled at the bottom to facilitate insertion into the ground. A 10 cm long flat iron crosspiece was welded 0.5 m from the bottom of each station at 90° from the main rod and was used to push the station into the ground with one's foot or a hammer. Angle iron was used for the stations because of its strength, size, ability to penetrate rocky earth, ability to withstand strong winds, and resistance to large animal damage. A 10 cm² iron plate was welded to the top of each stand and contained a 5 mm hole drilled through each corner. A plastic container (~ 11.5 x 17 x 4 cm, L x W x H) was nailed through the center onto a 25 cm² wooden plate. The wooden plates were affixed to the iron stand with screws or nails through each of the holes on the iron plate, making it easy to replace or repair the containers as needed. The stations were painted purple (Figure 2-1).

Each station was baited with a 1:3:3 mixture of honey, water, and sugar respectively and by volume. Pure honey was not used because of its expense and lack of availability in the study area. However, the honey used was from a single source to control for any differences in the attractiveness of honeys from various sources. The plastic container on each feeding station was filled with ~ 600 mL of bait into which sticks and twigs were placed to provide bees a platform from which they could drink without drowning (Figure 2-3). Once honey bees are attracted to the station, they typically will continue to return up to 7 days after the station is emptied (personal observation).

Feeding stations were placed systematically throughout each study site (Table 1-1) with a maximum of ten stations being used at any one site. Only Ezra Schoonbee's farm was used for the study site "Theo Harris/Ezra Schoonbee" while only "Carnavron Dale" was used from Amakhala Game Reserve. The stations were placed ~ 2 km away from each other throughout a study site. African honey bees typically forage within 1 km of the nest, though they can forage further distances (Schneider 1989, Schneider and Hall 1997; Hepburn, personal communication). Consequently, the stations may attract honey bee colonies nesting within a 1 km radius, minimizing the possibility that one colony will be attracted to two stations.

The locations for each station were selected before entering a site in order to prevent sampling bias. Station placement sites were selected using Google Earth v.5.1 (Google Inc. 2009). All proposed feeding stations were "pinned" and labeled on the map, thus allowing me to use the measure tool to calculate distances between stations. Since the different research sites were different sizes, the number of feeding stations

placed in each varied. I attempted to maximize the number of stations placed in each study area. Stations were placed close to fences only if the landscape was the same at a considerable distance from the fence into the adjacent property and/or the adjacent property was managed identically to that on which the station was placed. Stations on the site "Kwandwe" were placed along main park roads because the presence of lions and elephants prohibited me and rangers from walking off-road. All feeding stations were entered as waypoints into a Garmin GPSmap 60CSx (Garmin International Inc., Olathe, KS).

Stations were placed and baited at the pre-selected sites about 24 hours before monitoring. Data were collected only during sunny weather with little to no wind. If bees had removed the bait from the stations prior to data collection, the stations were refilled, causing bees to return almost immediately.

Population Index Data Collection

All population index data collection occurred from 8 April to 1 May 2010. Data collection lasted no longer than 60 minutes at each station. I counted the number of bee lines established at each feeding station and recorded the compass direction of each bee line and the weather at the time of data collection. A bee line is the flight path taken by honey bees to and from a food source and the colony. When the bees are familiar with the location of a food source, they fly almost directly to and from the colony from the food source (Edgell 1949). The number of bee lines suggests a possible number of colonies within the attraction radius of the feeding station. From my observations, bees will approach the stations directly from the colony but will circle around the station in order to face the direction the wind is blowing as they land. It was more useful to me to watch the directions that the bees fly when leaving the food, which seemed more direct

than when they landed. Bee lines were viewed best when standing level or below the station and watching the flight direction of the bees against the sky as they left the station. Flying bees are lost easily against a dark colored background such as vegetation or rocks (Figure 2-2). Each station was monitored until all established bee lines were noted.

I also collected a second set of data at each feeding station. I rated each station on a scale of 0 (no bees foraging) to 3 (many bees foraging) based on the intensity of honey bee foragers visiting a station. This was a qualitative scale and is called the “field rating.” Furthermore, I photographed each station during the estimated peak bee foraging activity. One photograph per feeding station was analyzed on a 15” MacBook Pro 4,1 (Apple Inc., Cupertino, CA) using iPhoto ’08 v.7.1.5. (Apple Inc. 2008). I rated each photograph (photograph rating) on a scale from 0 to 3. This rating was quantitative, based on the number of foraging bees observed in the photograph. The ratings were assigned as follows: (0) = zero foraging bees, (1) = 1-50 foraging bees, (2) = 51-200 foraging bees, (3) = \geq 200 foraging bees (Figure 2-3).

Statistical Analyses

Land use (reserve or livestock farm) effects on the number of bee lines at each feeding station were determined using a one-way ANOVA, weighted by the number of feeding stations at each site. A χ^2 analysis was used to determine if there was a difference between site ratings (both field and photograph) for feeding stations on the two land use types. A linear regression analysis was used to determine a correlation between the average number of foraging bees and the number of bee lines established per feeding station. For this analysis, all feeding stations with 0 foraging bees were

omitted. All analyses were conducted using the statistical software package JMP v 8.0 (SAS Institute 2009).

Results

The average number of bee lines observed per feeding station was not significantly different between livestock farms and game reserves (Table 2-1). The feeding stations on reserves exhibited a skewed distribution toward the highest rating of foraging bees (3) in the field rating and toward the highest two ratings of foraging bees (2, 3) in the photograph rating (Table 2-1). Photograph and field ratings were distributed evenly across all ratings for stations on farms (Table 2-1). The number of foraging honey bees was positively correlated to the number of bee lines established at each feeding station ($\# \text{ foraging bees} = 91 * (\# \text{ bee lines}) + 13$ foraging bees; $\beta = 91$, $R^2=0.33$, $F_{1,33}=16.5$, $P<0.01$) (Figure 2-4).

Discussion

Using the index method I developed, an effect of land use practices on the number of bee lines observed was not detectable. There are three possible reasons for this. First, it is possible that land use simply does not affect Cape honey bee population densities. The reserves used in the study had been reclaimed from farms in the past 15 years and livestock replaced with other large grazing animals. If these animals are in large abundance, they may have similar effects as cattle on farms and there may be no change in resource availability. On the other hand, it is possible that not enough time had elapsed from the farm conversion to allow the land to return to a pre-farming status where there would be a resource abundance that would support a large population. The landscape between the farms and reserves was similar since the reserves were recently reclaimed farms. Open grazing areas and thicket patches on farms are still open

grazing areas and thicket patches on the reserves. Therefore, the population density may remain the same within these patches.

Secondly, it is possible that the index I developed is not representative of actual population densities of Cape honey bees *in vivo*. For example, my index suggests a population density in the Eastern Cape considerably lower than those shown by other authors studying honey bees in Texas (12.5 colonies/km² - Baum et al. 2005), Australia (40-150 colonies/km² - Oldroyd et al. 1997), and the Kalahari (10.6 colonies/km² - Mortiz et al. 2008). There are possible reasons for this. First, if two colonies exist in close proximity to one another, their respective bee lines away from the feeding station may overlap too much to be distinguished separately. When I collected data in Crown River Safari Reserve, one bee line I counted headed in the exact direction of a cliff where I found five bee colonies nesting within ~ 100 m from one another. Second, the feeding stations may sample colonies within a much smaller radius than what I had hypothesized. When using the feeding stations to locate colonies, the colonies were rarely more than 500 m from the stations, possibly suggesting an increased population density. Regardless, the method I developed should be used as a comparative index of colony population density rather than an estimator of an actual colony number per unit area.

Finally, it is possible that land use practices do affect colony population density and that the sample size in this study was too small to represent true population densities accurately. This seems reasonable given the low *P* value (*P*=0.08) for the bee line analysis which was nearly significant at the established α level. Though I did not present the analyses, the average number of bee lines on reserves and farms was

significantly different when the means were not weighted by the number of stations on each site and when the stations were considered independent.

The field and photograph ratings indicated that there were more bees visiting feeding stations on reserves than on farms. Since the number of bees is positively correlated with the number of bee lines, the data suggest that the population density was higher on reserves. Consequently, it is possible and likely that land use practices tested in this study do have an impact on colony density, but one that was undetectable by reading bee lines considering the low sample size.

This increase in population density on reserves, determined from the index and field/photograph ratings, suggests that converting farms to game reserves does benefit Cape honey bees and possibly even the health of the entire ecosystem they support. This benefit may be even greater than what I found considering that the reserves were converted from livestock farms within the preceding 15 years. This could be verified if a density index were determined for land unaltered by humans in the surrounding area to compare those on livestock farms and reserves.

The accuracy of my index should be confirmed by comparing the results from the index (# bee line and field/photograph ratings) to the actual population density of honey bees colonies and to predictions made using the other estimation methods (Baum et al. 2005, Oldroyd et al. 1997, Mortiz et al. 2008). With this information in hand, the index methodology could be modified further to increase its predictive power. For example, I could adjust the distances between feeding stations, both shortening and lengthening that distance. All observed bee lines can be followed to their respective colonies to create a colony density map for an entire area. One could optimize feeding station

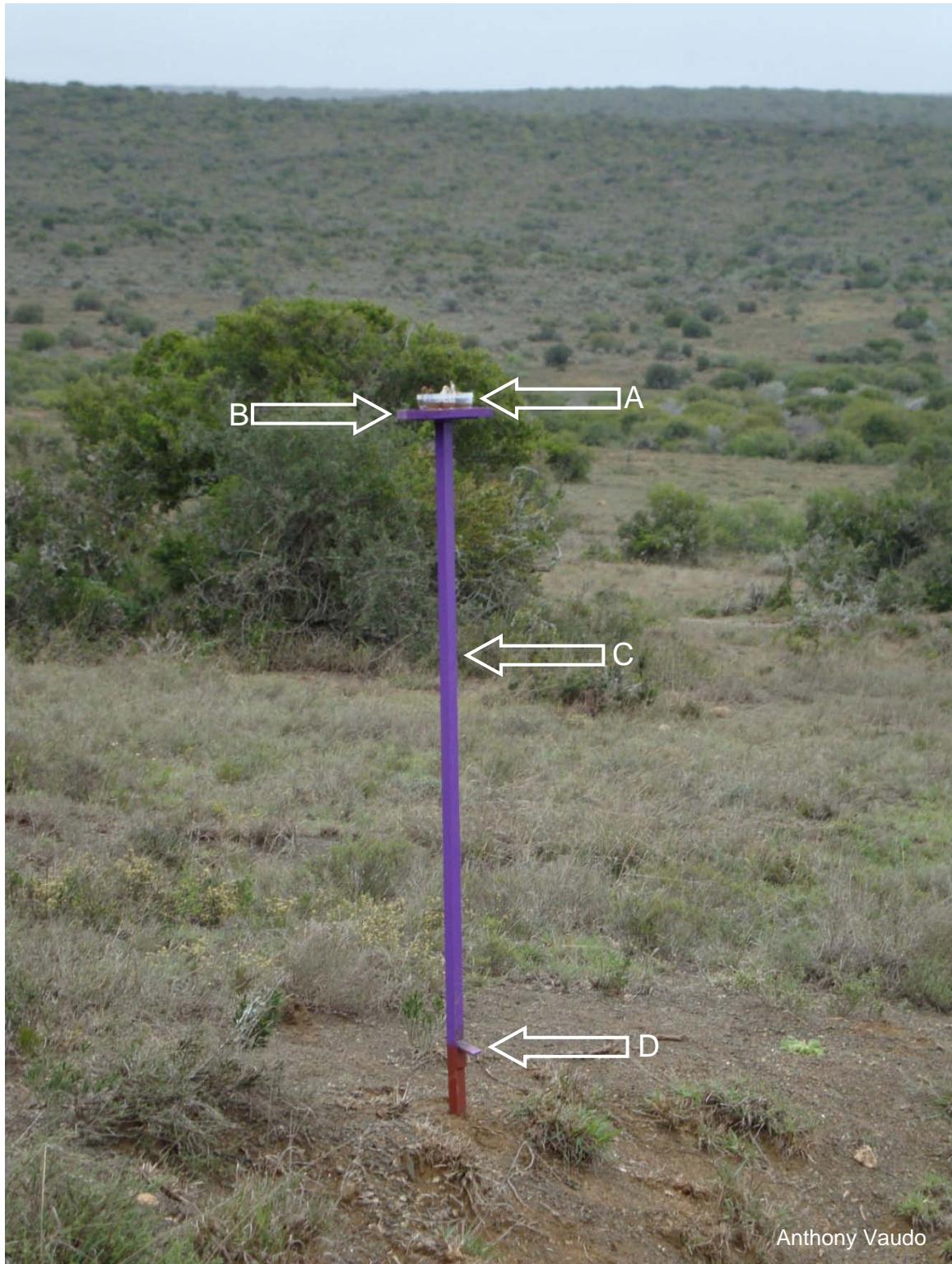
placement to avoid stations locating the same colonies while still sampling most colonies through the study site. Furthermore, the amount of bait provided at each feeding station was limited to the size of the container used. Sometimes, the bait was gone between establishing the stations one day and going to collect data the following day. In the future, more bait needs to be allotted to each station. This may stop the data collector from having to refill the station and wait for returning foragers, thus increasing the accuracy of the data by preventing the possible “loss” of bee lines previously established the day before.

Knowing the population density of honey bee colonies in an area is important. Being able to predict population densities of honey bees accurately would permit one to determine how land use practices, global climate trends, and other large-scale environmental issues affect wild populations of honey bees. For example, Oldroyd et al. (1997) suggested that population densities of honey bees may be reduced in drought conditions. This could be verified if methodology is developed to track fluctuations in population density over time. Then, scientists can use tools such as GIS technology, climate change data, etc. to determine how Cape bee populations are affected. Ultimately, such information could be used to develop conservation practices for wild honey bees, a worthy endeavor considering the plight of honey bees globally.

Table 2-1. Land use effects on Cape honey bee population density index parameters in the Eastern Cape, South Africa.

Parameter	Statistical Test	Reserves	Farms
Average # of bee lines per feeding station	ANOVA (weighted) $F_{1,6}=4.4; P=0.08$	2 ± 0.2 (4)	1.3 ± 0.3 (4)
Field rating	χ^2	0: 2 1: 1 2: 5 3: 13 $\chi^2(3,N=21)=16.9; P<0.01$	0: 3 1: 2 2: 8 3: 6 $\chi^2(3,N=19)=4.8; P=0.19$
Photograph rating	χ^2	0: 2 1: 1 2: 8 3: 10 $\chi^2(3,N=21)=11.2; P=0.01$	0: 3 1: 4 2: 7 3: 5 $\chi^2(3,N=19)=1.8; P=0.61$

Data in row one are mean \pm s.e. (N) number of bee lines. χ^2 data are number of feeding stations assigned to a given category. Field rating categories: 0 (no bees), 1 (few foraging bees), 2 (some foraging bees), and 3 (large number of foraging bees). Photograph rating categories: 0 (no bees), 1 (1-50 bees), and 2 (51-200 bees), and 3 (>200 bees).



Anthony Vaudo

Figure 2-1. A honey bee feeding station. Arrow A) the container partially filled with bait. Arrow B) the removable feeding plate. Arrow C) the main iron rod driven into the ground. Arrow D) the crosspiece used to hammer the station into the ground.



Chiithuli Makota

Figure 2-2. Identifying bee lines. It is best to have a level view of the feeding station or view it from below when identifying distinct bee lines. This station had three bee lines, one heading to the left of the photograph, one heading to the right, and one heading behind the photographer. Notice how the bees are “lost” when flying below the horizon.



Figure 2-3. Population density index field and photograph ratings. Figure A = Rating 0: 0 foraging bees. Figure B = Rating 1: 1-50 foraging bees. Figure C = Rating 2: 51-200 bees. Figure D = Rating 3: ≥ 200 foraging bees. Figures B, C, and D represent the approximate maximum amount of foraging bees for their respective ratings.

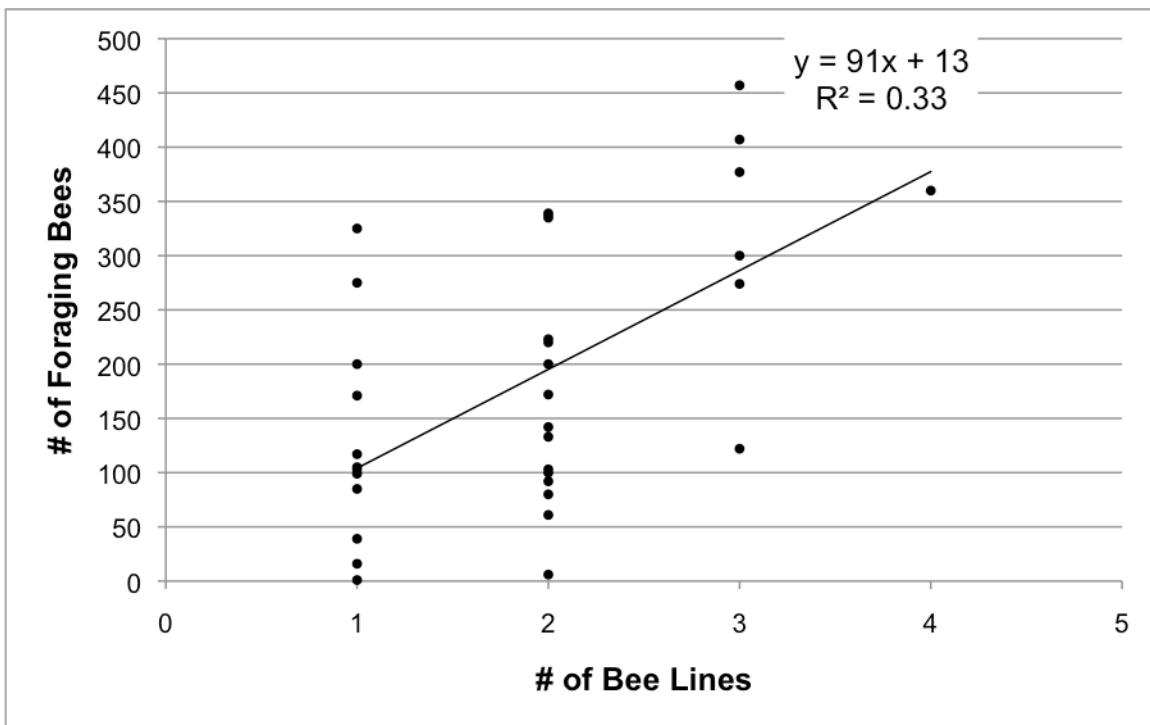


Figure 2-4. Number of foraging honey bees per bee line ($F_{1,33}=16.5$, $P<0.01$).

CHAPTER 3

CAPE HONEY BEE (*Apis mellifera capensis* ESCHOLTZ) NEST SITE SELECTION ON RESERVES AND LIVESTOCK FARMS IN THE EASTERN CAPE, SOUTH AFRICA

Introduction

Nest site selection is crucial to honey bee survival. Finding and inhabiting a suitable nest site completes the reproductive process, known as swarming, of a honey bee colony (Winston 1987). Proper nest selection is important for a number of reasons. Potential threats such as predation, parasitism, and harsh weather can disrupt, weaken, or even kill the colony (Morse and Flottum 1997, Blacshon et al. 1999). A good nest site should be protected and easily defended. Furthermore, a nest should be close to essential resources (Hansell 1993, Steinhause et al. 2005). Though bees fly from the nest to obtain food, water, and propolis for the colony, the closer these resources are to the colony, the more efficient the foragers are when foraging, thus potentially producing a stronger colony.

Honey bees (*Apis mellifera*) nest in a variety of habitats often nest in cavities, such as those in cliffs (Figure 3-1), underground, (Figure 3-2), or in trees (Figure 3-3) (Crane 1999). Honey bees also nest in many manmade structures, especially roofs and walls of buildings (Figure 3-4). Some Cape honey bee colonies build exposed nests, but this occurs less often (Figure 4-2).

Nest site selection and availability can be affected by a number of factors, possibly even including land use practices (Dietemann et al. 2009). For example, production agriculture generally involves transforming land through the removal of trees and large bushes (Whitmore and Sayer 1992). This results in fragmented natural areas (Mangnall and Crowe 2003), which may reduce the number of nest sites available to Cape bees since honey bees readily nest in tree cavities or ground cavities underneath trees

(Wilson 1971, Seeley and Morse 1976, Tautz 2008). Clearing land for agricultural use also may destroy potential ground cavity nesting sites.

In sharp contrast, game reserves may contain more nesting sites for bees since minimal-impact management schemes typically are practiced on reserves. Reduced-impact practices that should favor the preservation of bee nesting sites on reserves include maintaining sustainable stocking densities of large animals, reducing and preventing erosion, minimizing land clearing activities such as bulldozing trees (Langholz and Kerley 2006), and protecting wild colonies from honey hunters. Therefore, potential honey bee nesting sites on reserves may be more numerous and varied than on farms. If this is the case, bees nesting in natural areas should have more places available to them to establish nests.

The overall purpose of the current project was to determine if honey bee nest site selection differed between reserves and farms, which, if it occurs, may indicate a difference in potential nest site availability. Bees presented with many potential nesting sites are able to choose optimum nest sites more frequently (Seeley and Morse 1978). To address this purpose, I measured various parameters associated with nest sites, including height of the nest from the ground, where the nest was located (building, cliff, ground, tree, etc.), what cardinal direction the nest entrance faced, and the volume of the nest cavity, all standard nest site selection parameters (Seeley and Morse 1978).

In addition to colonies located in reserves and farms, I collected nest site selection data from Grahamstown, South Africa, a small urban community in the Eastern Cape. Though the data were collected only from one urban area, it did provide insight to the habits of Cape bees when nesting in urban settings. Overall, the data generated by this

chapter addressed the overall purpose of the project which was to determine if honey bee nest site selection is affected by land use.

Methods and Materials

Locating Honey Bee Colonies

Wild honey bee colonies were located in the 8 study areas (4 livestock farms, 4 game reserves) listed in Table 1-1 as well as in a single urban location (Grahamstown, South Africa). All colonies were located between September 2009 and March 2010. Some colonies were found by interviewing local landowners and employees. Most of the colonies were found using a bee-lining method modified from the one described originally in *The Bee Hunter* (Edgell 1949) and subsequently by others (Seeley and Morse 1976, Seeley et al. 1982, Seeley 1983, Visscher and Seeley 1989; Seeley, personal communication). Colonies in Grahamstown were located by searching and through interviews with homeowners and others who knew of existing colonies.

A bee line is defined as the direct flight path taken by honey bees to and from a colony from a particular resource, be it honey, water, or propolis. To establish bee lines to wild colonies, I baited feeding stations with a combination of honey, sugar, and water. A description of the feeding stations is provided in the Chapter 2 methodology.

To reduce bias, I placed the feeding stations throughout each study area so that some were close to cliffs, valleys, trees and open areas. Once the feeding stations were deployed, I established bee lines at each station and then followed the bee line away from the station to the wild nest. I was able to find ~90% of the colonies for whose bee lines I followed. At times, the bee lines would occur over long distances and through areas of dense thicket, thus making them difficult to follow. During these instances, I would reestablish a bee line with a secondary mobile feeding station (a feeding

container placed on top of a bucket), placed close to where the original bee line was lost. I repeated this procedure until bee-lining was no longer necessary and the colony was located. I also found colonies by following bees to their nest from a water source (Crane 1999). Colonies located this way tended to be close (within ~250 m) so no feeding stations were necessary. When narrowing in on a colony's location, I would inspect visually for bees entering and exiting from the ground, above the bushes, or from a cliff or tree or listen for bee activity. Using this method, I located 94 total colonies, 42 in reserves, 32 on farms, and 20 in Grahamstown.

Nest Site Data Collection

Once a nest was found, I recorded the following data:

- 1) GPS coordinates (to be able to relocate the colony for extraction and future GIS research) – recorded using a Garmin GPSmap 60CSx (Garmin International Inc., Olathe, KS) set to WGS 84 map datum,
- 2) nest location (building/man-made dwelling, cliff, ground, or tree),
- 3) surrounding habitat (reserve, farm, or urban),
- 4) Cardinal direction the entrance faced – determined for true north
- 5) height of the nest entrance from the ground (ground colonies were assigned a height of 0 m),
- 6) nest cavity volume – determined by extracting the nest of 19 colonies on farms, 18 colonies on reserves, and 4 colonies in Grahamstown. I estimated cavity volume by observing the general shape of each nest cavity, measuring various dimensions to the nearest centimeter, and using that information to calculate volume. For example, if the lower half of the cavity was spherical and the upper half cube-shaped, I took appropriate measurements necessary to determine the volume for both shapes and added them to derive the total volume of the cavity (in L). Only the volume occupied by the comb was calculated for colonies that were located in open spaces such as in an attic or roof.

Statistical Analyses

Nest entrance height (excluding colonies found in the ground) and cavity volume were compared between land use types (reserve, farm, and urban) using a one-way

ANOVA with the first analysis excluding colonies found in urban settings and the second analysis including colonies found in urban settings. In a second analysis, entrance height was assigned one of three categories: (1) “0” for entrances on or below the ground, (2) “1” for entrances >0 m but < 3 m and (3) “2” for entrances ≥ 3 m. The height categories then were compared by land use type (reserve, farm, and urban) using a χ^2 test. Nest locations (building, cliff, ground, and tree) were compared by land use type using a χ^2 test.

The average nest cavity volume was compared between nests in each land use type using a one-way ANOVA. Nest cavity volumes were calculated for 40 extracted colonies (18 in reserves, 18 on farms, and 4 in Grahamstown) and compared between each land use type using a one-way ANOVA with the first analysis excluding colonies found in urban settings and the second analysis including colonies found in urban settings.

Colony entrance directions were mapped on a compass and examined for trends (Figure 3-5). Nest entrance orientation was analyzed using χ^2 tests on 5 separate nest entrance comparisons, all based on “true” north (rather than magnetic north):

- 1) north vs. south (north = entrances facing $< 90^\circ$ and $> 270^\circ$, south = entrances facing $>90^\circ$ and $<270^\circ$),
- 2) east vs. west (east = entrances facing $>0^\circ$ and $<180^\circ$, west = entrances facing $>180^\circ$ and $<360^\circ$),
- 3) north vs. east vs. south vs. west (north = entrances facing $<45^\circ$ and $>315^\circ$, east = entrances facing $>45^\circ$ and $<135^\circ$, south = entrances facing $>135^\circ$ and $<225^\circ$, west = entrances facing $>225^\circ$ and $<315^\circ$),
- 4) northwest vs. southeast (northwest = entrances facing $<45^\circ$ and $>225^\circ$, southeast = entrances facing $>45^\circ$ and $<225^\circ$),
- 5) northeast vs. southeast vs. southwest vs. northwest (northeast = entrances facing $>0^\circ$ and $<90^\circ$, southeast = entrances facing $>90^\circ$ and $<180^\circ$, southwest =

entrances facing $>180^\circ$ and $<270^\circ$, northwest = entrances facing $>270^\circ$ and $<360^\circ$),

Colonies whose entrances were located on a line dividing two directions were split between the two directions if an even number of colonies fell on the line or one colony was omitted from the analysis and the remaining colonies split between the two directions if an odd number of colonies fell on the line. Using a χ^2 test, I determined if colony entrance direction was affected by land use type. All analyses were conducted using the statistical software package JMP v 8.0 (SAS Institute 2009).

Results

The average nest entrance height was significantly higher for Cape bee colonies nesting in reserves than for colonies nesting on farms (Table 3-1). When the colonies sampled in Grahamstown were factored into the analysis ($F_{2,85} = 12$; $P < 0.01$), bees in the urban area (5.8 ± 1 m high nest entrance, 19 colonies) nested higher above the ground more often than bees nesting on reserves or farms. When analyzed by height category (≤ 0 m, $0.1 - 3$ m, >3 m), colonies favored lower nesting sites when nesting on farms. Colonies nesting on reserves were distributed evenly amongst height categories (Table 3-1). In Grahamstown, colonies significantly favored ($\chi^2(2, N=21) = 10.6$; $P < 0.01$) higher nesting sites (# colonies nesting: ≤ 0 m = 3; $0.1 - 2.99$ m = 4; ≥ 3 m = 14). Colonies nesting on livestock farms favored ground cavities while colonies nesting on reserves showed no preference for nest location (Table 3-1). Colonies nesting in Grahamstown favored cavities in buildings (14 colonies) and trees (7 colonies) while none were observed nesting in the ground or cliffs.

The average cavity occupied by Cape bees was significantly larger on farms than on reserves (Table 3-1). When including colonies nesting in Grahamstown, urban (75.4

± 9.1 L cavity, 4 colonies) and farm-nesting colonies nested in larger cavities than did those nesting on the reserves ($F_{2,37}=8.15$; $P<0.01$).

Nest entrance directions seemed variably distributed for colonies nesting on reserves and farms while colonies nesting in Grahamstown favored cavities with easterly and southeasterly entrances (Table 3-2). When pooling entrance direction data for all land use types, bees nested more often in cavities having easterly and southeasterly entrances (Table 3-3). Pooled means of nest height, cavity volume, and entrance direction and the number of colonies nesting in a particular location on reserves and farms (including and excluding colonies nesting in manmade structures) are reported in Table 3-4.

Discussion

In this study, the height of bee nests may have been tied to nest site availability on livestock farms and reserves rather than bees exhibiting a true preference for cavities located at certain heights. Nesting in the ground and in trees is a common trait of *A.m. scutellata* (Schneider and Blyther 1988, McNally and Scheider 1996) and other African races of bees (Hepburn and Radloff 1998). Based on casual observation, the surveyed farms in this study tended to have less thick vegetation and old growth than did the surveyed protected areas. Consequently, there may have been more potential nest sites higher above the ground in the protected areas than on farms. In that case, higher nest site availability would be reflected in the presence of older and taller trees on reserves. In contrast, Seeley and Morse (1978) found under controlled conditions that honey bees nesting around Ithaca, NY chose to nest in cavities 5m above the ground more than they chose to nest in cavities 1 m above the ground. Despite this, the majority of nest entrances in wild bee colonies were near the ground, although variation

was high (Seeley and Morse 1976). Seeley and Morse (1976) suggested that this might be due to the observation that tree cavities or holes to access these cavities generally are closer to the ground while the cavities themselves extend upward. Regardless, a consistent bee preference for nest cavities at a certain heights across all study sites was not observed.

A similar trend for colonies choosing nest sites above the ground was observed for colonies nesting in Grahamstown. As before, this trend may be a reflection of nest site availability in the urban setting. Manmade structures often contain many cavities (chimney, walls, attics, etc.) that are favorable nesting sites for bees. Given the wide availability of nesting sites in an urban setting, many colonies in Grahamstown nested in roofs. Furthermore, urban settings in South Africa, such as Grahamstown, contain many large (often nonnative) trees that provide more nesting sites above the ground. Therefore, bees tended to have higher colonies when such nesting sites were available (urban setting), nest lower to the ground when high sites were unavailable (farm), nest randomly at all heights when high nesting sites were present but not abundant (reserves). To address nest height preference experimentally, one would need to provide swarming bees cavities at various levels while documenting which cavity height the bees prefer (Seeley and Morse 1978).

In the Northern hemisphere, there is a higher probability that honey bees will choose a nest site with an entrance that is located on the bottom third of the nest and facing southward (Seeley and Morse 1976, 1978). Seeley and Morse (1976, 1978) commented that beekeepers prefer to face their colonies southward. They do this because honey bees in the northern hemisphere often choose nest sites with entrances

facing south, presumably because the entrances will be exposed constantly to the sun for warmth and the bees will have a regular view of the sun which would help them find their foraging direction as they leave the nest. Nest entrances also may face east more often so that they can receive sun during early morning hours (Cambray, personal communication). Considering this information, I had predicted that Cape honey bees would prefer to nest in cavities whose entrances more often faced north (since South Africa is in the southern hemisphere) and/or east.

Though colony entrances were found facing many directions, there was a trend for colonies in this study to nest in cavities having an easterly and southerly orientation, especially in Grahamstown and when all of the data were pooled. My results are consistent with data on *A.m. scutellata* which generally nested in cavities having southerly facing nest entrances in Botswana (Schneider and Blyther 1988, McNally and Schneider 1996). To address bee preference for nesting in cavities experimentally, multiple potential nest cavities with entrances facing one of many directions could be made available to swarming colonies with the dependent variable being the frequency in which colonies inhabit boxes facing a particular direction.

Seeley and Morse (1976) reported that the average volume of wild honey bee colony nest cavities around Ithaca, New York was normally distributed around 45L. In choice tests, honey bees in New York, USA preferred cavities that were > 10 L and chose 40 L cavities over 100 L ones (Seeley 1977). This preferred volume for a nesting cavity can vary based on the availability of nest sites, which may be more or less than 45 L within a given area. In the present study, cavities not associated with manmade structures in which Cape bees nested averaged ~39 L in volume. When all cavities were

evaluated, the average cavity volume was ~44L. This is similar to the size of commercial hive bodies used in the United States which generally are ~40 L in volume because of observations of L.L. Langstroth who designed the original nest (Crane 1999). This is notable considering that nest cavity volumes have not been documented for Cape honey bees with the expectation that Cape honey bees, and Sub-Saharan honey bees in general, which are smaller than European races of honey bees, would make smaller nests and nest in smaller-sized cavities. However, the cavity volumes of this research were larger than those reported by Schneider and Blyther (1988) (~17L) and McNally and Schneider (1996) (~33L) for *Apis mellifera scutellata* colonies found in Botswana. Cavity volume may be related to population size, where a larger cavity would make it possible for bees to have a larger population. However, work by Seeley and Morse (1976) did not support this assertion. Regardless, Cape honey bees nest in cavities that tend to be larger than those in which other African bee races nest (Schneider and Blyther 1988, McNally and Schneider 1996). This topic is revisited in Chapter 4.

Though not measured directly in my project, I observed that many colonies nesting in the ground had entrances covered or surrounded by plants, which were often thorny (Figure 3-6). Many of the plants had to be removed to access the entrance and remove the nest. It seems logical that a protected (in this case by thorny plants) and/or camouflaged nest entrance would increase the safety of the nest site and reduce its accessibility to predators. In the future, researchers could investigate this topic, thus determining the usefulness of entrance composition to colony nesting success. Seeley and Morse (1978) noted that scout bees searching for new nest sites fly and land on the

vegetation surrounding the nest site, possibly indicating that scout bees assess cavity cover.

Though nest entrances in cliff and tree colonies typically do not have entrance obstructions, most colonies nesting in these locations reduced their nest entrance to holes ~2-3 cm in diameter using propolis (Figure 3-7) consistent with Ellis and Hepburn (2003). This is especially true for colonies nesting in cliffs where propolis “walls” were constructed to enclose the comb of the colony (Figure 3-7, Figure 4-2). Furthermore, the inside of most cavities in which the bees nested was sealed with propolis, which may have served to prevent entry and invasion by termites, ants, and possibly a number of other small animals. For example, I found dead beetles encapsulated in propolis at the bottom of some nests. Colonies nesting in the ground tended to inhabit cavities under abandoned termite mounds (Figure 3-8), cavities created by aardvarks or other burrowing animals (Figure 3-2), or were remnants from partially uprooted trees (Figure 3-2). Propolis use is clearly important for Cape bees.

In conclusion, future research on Cape honey bee nest site selection could be viewed at a larger scale to determine topography, canopy cover (Baum et al. 2005), vegetation biome and structure, proximity to water, etc. effects on nest site selection. The landscape of the farms and reserves studied was somewhat similar because of the recent conversion to reserves from farms. Useful data should be obtained from unaltered landscapes as a basis for comparison. Nest site selection parameters may be independent of “artificial” land use (livestock farming, private reserves), but more dependent on the “actual” landscape. GIS analysis would help reveal trends not observed readily.

Table 3-1. Land use effects on Cape honey bee nest site selection in the Eastern Cape, South Africa.

Colony Parameter	Statistical Test	Reserves	Farms
Height from ground (m) (all colonies)	ANOVA = $F_{1,67}=4.1; P<0.05$	2.3 ± 0.7 (38)a	0.75 ± 0.32 (31)b
Height category	χ^2	$\leq 0\text{m}$: 18 $0.1\text{-}3\text{m}$: 9 $\geq 3\text{m}$: 14 $\chi^2(2,N=41)=3; P=0.2$	$\leq 0\text{m}$: 19 $0.1\text{-}3\text{m}$: 10 $\geq 3\text{m}$: 3 $\chi^2(2,N=32)=12.1; P<0.01$
Nest location	χ^2	Building: 6 Cliff: 13 Ground: 16 Tree: 6 $\chi^2(3,N=41)=7.5; P=0.06$	Building: 5 Cliff: 5 Ground: 17 Tree: 5 $\chi^2(3,N=32)=13.5; P<0.01$
Cavity volume (L)	ANOVA = $F_{1,34}=6; P=0.02$	32.1 ± 4.3 (18)b	48.8 ± 5.3 (19)a

Data are mean \pm s.e.(N) for ANOVA analyses and # colonies nesting in a given height category or nest location for χ^2 analyses. For χ^2 tests, P values ≤ 0.05 indicate that the data within the cell are not distributed randomly.

Table 3-2. Direction of nest entrances for Cape honey bee colonies nesting on reserves, farms, and an urban area in the Eastern Cape, South Africa.

Direction	Reserves	Farms	Urban
North vs. South	North: 18 South: 23 $\chi^2(1, N=41)=0.6; P=0.43$	North: 14 South: 16 $\chi^2(1, N=30)=0.1; P=0.72$	North: 5 South: 14 $\chi^2(1, N=18)=5.6; P=0.02$
East vs. West (True)	East: 23 West: 17 $\chi^2(1, N=40)=0.9; P=0.34$	East: 17 West: 13 $\chi^2(1, N=30)=0.5; P=0.47$	East: 14 West: 5 $\chi^2(1, N=19)=4.3; P=0.04$
North vs. East vs. South vs. West (True)	North: 9 East: 13 South: 10 West: 9 $\chi^2(3, N=41)=1; P=0.79$	North: 6 East: 8 South: 9 West: 7 $\chi^2(3, N=30)=0.7; P=0.88$	North: 3 East: 5 South: 8 West: 3 $\chi^2(3, N=19)=3.5; P=0.32$
Northwest vs. Southeast (True)	Northwest: 18 Southeast: 23 $\chi^2(1, N=41)=0.6; P=0.43$	Northwest: 13 Southeast: 18 $\chi^2(1, N=31)=0.8; P=0.37$	Northwest: 6 Southeast: 13 $\chi^2(1, N=19)=2.6; P=0.11$
Northeast vs. Southeast vs. Southwest vs. Northwest (True)	Northeast: 9 Southeast: 14 Southwest: 9 Northwest: 8 $\chi^2(3, N=40)=2.2; P=0.53$	Northeast: 6 Southeast: 10 Southwest: 6 Northwest: 8 $\chi^2(3, N=30)=1.5; P=0.69$	Northeast: 3 Southeast: 10 Southwest: 4 Northwest: 1 $\chi^2(3, N=18)=1.5; P=0.02$

Data are the number of colonies with entrances facing a given direction. Analyses are presented for entrance directions based on a true, rather than magnetic, compass direction. For χ^2 tests, P values ≤ 0.05 indicate that the data within the cell are not distributed randomly. Colonies whose entrances were located on a line dividing two directions were split between the two directions if an even number of colonies fell on the line or one colony was omitted from the analysis and the remaining colonies split between the two directions if an odd number of colonies fell on the line.

Table 3-3. Direction of nest entrances for all Cape honey bee colonies found during the study.

Direction	# of Colonies	Statistical Test
North vs. South	North: 37 South: 54	$\chi^2(1,N=91)=3.2; P=0.07$
East vs. West	East: 54 West: 37	$\chi^2(1,N=91)=3.2; P=0.07$
North vs. East vs. South vs. West	North: 18 East: 26 South: 28 West: 19	$\chi^2(3,N=91)=3.3; P=0.35$
Northwest vs. Southeast	NW: 37 SE: 54	$\chi^2(1,N=91)=3.2; P=0.07$
Northeast vs. Southeast vs. Southwest vs. Northwest	NE: 19 SE: 34 SW: 19 NW: 18	$\chi^2(3,N=90)=7.9; P=0.05$

Data are the number of colonies with entrances facing a given direction. Analyses are presented for entrance directions considering true (rather than magnetic) compass directions. For χ^2 tests, P values ≤ 0.05 indicate that the data within the cell are not distributed randomly. Colonies whose entrances were located on a line dividing two directions were split between the two directions if an even number of colonies fell on the line or one colony was omitted from the analysis and the remaining colonies split between the two directions if an odd number of colonies fell on the line.

Table 3-4. Summary nest site parameter data for Cape honey bee colonies nesting on game reserves and farms in the Eastern Cape, South Africa.

Parameter	Colonies not Nesting in Manmade Structures	All Colonies
Height (m) of nests above ground level (ground colonies excluded)	3.7 ± 1 (26)	4.6 ± 0.6 (48)
Nest cavity volume (L)	38.6 ± 3.5 (35)	44.1 ± 3.8 (41)
Entrance direction ($^{\circ}$) based on true north	173.5 ± 12.4 (62) Median = 157.5	164.2 ± 9.9 (91) Median = 150
Nest location	Cliff: 18 Ground: 33 Tree: 11	Building: 25 Cliff: 28 Ground: 33 Tree: 18

Data are mean \pm s.e.(N) for height, volume, and entrance directions. Medians are included for entrance directions. The number of colonies found in each nest location are included. The first data column excludes colonies nesting in manmade structures in reserves and farms. The second column includes all colonies measured including manmade structures on reserves, farms, and in Grahamstown.



Figure 3-1. Cape honey bee colonies nesting in cliffs. Figure A shows a colony nesting in a cavity having vertical entrance while Figure B shows the entrance of a second nest that extends to a deep rock cavity.

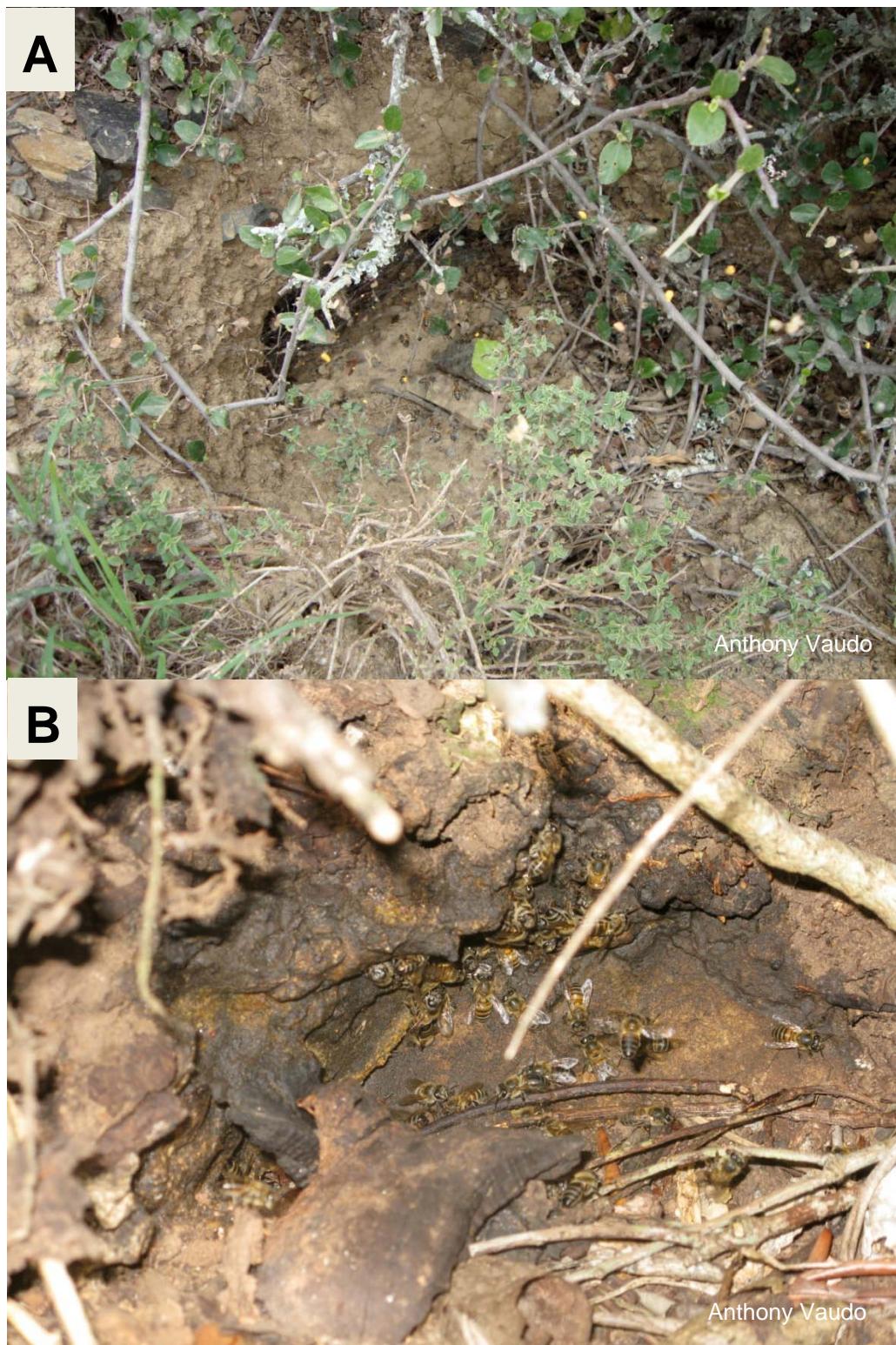


Figure 3-2. Cape honey bee colonies nesting in the ground. Figure A shows a colony nesting in what may have been an abandoned aardvark burrow while Figure B shows a colony nesting in a cavity created by a partially uprooted tree.



Figure 3-3. Cape honey bee colonies nesting in trees. Figure A shows the colony entrance in a broken branch. Figure B shows two colony entrances leading into the hollow trunk of a dead tree.

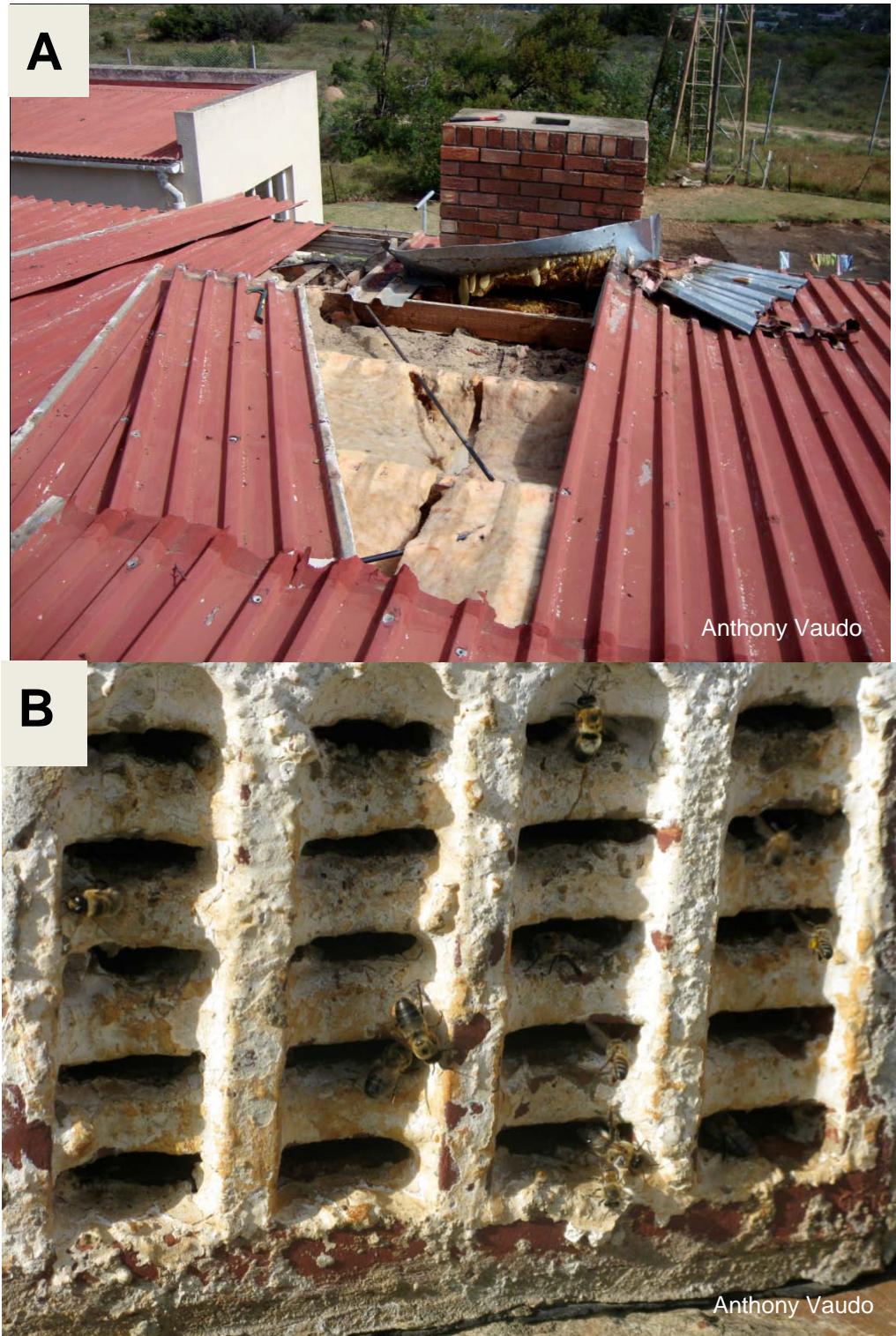


Figure 3-4. Cape honey bee colonies nesting in man-made structures. Figure A shows the roof panel removed to expose the colony nesting between the chimney and roof beam. Figure B shows bees nesting in a wall vent leading underneath the floorboard of the building.

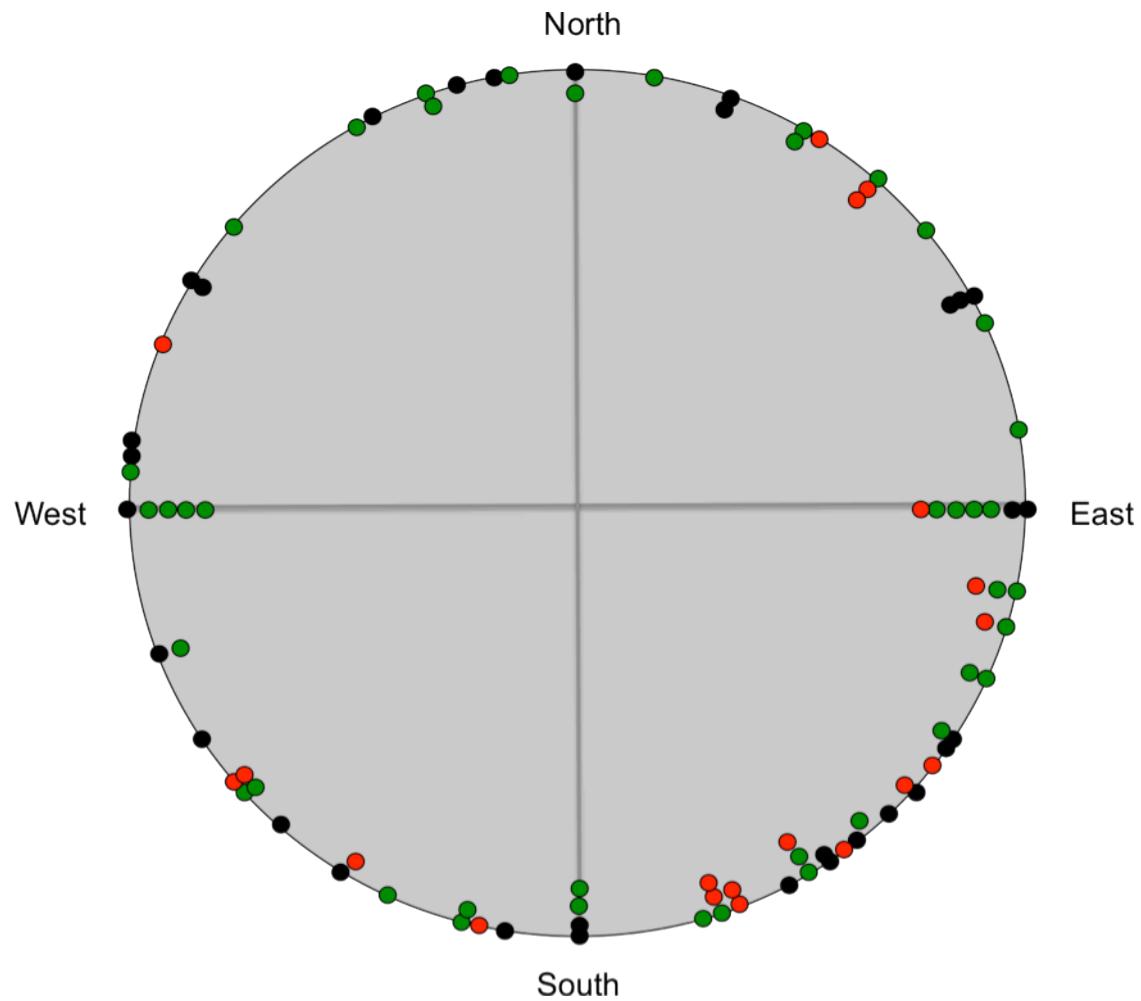


Figure 3-5. The directions of colony entrances for Cape honey bees nesting in the Eastern Cape, South Africa. Green dots represent colonies nesting on reserves. Black dots represent colonies nesting on farms. Red dots represent colonies nesting in Grahamstown, South Africa.

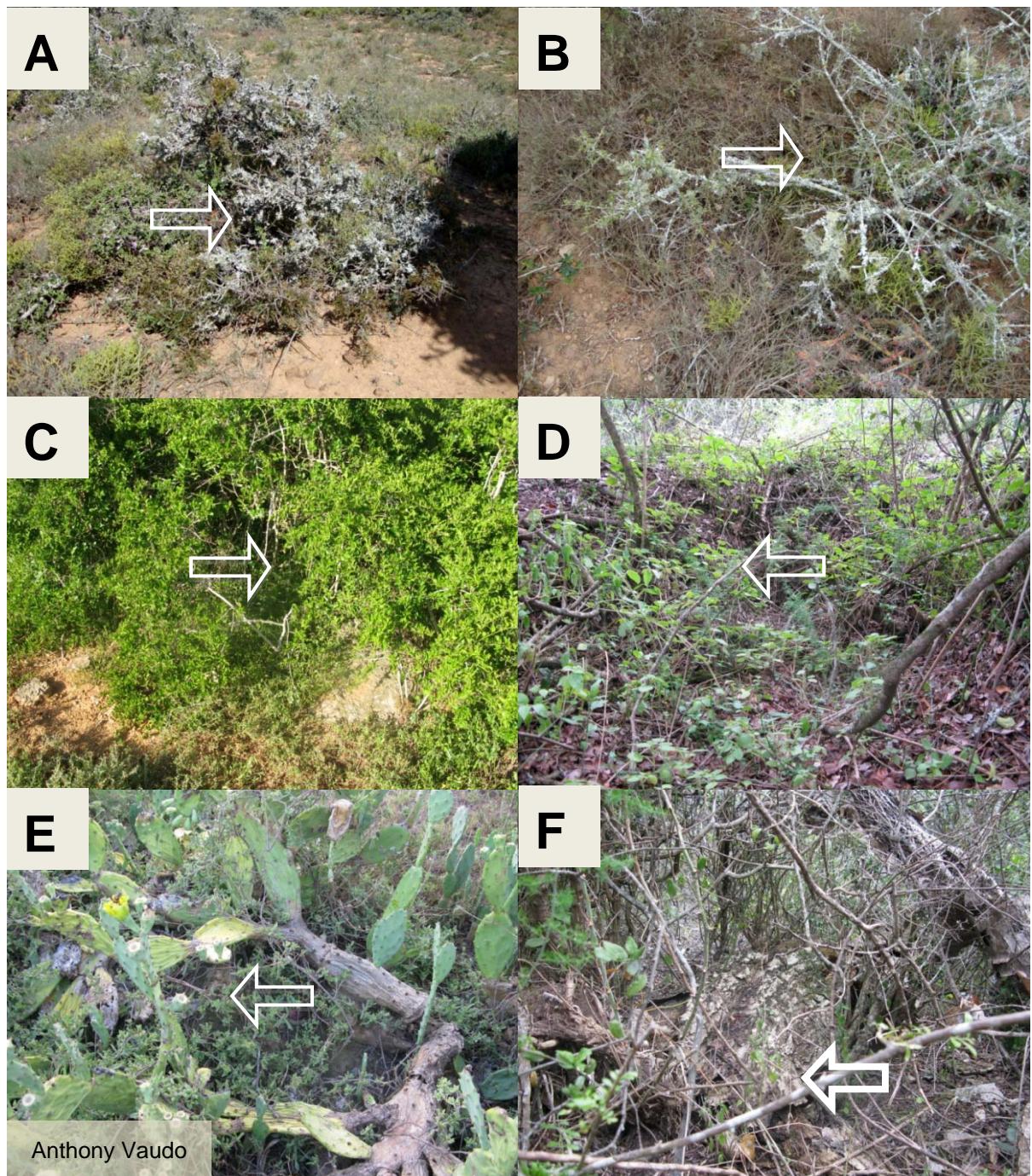


Figure 3-6. Examples of ground nesting Cape honey bee colonies whose entrances are well covered and not visible from a distance. White arrows indicate the approximate site of the nest entrances.

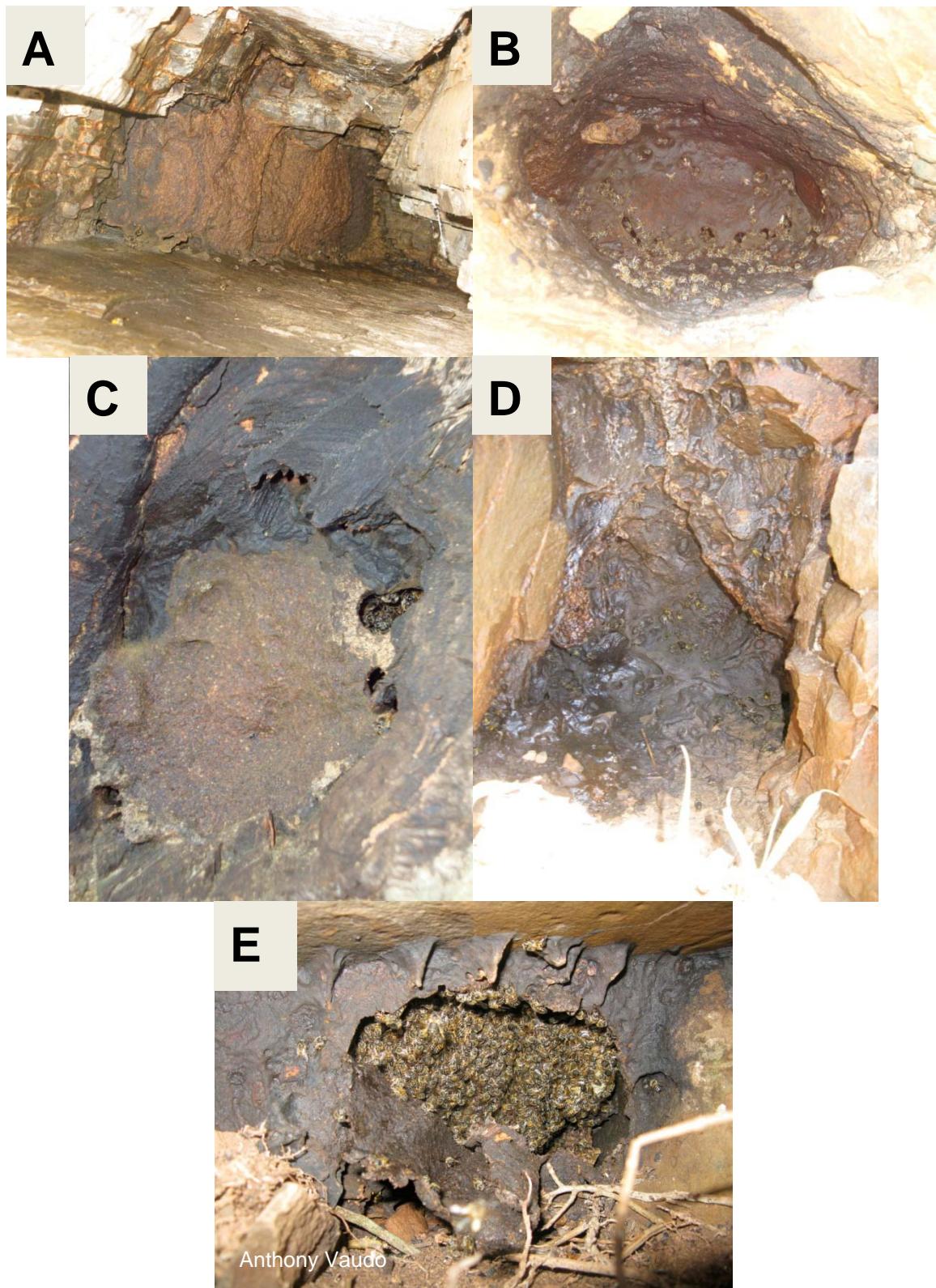


Figure 3-7. Examples of Cape honey bee colony nest entrances reduced by the bees' addition of propolis. Figure E shows the sheet of propolis broken and peeled away to reveal the colony behind.

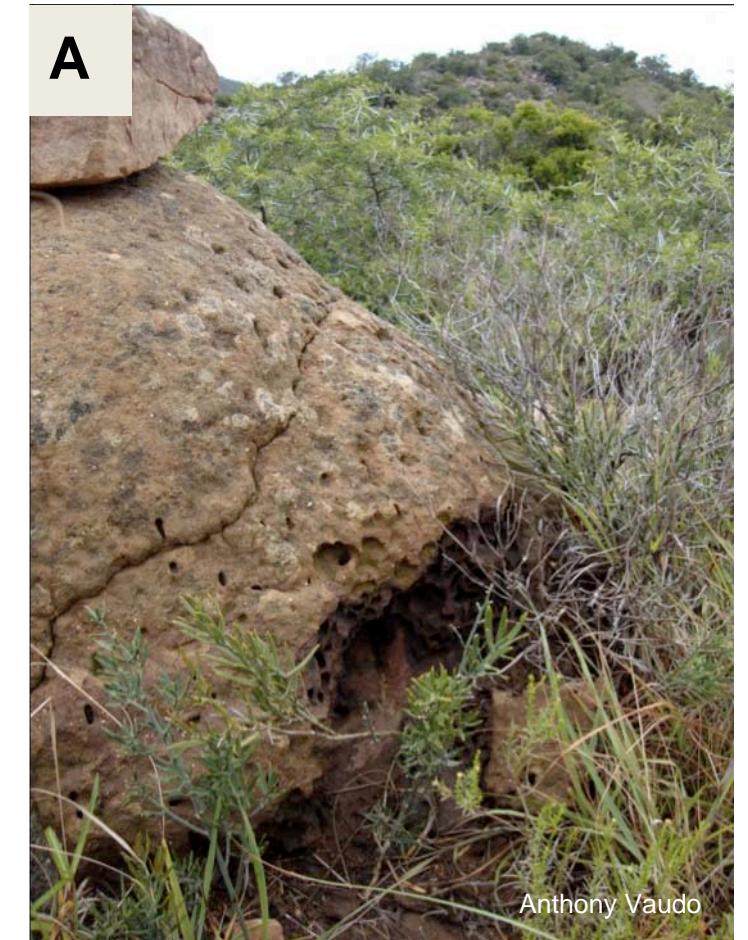


Figure 3-8. Examples of Cape honey bee colonies nesting in abandoned termite mounds. Both colonies hung their comb from a sheet of propolis built on the inside of the old mounds.

CHAPTER 4
LAND USE EFFECTS ON CAPE HONEY BEE (*Apis mellifera capensis* ESCHOLTZ)
COLONY STRENGTH PARAMETERS

Introduction

Converting land to agricultural use can cause the destruction of habitat and natural resources. Agriculture can affect population structures, wildlife diversity, plant communities, abiotic material, and encourage the spread of disease and use of toxic substances (e.g. pesticides)(Matson et al. 1997, Williams et al. 2002). The possibility of species extinction and climate change is magnified through deforestation which often accompanies agriculture (Whitmore and Sayer 1992). In the Eastern Cape, South Africa specifically, livestock farming can affect wildlife populations and plant structure and diversity negatively for small animals such as lizards and arthropods (Kerely et al. 1995, Fabricius and Burger 1996a, 1996b, Fabricius et al. 1996a, 1996b, Mills et al. 2005, Lechmere-Oertel et al. 2005), but its effects on honey bee colonies in the Eastern Cape is unknown.

If resources are limited and bee colonies on livestock farms are affected negatively, their poor health may be apparent in their stored resources (honey and pollen) or lack thereof. Lee and Winston (1985) found a positive correlation between adult bee population size and worker weight. They stated that lighter worker weight may be due to poor nutrition because of the lack of workers available for foraging and brood rearing. Also, adverse environmental conditions can lead to lighter brood weight (Blaschon et al. 1999) and therefore lighter adults. Brood patterns of honey bees are affected by inbreeding, which would occur in instances of low population densities (Chapter 2) (Mattila and Seeley 2007). The number of bees per colony may indicate the relative success of that particular colony. Quantifying the amount of brood in a colony

can indicate the colony's health and resource dependent productivity (Brodshneider and Crailsheim 2010) and presence of diseases (Aronstein and Murray 2010, Czekonska 2000, Forsgren 2010). When an abundance of honey, pollen, and brood are in a colony, more comb will be built to compensate for the influx of resources and brood (Pratt 1999).

In this project, I investigated the effects of land use practices (livestock farming and game reserves) on Cape honey bee colony strength parameters as discussed above, hypothesizing that livestock farming would affect colony health negatively while game reserves would optimize colony strength parameters. I predicted this because livestock farming may reduce the availability of resources in the environment, especially if bee-important plant communities have been removed or damaged by grazing. If this were the case, colony food stores (honey and pollen), adult bee population, and total brood may be affected. To test my hypothesis, I located wild colonies of Cape honey bees on livestock farms and game reserves in the Eastern Cape, South Africa and measured various colony strength parameters to determine how land use practices affect colony health.

The Eastern Cape provides one the opportunity to isolate and record land use effects on honey bee populations. First, livestock farming (particularly cattle, sheep, and goats) is common in the Eastern Cape. People in the area have been livestock farming since the 1700s, significantly changing the landscape from that which was originally settled (Beinart 2003). Second, many livestock farmers in the Eastern Cape are converting their farms to game reserves as tourism increases in the area and reserves become more profitable (Langholz and Kerley 2006). This gives one the opportunity to

investigate how conservation practices (those used on game reserves) affect Cape honey bee populations, especially since reserves and farms can occur immediately next to one another thus providing a before/after picture of conservation effects on honey bee health.

Methods and Materials

To address my hypothesis, I located wild colonies of Cape honey bees (procedure described in Chapter 3) on 4 farms and 4 game reserves in the Eastern Cape, South Africa (Table 1-1). I determined the following parameters for each experimental colony: number of bees, weight per bee, total comb area, cm² honey, cm² brood, cm² pollen, cm² filled comb, cm² empty comb, brood pattern, the number of bees per nest volume, and proportion of comb used for brood, honey, and pollen.

Colony Dissection

Thirty-three colonies (17 from reserves and 16 from farms) were extracted from the cavity in which they nested and dissected to conduct colony strength readings. These colonies were located using the methods described in Chapter 3. Though more than 33 colonies were found, up to five colonies from each study site were selected randomly for extraction. If the colonies were difficult to access, another colony was selected in its place. For instance, some colonies in cliffs were either too difficult to access or too deep into a cavity to remove. All colonies were extracted between 7 May 2010 and 7 June 2010. I did this in an effort to ensure that colony life cycles were similar for all colonies at the time of removal. This allowed me to control for seasonal differences that would occur in colony brood rearing, honey production and storage, wax production, and pollen storage and to precede the swarming season between August and December (Hepburn and Radloff 1998).

The materials used for each removal differed depending on the need and location of each colony. Before all removals, smoke was pumped into the colony entrance.

Removal of ground-nesting colonies was accomplished by opening the entrance to the colony using a chisel or pick if necessary and efforts were taken to not allow the earth to collapse onto the colony during the removal process. The comb was removed from the cavity ceiling by cutting it with a knife or by rocking it back and forth until it became dislodged (Figure 4-1). Colonies nesting in cliffs were extracted by removing the propolis covering over the nest entrance (Figure 4-2) and then using a “honey gathering stick” (made of fencing wire with a hook at the end) (Figure 4-3) and/or “Kwandwe staff” (a machete attached to the end of a long branch) to cut and remove the comb from the cavity ceiling. Colonies nesting in trees were more difficult to remove. Often, their extraction involved using a machete, handsaw, and/or chisel to gain access to the cavity. This allowed me to remove the comb without damaging it. The opening was extended down the branch or trunk as needed to access more comb (Figure 4-4, Figure 4-5). The combs were stored and in 20 L buckets. The combs were stacked by colony side by side and right side up in the buckets to prevent damage and limit honey leakage. The buckets were placed in a freezer (-10°C) until ready to be measured.

Once the combs were removed from the cavity, I attempted to collect the bees to determine the number of bees in the nesting colonies. Once dissected, the bees from the extracted colony would form a cluster similar to that of a swarming colony either inside the nest cavity or in a nearby bush or tree (Figure 4-6). Such clusters were collected from 19 of the extracted colonies (10 from reserves and 9 from farms) and placed into a cardboard box. I collected as many clusters as possible, but not all

clusters were obtainable. Some were too difficult to reach; others absconded.

Sometimes, too many bees were killed during the extraction process to collect and measure their populations accurately.

There were multiple ways to collect the clusters. Often, after the comb was extracted, I would fill the nest cavity with smoke until the colony decided to vacate the nest. As they left, I looked for the queen. Once found, she was placed in a preweighed box and the remaining bees would cluster around her (Figure 4-6, Figure 4-7). Other times, the cluster formed naturally after the colony was extracted and I could move it into a box by shaking or brushing the bees off the substrate on which they clustered. Finally, if the bee cluster would not leave the nest cavity, I reached into the cavity and collected the bees manually, scooping them with my hands into the box. Once as many of the bees were collected in the box as possible, the box was weighed (g) in the field on a triple beam scale (Figure 4-8). A small sample, 30 – 200 worker bees, was collected randomly from the cluster in a pre-weighed plastic jar, then stored in a freezer (-10°C) until measurements were made. The cavity volume was determined using the methodology outlined in Chapter 3. The weighed bees were returned to the nest cavity.

Colony Strength Measurements

The sample of bees collected from each colony cluster was weighed and the number of bees counted. This permitted me to determine an average weight per bee (g) and provided a way to estimate the number of bees in each colony. The latter was accomplished by dividing the cluster weight by the weight per bee. The colony population was divided by the cavity volume to determine the number of bees/L nest cavity.

A transparent 500 cm² grid (vertical and horizontal lines every 1 cm) was used to determine the total surface area of comb (cm²), cm² honey, cm² pollen, and cm² brood (eggs, larvae, and pupae) for each comb from a nest (Figure 4-9). The amount of filled comb was calculated by adding the amount of comb containing honey, brood, and pollen. The amount of empty comb was calculated by subtracting the amount of filled comb from the total comb area. The data were used to determine the proportion of comb that contained honey, brood, or pollen or was otherwise empty.

The brood pattern (roughly, the percent of brood comb that contained brood) of each extracted colony was determined using a 3 point scale. A rating of 1 indicated a very poor brood pattern, with many empty cells (>50% empty), and/or indications of disease. A rating of 2 was assigned to colonies having a somewhat spotty brood pattern (20 - 50% empty cells). A rating of 3 was assigned to combs with a solid brood pattern (<20% empty cells), even distribution of eggs, larvae, and pupae, and no visible diseases (Figure 4-10).

Statistics

The effects of land use (reserves or livestock farms) and nest site (ground, tree, and cliff) on colony strength parameters was determined using a one way ANOVA recognizing land use or nest site as the main effects and the following parameters as dependent variables: weight per bee (g); # bees/colony; # bees/L cavity volume; cm² honey, brood, pollen, empty (nothing in cells), or filled (contained anything in cells); total comb area; and the proportion of comb that contained honey, brood, pollen, nothing, or was filled. Proportion data were arcsin \sqrt{x} transformed prior to analysis though untransformed means are reported in this manuscript. The distribution of brood pattern ratings was compared within land use types using a Chi-square test. A single queenless

colony was omitted from brood analyses. The brood pattern ratings of 0 that had no data could not be included in the analysis, and were not used for reserve, ground, and cliff analyses. A linear regression analysis was conducted to determine if the concentration of bees in the colony (bees per liter cavity volume) was related to nest cavity volume. All analyses were conducted using the statistical software package JMP v 8.0 (SAS Institute 2009).

Results

Land use (reserve or livestock farm) did not affect any measured strength parameter significantly (Table 4-1). Brood pattern ratings were generally higher in colonies nesting on protected areas than those nesting on farms (Table 4-1). Means and standard errors for colony strength parameters pooled regardless of where the colony nested are reported in Table 4-2.

Nest site (ground, tree, or cliff) significantly affected cm^2 honey, pollen, and total comb filled and the proportion of comb containing honey, that was empty, or that was filled (Table 4-3). Colonies nesting in cliffs contained more honey than colonies nesting in the ground colonies, more pollen than colonies nesting in the ground or trees, had more area of its comb filled than colonies nesting in the ground or trees, and had a higher proportion of its comb filled than colonies nesting in the ground. Colonies nesting in trees had a larger proportion of their comb containing honey than did colonies nesting in the ground. No other colony strength parameters were affected by nest site (Table 4-3). Overall, nest cavity volume and the number of bees per liter of nest cavity was negatively correlated ($\# \text{ bees/L cavity volume} = -5.8*(\text{volume in L}) + 619 \text{ bees/L}$; $\beta = -5.8$, $R^2=0.43$, $F_{1,15}=11.5$, $P<0.01$) (Figure 4-11).

Discussion

Overall, the data suggest that land use practices did not affect the colony strength parameters measured in this study. Because colony strength could reflect the health of surrounding ecosystems, the lack of significant effects of land use on nesting colonies suggest that livestock farming has minimal impact on individual Cape honey bee colony strength. However, most trends in strength parameters favored colonies nesting on reserves over those nesting on farms, with the exception of the total amount of brood in colonies and the weight per bee (Figure 4-12). As such, the data present a dichotomy: no significant effects of land use on colony strength, but a number of trends that suggest otherwise. I discuss both possibilities.

There are a number of possible reasons that land use does not affect the strength of Cape honey bee colonies. First, the game reserves and farms tested in the study may not have differed significantly in land composition. The game reserves used in the study were converted from livestock farms within the previous 15 years. Therefore, it is possible that the land on game reserves did not have enough time to recover or affect nesting bee colonies significantly. To address this possibility, one should continue the research on undisturbed and natural habitat (as much as this is possible), thus giving one baseline data for Cape bee colonies nesting in unaltered landscapes.

Second, though the health status of honey bee colonies was not affected by land use, the colony density was. As such, livestock farms may have less resources available to nesting Cape honey bees, thus affecting nest density per unit area (Chapter 2). Because nest density was lower on livestock farms, the limited resources available to colonies there were sufficient to support the reduced number colonies nesting on the

farms. This would result in colonies similar in strength to those nesting on reserves, but just fewer of them.

The third possible reason that the strength of Cape honey bee colonies was unaffected by land use is that the farms tested in this study bordered reserves and/or had patches of unaltered land on the farm (especially in valleys where livestock would not graze). Consequently, the livestock farms were not truly homogenous and equally resource-poor but rather heterogeneous, with many habitat compositions available. Honey bees may have been accessing these areas in order to obtain their resources. To determine this further, one would have to employ GIS technology to see if colony strength can be predicted accurately by land use practices rather than simply recognizing “farm” and “game reserves” as all-encompassing terms.

On the other hand, there is some evidence that land use practices did affect colony strength parameters, at least numerically. All but one of the colonies nesting on reserves were assigned a brood pattern rating of 3 while the pattern ratings were distributed more evenly on colonies nesting on livestock farms. This may have resulted from poor resource availability on farms or other similar factors. For example, pesticides can affect honey bee brood, possibly resulting in spotty brood patterns (Toth and Ellis, unpublished data). Pesticides for cattle and crops were used on the test farms while not on the reserves. Furthermore, inbreeding is a significant contributor to spotty brood patterns (Moritz 1984). With lower colony densities on farms than on game reserves (Chapter 2), one would expect inbreeding to be more frequent on farms. Despite the differences in brood pattern ratings between colonies nesting on farms and game reserves, the average brood rating across all colonies was 2.7 (Table 3-2), suggesting

that wild Cape bee colonies generally had healthy queens, no visible brood diseases, etc.

Though land use did not, nest site did affect some colony strength parameters significantly. Colonies nesting in cliffs stored large quantities of honey and pollen and used most of their available comb. This may have been an artifact of nest cavity volume as colonies nesting in cliffs nested in cavities with numerically larger volumes than colonies nesting in trees or the ground (more cavity space = more storage space for honey and pollen). However, this likely was not the case as bees nesting in cliffs used proportionately more of their comb (Table 4-2). Additionally, colonies nesting in cliffs may be more protected in general than colonies nesting in the ground or in trees because of the difficulty in accessing cliff colonies. Cliff colonies may be protected from ground and tree dwelling organisms; certainly they are harder for predators and humans to reach.

As reported in Chapter 3, the mean cavity volume for colonies nesting in any cavity (including manmade structures) was ~ 44 L while colonies nesting in natural cavities exclusively (trees, ground, cliffs, etc.) had a mean cavity volume of ~ 38.6 L. This finding is consistent with previous ones made others for feral colonies in the northeast U.S. (Seeley and Morse 1976, Seeley 1977). However, the same authors reported that volume was not related to colony population size though my data indicated otherwise for Cape honey bees. Volume may affect honey bee strength significantly because bees may choose a nest cavity of sufficient size to support a strong colony population. The “optimal” volume may prevent the overcrowding of bees and allow for

population fluctuations and resource storage while at the same time not leave the colony exposed to infiltration of pests or limit colony growth.

The data I collected also permit me to discuss the size of wild Cape bee colonies in relation to feral European honey bee colonies in the U.S and wild *A. m scutellata* in Botswana. In general, European colonies had more bees (~19000 bees/European bee colony; ~12000 bees/Cape bee colony) and total comb area (~23,000 cm²/European bee colony; ~9000 cm²/Cape bee colony) than did Cape bees (Seeley and Morse 1976) where *A. m. scutellata* had less bees and total comb (~6500 bees/*A. m. scutellata* colony; ~6000 cm²/*A. m. scutellata* colony) (Schneider and Blyther 1988, McNally and Schneider 1996) (Table 4-3). The percentage of comb utilized for brood was similar between the European and Cape honey bees with ~25% of the comb utilized for brood in European colonies and ~22% of the comb utilized for brood in Cape bees. These values were much less than the percentage brood (~55%) found in *A. m. scutellata* colonies (Table 4-3). The amount of empty comb and the use of combs by the three types of honey bees for honey and pollen storage differed. Seeley and Morse (1976) found that European bees use ~55% of the comb for honey and pollen storage with ~20% of the comb remaining empty. I found that Cape bees use ~43% of the comb for honey and pollen storage with ~36% of the comb remaining empty. McNally and Schneider found that *A. m. scutellata* colonies use ~24% of the comb for honey and pollen storage with ~22% of the comb remaining empty (Table 4-3).

There are a number of potential explanations for these results though I discuss four here. First, the three bee races have different natural histories, thus possibly explaining the differences in comb use. African races of honey bees can migrate

throughout a season as resources become limited in a given habitat (Hepburn and Radloff 1998) and abscond frequently because of high rates of predation causing them to construct less comb and store less food (McNally and Schneider 1996). Some of the sampled Cape and *A. m. mellifera* colonies could have been at their second nesting site, thus making the colony smaller in general, and having stored fewer resources over time. Second, the Eastern Cape and Okavango River Delta are semiarid environments (Schneider and Blyther 1988) where flowering plants exist much of the year and therefore, Cape bees and *A. m. scutellata* colonies would be pressured less to hoard honey/pollen. On the other hand, Seeley and Morse (1976) studied wild colonies in temperate New York, U.S. where winters are cold and bee colonies must hoard resources and have large populations in order to survive. Third, given that African honey bees have available flowering plants available year round, they can have long swarming periods where several reproductive swarms are produced with potentially several afterswarms (McNally and Schneider 1996, Hepburn and Radloff 1998), thus keeping populations lower than those of European honey bees. Finally, the Cape bee appeared to have an intermediate nesting biology between the European and *A. m. scutellata* colonies regarding # bees/colony, total comb constructed, and food storage (Table 4-3). This may be an effect of the environmental conditions where New York's climate is temperate, Botswana's is subtropical, and the Eastern Cape's represents a Mediterranean climate (Hepburn and Radloff 1998), where the seasons are less defined by temperature and floral bloom than New York, but more so than Botswana. Differences between observed nesting parameters for Cape bees, European bees, and *A. m. mellifera* colonies could be based on the time of colony harvesting and measuring.

While Seeley and Morse (1976) extracted colonies in the summer and *A. m. scutellata* colonies were sampled over a 12 month period (Schneider and Blyther 1988), I extracted the Cape honey bees in autumn. .

In conclusion, Cape bee colonies appeared slightly healthier when nesting on reserves than when nesting on livestock farms, though the differences between colonies nesting in both locations were not significant. To address this topic further, similar projects should be repeated including an analysis of colonies on undisturbed lands. That said, population densities may be a more useful estimator of land use effects on Cape bee colonies as land may not affect the strength of colonies overall but rather the total number of colonies an area can support. Finally, differences were found between strength parameters of wild Cape honey bee colonies, wild *A. m. scutellata*, and feral European honey bee colonies which likely reflect different environments in which the bees live and the differing life history strategies of the different honey bee races.

Table 4-1. The effects of land use on Cape honey bee colony strength parameters.

Strength Parameter	Reserves	Farms	ANOVA
Weight per bee (g)	0.09 ± 0.003 (10)	0.1 ± 0.011 (9)	$F_{1,17}=3.1; P=0.1$
# bees/colony	12700 ± 2057 (9)	11420 ± 1445 (9)	$F_{1,16}=0.3; P=0.62$
# bees/L cavity volume	631 ± 127 (9)	337± 76 (9)	$F_{1,16}=3.9; P=0.06$
cm ² brood	1672 ± 243 (16)	1733 ± 270 (16)	$F_{1,30}=0.03; P=0.87$
cm ² honey	4057 ± 726 (17)	3215 ± 425 (16)	$F_{1,31}=1; P=0.33$
cm ² pollen	417 ± 83 (17)	372 ± 90 (16)	$F_{1,31}=0.1; P=0.72$
cm ² empty	2514 ± 457 (17)	3932 ± 704 (16)	$F_{1,31}=2.9; P=0.1$
cm ² filled	6047 ± 875 (17)	5320 ± 555 (16)	$F_{1,31}=0.5; P=0.49$
cm ² total comb	8562 ± 1110 (17)	9252 ± 968 (16)	$F_{1,31}=0.2; P=0.64$
Proportion of comb containing brood	0.25 ± 0.04 (16)	0.18 ± 0.02 (16)	$F_{1,30}=1.2; P=0.28$
Proportion of comb containing honey	0.42 ± 0.05 (17)	0.36 ± 0.05 (16)	$F_{1,31}=0.6; P=0.46$
Proportion of comb containing pollen	0.05 ± 0.01 (17)	0.04 ± 0.01 (16)	$F_{1,31}=0.7; P=0.42$
Proportion of comb empty	0.3 ± 0.04 (17)	0.41 ± 0.05 (16)	$F_{1,31}=3.2; P=0.08$
Proportion of comb filled	0.7 ± 0.04 (17)	0.59 ± 0.05 (16)	$F_{1,31}=3.3; P=0.08$
Brood pattern rating	1: 0* 2: 1 3: 15 $\chi^2(1, N=16) = 12.3;$ $P<0.01$	1: 1 2: 7 3: 8 $\chi^2(2,N=16) = 5.4;$ $P=0.07$	

Data are mean ± s.e. (N number of colonies) for ANOVA tests and # colonies assigned a given brood pattern rating for χ^2 analyses. For χ^2 tests, P values > 0.05 indicate a random distribution of brood pattern ratings among colonies. Data labeled with an asterisk were excluded from analysis because χ^2 tests do not recognize "0". For brood pattern ratings: 1= very spotty brood (>50% empty cells), 2= somewhat spotty brood (20 - 50 % empty cells) and 3= solid pattern (<20% empty cells).

Table 4-2. Nest site effects on Cape honey bee colony strength parameters.

Strength Parameter	Ground	Tree	Cliff	Result
Volume (L)	35.3 ± 4.4a (19)	36 ± 10.9a (7)	44.3 ± 6.7a (6)	$F_{2,29}=0.4; P=0.65$
Weight per bee (g)	0.1 ± 0.003a (11)	0.1 ± 0.004a (7)	0.09**	$F_{1,16}=0.04; P=0.84$
# bees/colony	11262 ± 1640a (10)	12048 ± 1883a (7)	20118**	$F_{1,15}=0.1; P=0.76$
# bees/L cavity volume	439a ± 65a (10)	526 ± 191a (7)	636**	$F_{2,15}=0.2; P=0.63$
cm ² brood	1700 ± 235a (19)	1201 ± 204a (7)	2296 ± 492a (6)	$F_{2,29}=2; P=0.15$
cm ² honey	2844 ± 450b (19)	4211 ± 371ab (7)	5785 ± 1565a (6)	$F_{2,29}=5.1; P=0.03$
cm ² pollen	364 ± 65b (19)	237 ± 120b (7)	724 ± 130a (6)	$F_{2,29}=4.2; P=0.03$
cm ² empty	3764 ± 638a (19)	2045 ± 393a (7)	2769 ± 1005a (6)	$F_{2,29}=1.4; P=0.27$
cm ² filled	4908 ± 607b (19)	5649 ± 3594b (7)	8805 ± 1549a (6)	$F_{2,29}=4.9; P=0.01$
cm ² total comb	8671 ± 1080a (19)	7694 ± 1080a (7)	11574 ± 1659a (6)	$F_{2,29}=1.6; P=0.23$
Proportion of comb containing brood	0.24 ± 0.04a (19)	0.16 ± 0.03a (7)	0.21 ± 0.12a (6)	$F_{2,29}=0.6; P=0.53$
Proportion of comb containing honey	0.3 ± 0.04b (19)	0.55 ± 0.04a (7)	0.48 ± 0.1ab (6)	$F_{2,29}=5.6; P=0.01$
Proportion of comb containing pollen	0.04 ± 0.01ab (19)	0.03 ± 0.01b (7)	0.07 ± 0.02a (6)	$F_{2,29}=3.2; P=0.06$
Proportion of comb empty	0.42 ± 0.04a (19)	0.26 ± 0.04b (7)	0.24 ± 0.09b (6)	$F_{2,29}=4.3; P=0.02$
Proportion of comb filled	0.58 ± 0.04b (19)	0.74 ± 0.04a (7)	0.76 ± 0.09a (6)	$F_{2,29}=4.3; P=0.02$
Brood pattern rating	1: 0* 2: 5 3:14 $\chi^2(1,N=19)=4.3;$ $P=0.04$	1: 1 2: 2 3: 4 $\chi^2(2,N=7)=2; P=0.37$	1: 0* 2: 1 3: 5 $\chi^2(1,N=6)=2.7; P=0.1$	

Data are mean ± s.e.(N number of colonies) for ANOVA tests and # colonies assigned a given brood pattern rating for χ^2 analyses. Row data followed by the same letter are not different at $\alpha = 0.05$. For χ^2 tests, P values > 0.05 indicate a random distribution of brood pattern ratings among colonies. *Data were excluded from analysis because χ^2 tests do not recognize "0". **Data were excluded from analyses because only 1 colony was sampled. For brood pattern ratings: 1= very spotty brood (>50% empty cells), 2= somewhat spotty brood (20 - 50 % empty cells) and 3= solid pattern (<20% empty cells).

Table 4-3. Honey bee colony strength parameters pooled across all extracted Cape honey bee colonies, colonies from Okavango River Delta, and New York.

Parameter	Eastern Cape (Cape honey bee)	Okavango (<i>A. m. scutellata</i>)	New York (European honey bee)
Weight per bee (g)	0.983 ± 0.002 (19)	-	-
# bees/colony	12060 ± 1229 (18)	6462 ± 1336 (31)*	18804 ± 2853 (5)
# bees/L cavity volume	484 ± 340 (18)	-	-
cm ² brood	1702 ± 179 (32)	-	-
cm ² honey	3649 ± 427 (33)	-	-
cm ² pollen	395 ± 60 (33)	-	-
cm ² empty	3202 ± 427 (33)	-	-
cm ² filled	5695 ± 521 (33)	-	-
cm ² total comb	8896 ± 731 (33)	6061 ± 484 (80)	23400 ± 2470 (8)
Proportion of comb containing brood	0.22 ± 0.14 (32)	0.55 ± 0.03 (81)	0.25 ± 0.03 (8)
Proportion of comb containing honey and pollen	0.43 ± 0.03 (33)	0.24 ± 0.02 (81)	0.55 ± 0.05 (8)
Proportion of comb containing honey	0.39 ± 0.03 (33)	-	-
Proportion of comb containing pollen	0.04 ± 0.01 (33)	-	-
Proportion of comb empty	0.36 ± 0.03 (33)	0.22 ± 0.02 (81)	0.2 ± 0.03 (8)
Proportion of comb filled	0.64 ± 0.03 (33)	0.78 ± 0.02 (81)	0.8 ± 0.03 (8)
Brood pattern rating	2.7 ± 0.1 (32)	-	-

Data are mean ± s.e.(N). Data for Okavango (*A. m. scutellata*) are from McNally and Schneider (1996). Data for New York (European honey bee) are from Seeley and Morse (1976). Data marked with * are from Schneider and Blyther (1988).

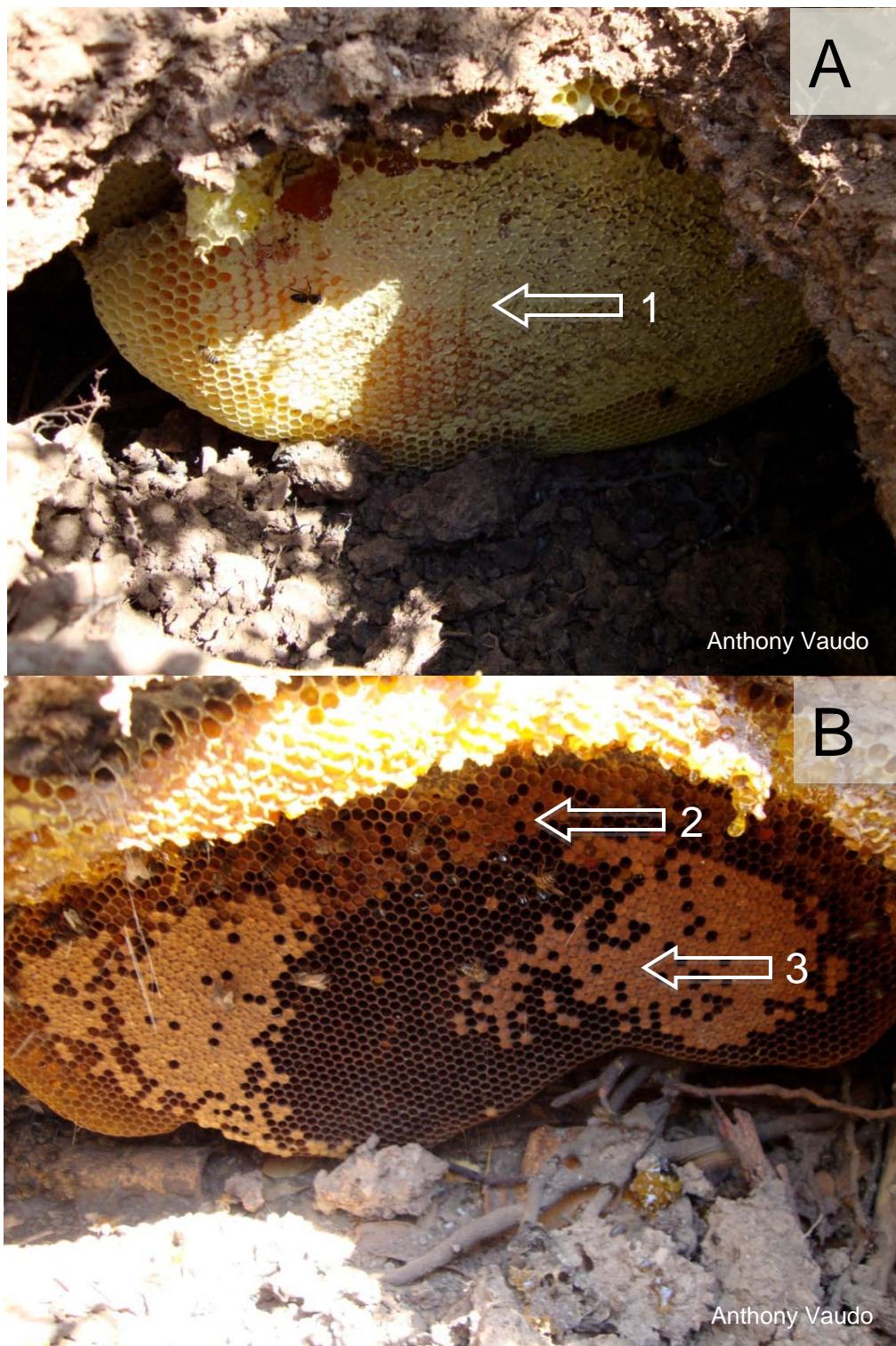


Figure 4-1. Cape honey bee colony nesting underground. The colony is visible because a section of ground was removed. Figure A shows the outermost comb filled with honey. Figure B shows the brood comb. Arrow 1 points to capped honey, arrow 2 points to stored pollen, and arrow 3 points to the capped brood.



Figure 4-2. Cape honey bee colony nesting in a cliff cavity. Figure A shows the comb covered with a layer of propolis. Figure B shows the comb exposed after the propolis was removed.



Riaan Boucher

Figure 4-3. Removing comb from a cliff colony using a honey gathering stick.



Riaan Boucher



Anthony Vaudo

Figure 4-4. Accessing a tree cavity where Cape honey bees were nesting.



Anthony Vaudo

Figure 4-5. A hole cut in a tree to facilitate comb removal. The photograph shows the top of the comb of the honey bee colony.



Figure 4-6. Examples of colony clusters. Figure A shows the cluster remaining in the nest cavity after comb removal. Figure B shows the cluster placed in a box to be weighed.



Anthony Vaudo

Figure 4-7. A Cape honey bee cluster in a box and prepared for weighing. The queen is present in the box.



Anthony Vaudo

Figure 4-8. Triple beam scale used for weighing bee clusters in a box. The box contains the honey bee cluster. The jar contains a subsample of honey bees from the cluster.



Remy Raitt

Figure 4-9. Measuring the amount of honey in a comb using a 500 cm^2 grid.

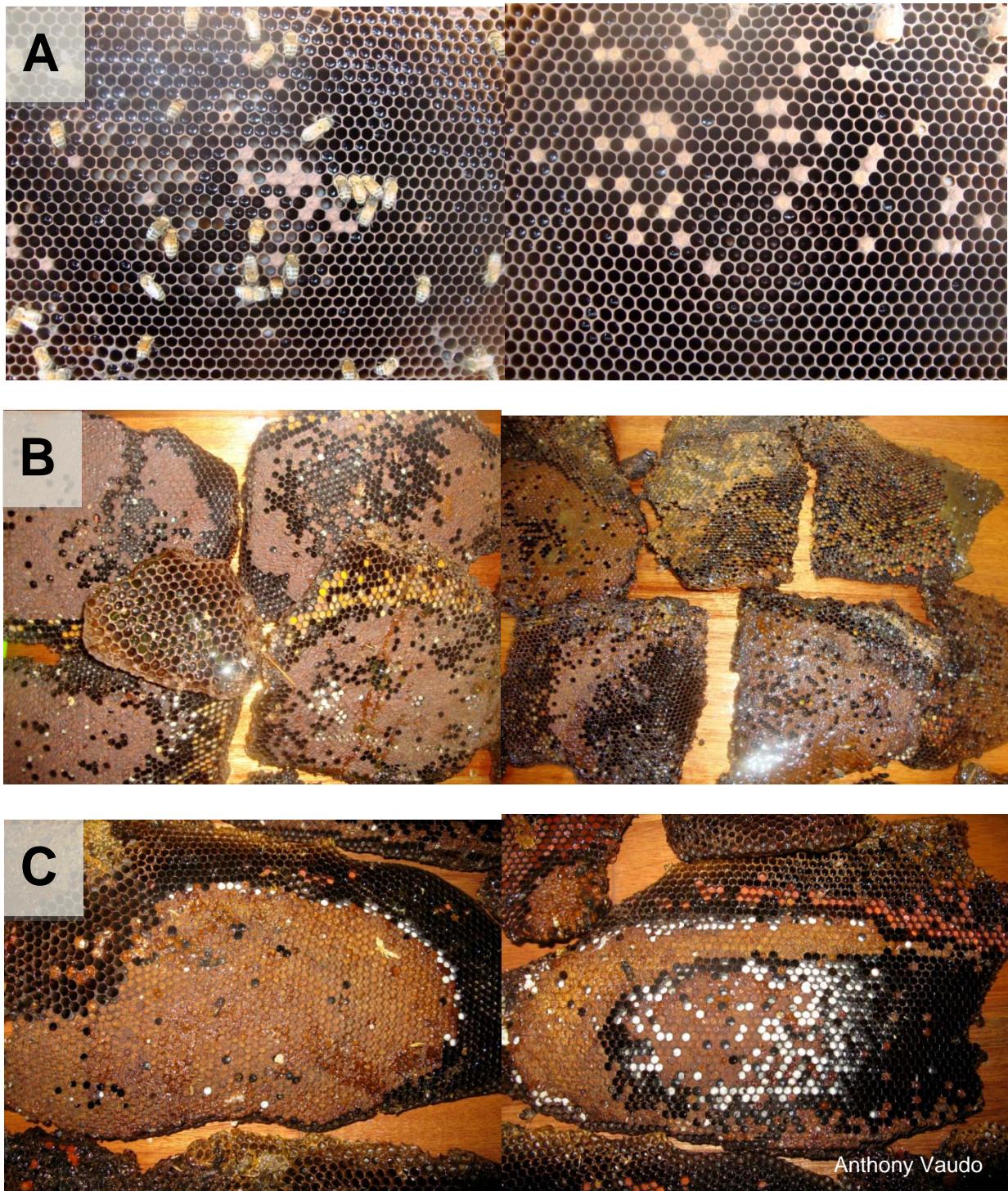


Figure 4-10. Brood pattern ratings. Figures in row A represent brood pattern #1 (very spotty brood; >50% empty cells). Figures in row B represent brood pattern #2 (somewhat spotty brood; 20-50% empty cells). Figures in row C represent brood pattern #3 (solid pattern; <20% empty cells).

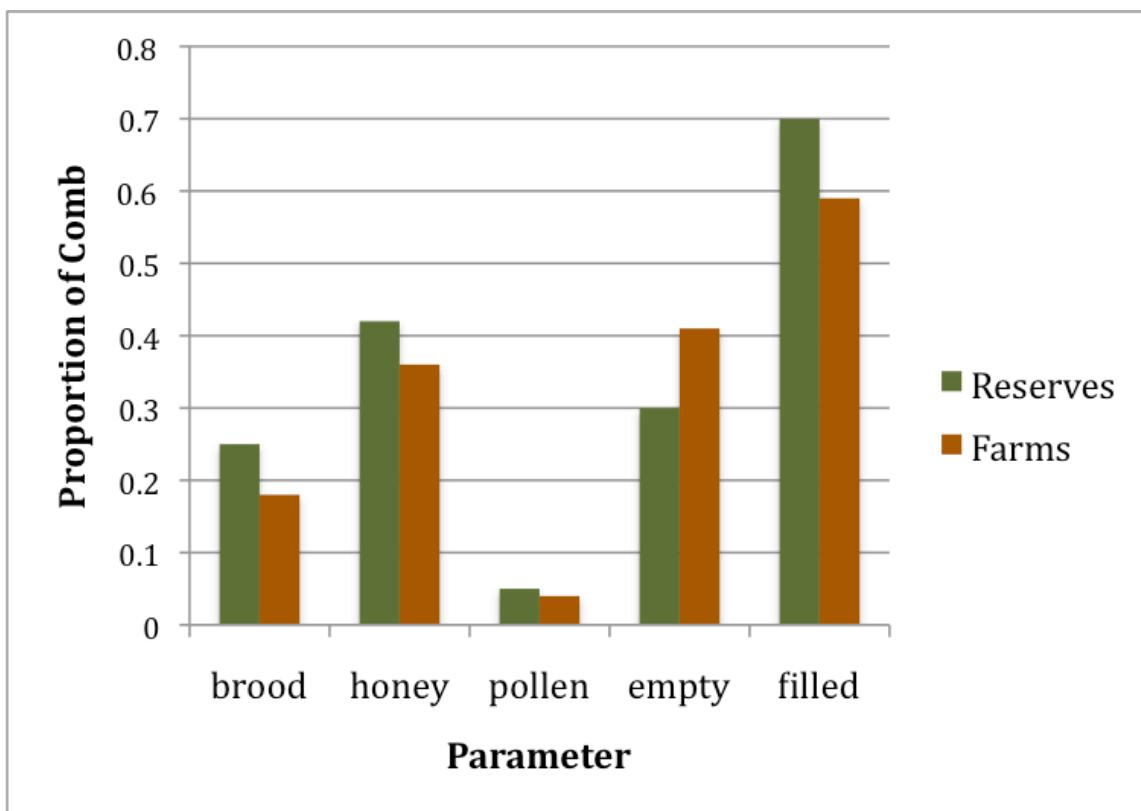


Figure 4-11. Mean proportions of colony strength parameters by land use type. In this figure, the trends in strength parameter means favoring colonies on reserves are apparent.

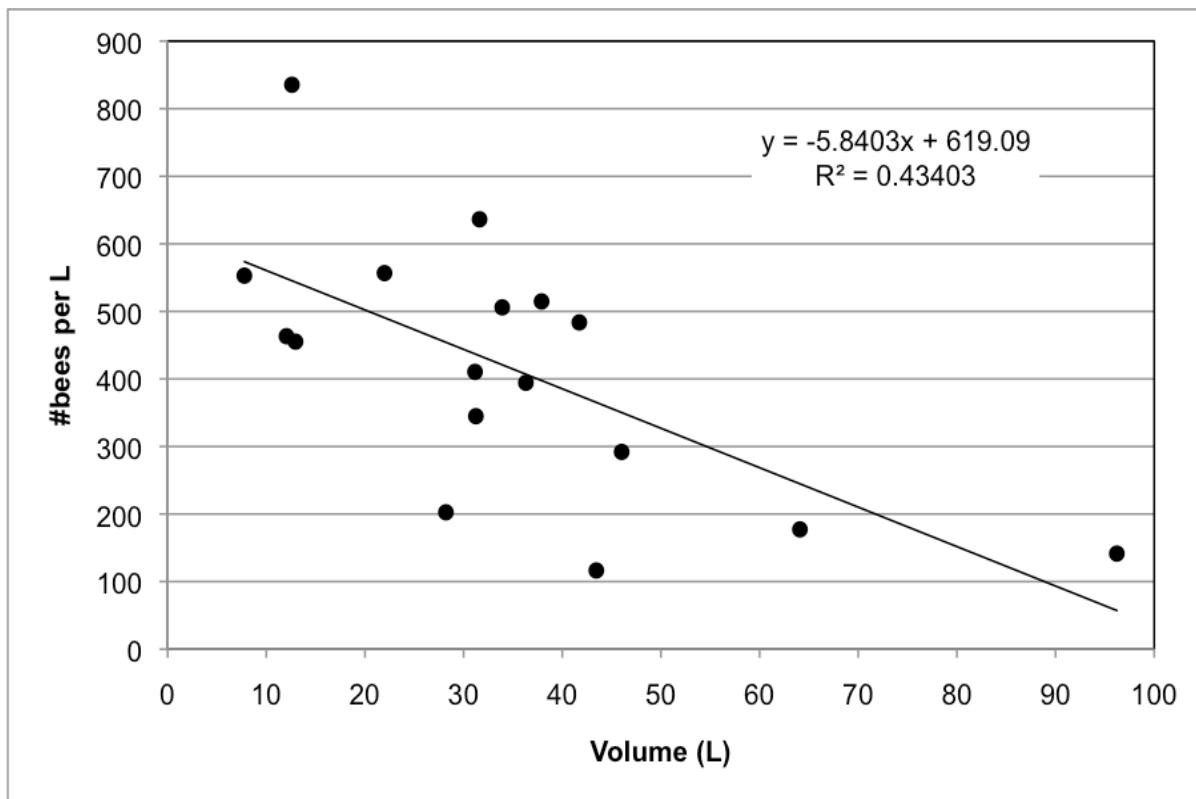


Figure 4-12. Concentration of bees by L of cavity volume ($F_{1,15}=11.5$, $P<0.01$).

CHAPTER 5 DISCUSSION

The purpose of the research efforts reported in this thesis was to determine potential land use effects on the population density, nest site selection, and colony strength of Cape honey bees in the Eastern Cape, South Africa. To do this, I developed, modified, and employed various methodologies for use in the research. In particular, I investigated how livestock farming affected Cape bee nesting dynamics, using reclaimed farms (private game reserves) as standards for comparison.

Land Use Effects

Collectively, the data suggest that Cape bee colonies were affected negatively when nesting on livestock farms compared to when nesting on recently reclaimed land used as nature reserves. Because some of the specific trends were suggestive and not statistically significant, the research should be replicated on a larger scale in order to verify or refute the results obtained. Data from more colonies on varied livestock farms and reserves should be included; though dissecting a large number of wild colonies should be done only if necessary as destructively sampling colonies may affect surrounding ecosystems. Data on wild colonies could be collected responsibly, with brood measurements being made in the field and brood returned to colonies. Regardless, some methodologies (such as the population index) should be improved to increase the accuracy of the collected data. In this chapter, I will discuss my findings of land use effects on Cape bee nesting dynamics in a larger context, further emphasizing the role of honey bees as bioindicators.

Population Density

The data discussed in Chapter 2 suggest that land use negatively impacted colony population densities. This potential reduction in population density may have resulted from diminished nectar and pollen availability due to a presumed reduction in plant community structure on livestock farms – an effect known to happen due to land transformation through clearing, overgrazing, and erosion on farms (Kerley et al. 1995, Le Roux et al. 2008).

Knowing the population density of honey bee colonies in an area can provide useful information about bee ecology, bee population fluctuations over time, the carrying capacities for bee colonies in varying regions, landscape structure, effects of predation on colonies, spatial distribution of colonies, swarming dynamics, etc. Also, areas having larger honey bee populations, which may be associated with resource availability (Dempster and Pollard 1981), should be genetically diverse which promotes population growth, foraging efficiency, and resource storage (Mattila and Seeley 2007).

The effect of land use habits on Cape honey bee colonies was easiest to observe when considering the feeding station ratings obtained from visual estimates of bee intensity and photographs allowing me to determine the number of bees at a particular station (Chapter 2). Though counting bee-lines ultimately may be an effective method of comparing population densities of honey bees, there remains the potential that not all bee-lines can be observed if two or more colonies are nesting in the same direction away from the feeding station. If counting bee-lines is to be used in the future, the distance between feeding stations probably should be adjusted to maximize the accuracy of the technique. Furthermore, the population index ultimately must be correlated closely with the actual colony density in an area.

Nest Site Selection

Some parameters associated with nest site selection appeared to be influenced by land use practices. These included nest location (building, cliff, ground, and tree) and nest cavity volume (Chapter 3). The height of nests above the ground was influenced by nest location. There were more colonies found in cliffs and trees on reserves than on livestock farms, thus increasing average nest height on reserves. The results further suggest nesting preferences by bees nesting in the single urban site, Grahamstown, South Africa. Colonies nesting in Grahamstown, a location with numerous potential nesting sites, were almost always high above the ground in buildings and trees. On farms where potential nest sites were limited due to land use habits, colonies nested more often in ground cavities. That honey bees prefer higher nests has been supported by others (Seeley and Morse 1976, 1978, Schneider and Blyther 1988, McNally and Schneider 1996, Oldroyd et al. 1997, Crane 1999, Baum et al. 2005, Kajobe 2006).

When ignoring land use practices altogether, it is important to consider nest site selection among Cape bees as a general phenomenon. As stated, there was a tendency for Cape bees to nest high above the ground in cavities ~ 40 L in volume, a trend shown by others for European honey bees (Seeley and Morse 1976, 1978, Caron 1999). Why honey bees in general nest in volumes this size remains unclear. Forty liters may be “optimal”, helping to maintain nest homeostasis and limiting nest overcrowding.

Seeley and Morse (1978) suggested that feral European honey bees in the U.S. tended to nest in cavities with high exposure and visibility, though this may be an artifact of the ease with which these nests can be found by causal observation. In my study, Cape bees nesting in the ground often occupied cavities whose entrances often were

hidden by thorny plants, woody shrubs, etc. This could camouflage nest entrances and protect the otherwise vulnerable nests (Figure 3-6).

Finally, Cape honey bees habitually chose nests whose entrances faced south, east, or southeast. This is consistent with findings by others for European and African honey bees whose nest entrances tend to face south in both the Northern and Southern Hemispheres (Seeley and Morse 1976, Schneider and Blyther 1988, McNally and Schneider 1996). The data suggest that honey bees do not prefer nest locations where the entrance faces the equator (thereby maximizing entrance sun exposure) but rather prefer nesting in cavities with entrances facing the rising sun though this preference needs to be tested further.

Colony Strength

Many of the methods I used to determine strength parameters have been used by other investigators to determine how pests, parasites, pesticides, management stresses, etc. affect managed honey bee colonies (Delaplane and Hood 1997). Most colony strength parameters measured in Chapter 4 were not affected by land use habits though most data numerically favored colonies nesting on reserves. Brood patterns in reserve-nesting colonies generally were better than those in farm-nesting colonies. The lack of significant effects may have resulted from the relative youth of the tested game reserves which all were less than 15 years old, thus minimizing any effects of land use reclamation that may need more time to materialize. Also possible is that carrying capacity (population density – Chapter 2) is affected by land use practices. Resource-poor habitat (like that on livestock farms) supports fewer colonies, colonies which are otherwise healthy. Therefore, Cape honey bees might distribute their nests in a particular habitat to maximize resource usefulness. Fewer colonies per unit area may be

subject to inbreeding, which could have resulted in the spotty brood patterns seen in colonies nesting on livestock farms (Moritz 1984).

In contrast to land use effects, the type of nest site (cliff, ground, or tree) in which bees chose to nest did affect some colony parameters where colonies nesting in cliffs were observed to have the largest volume of honey and pollen stores and utilized more comb (Chapter 4). It is not immediately clear why this was the case, especially since land use did not affect these parameters. It could be that colonies nesting in cliffs were in locations that could not be grazed or cleared and there were more resources available for the colonies in these locations. In addition, colonies nesting in the ground tended to be the weakest colonies (Chapter 4). This may indicate that colonies on farms were generally weaker because colonies on farms nested in the ground at a higher frequency than colonies on reserves (Chapter 2).

Another factor affecting the study area, thus potentially affecting my data, is that a region-wide drought was ongoing during the time of data collection. This may have caused lower populations of honey bees and affected individual colony strength because of drought impact on flowering plants and negative effects on colony homeostasis. Consequently, the study should be replicated multiple years and seasons with a goal of sampling more colonies and study sites.

Honey Bees as Bioindicators

Though not investigated directly, a peripheral goal of the research project was to begin developing methodologies for using honey bee colonies to assess the health of terrestrial ecosystems, ie. as “bioindicators”. Honey bees as generalist pollinators help maintain plant communities in the Eastern Cape (Hepburn and Radloff 1998), making them an essential component of the region. Furthermore, honey bees and various

components of their nests also are sources of food for other animals. Advantages of using honey bees as bioindicators include: (1) the ease with which one can study their foraging behavior and the pollination services they provide to different plants, (2) their nests can be found easily, (3) beekeepers maintain colonies that can be used readily, (4) colonies contain thousands of individuals that can be sampled without threatening the health of the colony, (5) methods for measuring colony strength parameters are known, and (6) a considerable body of knowledge is available on the bee. With the population density index I developed, one now can begin estimating population densities in different areas, thus providing another valuable tool when using honey bees as bioindicators.

Although I have discussed the age of the game reserves already, it is pertinent to discuss the issue further as this may affect bees' use as bioindicators. The game reserves used in the study were converted from livestock farms less than 15 years before data collection for this study. This short time period may or may not have allowed the game reserves to return to pre-livestock farming conditions, though successional plant regrowth may have initiated (Avis and Lubke 1996). Converting livestock farms to game reserves in the Eastern Cape consists of removing livestock and replacing them with other large herbivores such as elephant, bovine varieties, giraffe, rhinoceros, zebra, etc. So, it is possible that game reserves are grazed as heavily as livestock farms. For example, elephants can be detrimental to vegetation when plants are in low abundance while white rhinoceros and giraffe, which are not native to the Eastern Cape, could stunt regrowth and promote additional overgrazing (Langholz and Kerley 2006). Landowners may promote a false savannah-like environment so tourists can view

charismatic animals (Langholz and Kerley 2006), thus affecting land more so than does livestock farming. Further, little attention often is placed on native vegetative restoration on game reserves. It is important that those managing game reserves not focus solely on the management of game reserves for large herbivores/carnivores, but also focus on vegetation and insect restoration. At the end of the day, reserve ecosystems may not be altogether different from those on farms, emphasizing the need to employ other technologies when determining what factors affect Cape bee nesting habits.

Geographic Information System (GIS) technology could be used to determine other parameters that affect Cape bee nesting dynamics more accurately. For example, bees may be impacted less by livestock farming than they may be by proximity to water, topography, vegetation patterns, etc (Bamford et al. 2009, Radovic and Mikuska 2009, Stralberg et al. 2009). These effects could be seen more clearly by mapping and analyzing nest site selection of Cape honey bees using GIS, thus allowing one to identify large scale trends. It is possible, for example, that livestock farming does not affect nesting behavior overall because most of the tested livestock farms, though they contained large grazing areas, remained diverse habitats where cliffs, trees and varied vegetation patterns and topography remained. GIS would allow one to determine what characteristics most correlate with nesting behavior and population densities while ignoring artificial designations such as “livestock farming”, “game reserves”, etc. Furthermore, GIS technology would permit one to study ecosystem differences and their effects on Cape and other honey bees temporally. In truth, GIS data may indicate that livestock farms and game reserves in the Eastern Cape are not altogether different, especially considering that most game reserves were livestock farms at one time and

have simply substituted cattle grazers for other large ungulate grazers. That said, key differences do exist between the two, such as pesticide use, the presence of humans, and more intensive management on farms.

It is possible that vegetative restoration on game reserves can be achieved by the reintroduction or augmentation of honey bee populations. Certain types of region-specific, native vegetation that is pollinated by honey bees can be replanted and honey bees moved to the area to expedite the establishment of those plants. By observing bee responses to available vegetation and *vice versa*, we can increase our knowledge of Cape bee ecology and its impact on the vegetation of the region. In addition, studies on honey bee foraging and pollen collection habits may provide an idea of the floral diversity and abundance in the field; the health of colonies is dependent on floral resources.

The research presented herein was initiated to start a discussion on analyzing the health of an ecosystem based on the nesting dynamics of the Cape honey bee. Carrying capacity, nest site availability, and resource availability of the ecosystems may have been reflected in the various colony parameters discussed so far. There were small differences in the Cape bee's nesting dynamics within the study sites suggesting there might be only small differences between game reserves and livestock farms. However, an index will need to be developed for each colony parameter to define the impact of ecosystem health on each. From there, we can state more strongly how honey bee nesting dynamics reflect the habitat in which they live.

Conclusion

When considering the data collectively, livestock farming appeared to affect Cape honey bee nesting parameters in the Eastern Cape, South Africa. The data contributed

to the understanding of Cape honey bee ecology and provided background information on Cape bees useful for promoting their health and conservation.

The modified bee nest hunting process I describe in this thesis can be used by those wishing to locate wild honey bee colonies. The methodology employed for measuring nest site selection and colony strength parameters were simple and can be used in the field by researchers and beekeepers after their accuracy is established. The population index method I developed can be used to compare bee populations in two or more areas but the methodology needs refining and further field testing. With modification, it could eventually be a useful tool for researchers, one not available previously.

Finally, there is potential to use honey bees as bioindicators of the general health of an ecosystem. Data collected using the methodology outlined within this thesis may be indicative of the status honey bees and the environment in which they live and forage. Further research must be conducted to model the relationship between honey bee colonies and their environment.

The biomes in the Eastern Cape and the Cape honey bee itself are unique. The Cape bee is a generalist pollinator that may be essential to the plant communities and ecosystems in the region. The area is being threatened by agricultural land use but many landowners are converting their land to game reserves for economic reasons. In order to protect the Cape bee and reverse negative land use practices in the region, one must understand the effects of land use patterns on bees so that one can outline best management practices for conserving Cape bees.

The observations made on wild Cape honey bees in the Eastern Cape described within this thesis may be used a catalyst for ongoing research on the topic. I trust that this will inspire and motivate researchers and enthusiasts to practice better land management and conservation practices, not just for honey bees, but the entire natural environment.

APPENDIX FIELD NOTES

Nest Site Selection

I made some cultural and personal observations regarding honey bee nest sites. Regarding nest height, beekeepers in South Africa tend to use “catch boxes,” usually just a Langstroth-style brood box, to attract and catch swarming colonies that then can be used for beekeeping (Cambray, personal communication; personal observation). These boxes are usually placed in high places such as roofs of buildings or in trees. I have observed that honey bees will inhabit boxes and ground cavities in urban areas such as Orlando, FL and Grahamstown, South Africa, and, of course, hives managed by beekeepers are kept on the ground. During my trip to the Democratic Republic of Congo in March, 2010, local inhabitants communicated that honey bee colonies generally were found in trees. The field site in the DRC was a wooded area, but colonies also have been found nesting in the ground. At this point, it appears that honey bees in the Eastern Cape choose nest sites heights based on availability.

There was an urban legend regarding honey bees based on the location of their nest and I noticed it through my own experience as well. There seemed to be behavioral differences between colonies that were nesting in different types of cavities. From what I noticed, colonies in cliffs and trees tended to be more defensive than colonies nesting in the ground. I never received a sting when approaching a ground colony whereas I received numerous stings when standing close to cliff and tree colonies. Also, when taking pictures of the colony entrances, honey bees from come cliffs and trees would “attack” the black camera whereas it did not happen when taking photos of ground colonies. It appears that colonies in cliffs and trees are better defended by the nest

location alone than the ground colonies; cliffs and tree colonies are less accessible and hard to attack and open than those on the ground. However, in that case it would seem that the ground colonies should be more defensive, but my own experience and others' descriptions have indicated that there is less of a defensive response. I conducted a few colony dissections from the ground without using gloves or veil and/or no smoke. The defensive responsiveness of colonies in some trees, cliffs, or buildings would not allow me to do the same. It is possible that ground colonies are more likely to be attacked and may be less defensive because of their ability or tendency to abscond or migrate (Hepburn and Radloff 1998), but this has yet to be shown. It has been discussed and suggested by locals, beekeepers, and scientists that "cliff colonies" may be different subspecies because they appear smaller, darker in color, and more defensive than ground nesting colonies. However, this is speculation and has yet to be tested.

Twelve of the 15 colonies that were not present when I returned to conduct the removals were in the ground or had entrances just above ground level. Two of the others were in buildings that were easily accessible by humans; one of them having been removed from a lodge on the Emlanjeni reserve by the manager. The final one was a tree cavity. A few had appeared to have absconded or died because the cavity appear intact, but 12 of these colonies seemed to have been robbed by man or possibly another animal such as a baboon or honey badger (Hepburn and Radloff 1998). It is known that local people groups living in the area do eat honey, pollen, and brood from wild colonies, so it is likely that they were removed by people. For instance, at Emlanjeni, seven of the eight of the colonies I originally found, excluding two that were shown to me by the manager, were no longer present. They were ground colonies with

the cavities having been completely opened and no comb left over whatsoever. There is a possibility that other honey bee colonies robbed the remainder of the comb. I did locate one colony that I did not notice during the bee hunting phase of my research while walking to conduct one of the removals at Emlanjeni. I removed the comb from this colony and the comb was very new and small, it appeared that this was one of the colonies that had been robbed and absconded to a new area, considering it was in June, which was well after the swarming season (Hepburn and Radloff 1998).

Bee Hunting

Often, multiple methods were used when attempting to locate a wild colony. I will provide one example of a relatively intense hunt that took approximately 3 hours on Theo Harris's farm. First, bees were baited to a feeding station and a beeline was established. I followed the beeline to the edge of a steep slope into a heavily wooded area with a riverbed at the bottom and was unable to locate the colony. I used secondary bait and established a new beeline at the edge of the hill. Using binoculars, I saw that the bees were travelling straight out into the valley and then diving downward after about 200m. The valley was composed of thicket and afromontane forest with tall trees, bushes, and cliffs. It was difficult getting down to the valley floor, and there was no way to carry secondary bait. I searched all potential nest sites that I could see such as holes in trees, the ground, and rock faces. When I could get to a point where I could see the sun again through the canopy, I saw the bee line. I followed this line twice, the first time unsuccessfully, but the second time I looked through another break in the canopy and saw a number of bees flying in and out of the woods. I felt that I was close to the entrance of the colony because of the number of bees travelling back and forth. When I arrived at the location, it was not a colony but a small pool of water in the

otherwise dried river. From the water, I watched the honey bees fly up through the trees and away, back in the direction from which I had just traveled. I knew that the nest was close. I then had to do some haphazard searching. I climbed up one side of the hill and cliff and heard the buzz of the colony entrance. An active colony will make a lot of noise because of the larger number of foragers flying into and out of the nest. By listening to the hum or buzz of a colony, one can direct their search to the colony. In thick bush, it is difficult to see the bees entering and exiting the colony from a distance. I moved beside the cliff and then spotted the entrance of the colony in the rocks. From about 7m away, they started buzzing me heavily and I received a few stings (which was rare during my experience locating colonies).

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BIOGRAPHICAL SKETCH

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