Insect. Soc.
DOI 10.1007/s00040-012-0223-0

Insectes Sociaux

RESEARCH ARTICLE

Honey bee (*Apis mellifera capensis/A. m. scutellata* hybrid) nesting behavior in the Eastern Cape, South Africa

A. D. Vaudo · J. D. Ellis · G. A. Cambray · M. Hill

Received: 4 April 2011 / Revised: 15 January 2012 / Accepted: 20 January 2012

Abstract Little is known about the natural history of wild honey bee (*Apis mellifera*) colonies in the Eastern Cape Province of South Africa. The goal of this research was to examine nest site characteristics of honey bee (*A. m. capensis*/*A. m. scutellata* hybrid) colonies sampled from a variety of habitats (nature reserves, livestock farms, and an urban setting) in the Eastern Cape. We also determined how nest site location related to various colony strength parameters. In general, colonies not nesting in ground cavities tended to nest in locations >6 m high when nesting in cliffs and buildings and >2 m high when nesting in trees. Colonies typically nested in cavities whose entrances faced a southeasterly direction and were ~40 L in volume. We sampled a subset of colonies to determine the relationship between nest type and the following colony strength parameters: total area of comb in the colony, the volume of stored honey, pollen, and brood, adult bee population, the weight per adult bee, and the bee/nest cavity volume ratio. In general, colonies nesting in cliffs tended to be stronger than those nesting in the ground or trees. Our findings provide new insights into the nesting biology of honey bees in the Eastern Cape, South Africa, perhaps leading to the formation of conservation recommendations for honey bees in this region.

Keywords *Apis mellifera* · Nest site selection · Colony health · South Africa

Introduction

The Eastern Cape Province of South Africa is home to two subspecies of Western honey bee, *Apis mellifera capensis* Escholtz (the Cape honey bee) and *A. m. scutellata* Lepeletier (Hymenoptera: Apidae). The Cape honey bee's native distribution is restricted to the Western and Eastern Cape Provinces in South Africa (Hepburn and Radloff, 1998). A hybrid zone occurs on the northern boundary of the Cape honey bee's distribution where *A.m. capensis, A. m. scutellata,* and hybrids of the two are found (Hepburn and Radloff, 1998). The distribution of *A. m. scutellata* occurs north and east of this transition zone throughout South Africa and into east/central continental Africa. Both honey bee races are important pollinators in areas where they are distributed naturally. For example, in the dry savanna climatic zone of Africa, which extends into the study area of the current project, honey bees pollinate at least 18% of the herbs, 29% of the shrubs, and 52% of the trees (Hepburn and Radloff, 1998). Consequently, investigations into the natural history of honey bee nesting behavior in the Eastern Cape are important for understanding their contributions to

A. D. Vaudo (✉) · J. D. Ellis
Department of Entomology and Nematology, University of Florida, P.O. Box 110620, Gainesville, FL 32611, USA
e-mail: advaudo@gmail.com
URL: http://entnemdept.ifas.ufl.edu/honeybee/index.shtml

J. D. Ellis
e-mail: jdellis@ufl.edu
URL: http://entnemdept.ifas.ufl.edu/honeybee/index.shtml

G. A. Cambray
Makana Meadery, PostNet Suite #90, Private Bag x1672, Grahamstown 6140, South Africa
e-mail: meadery@gmail.com
URL: http://www.iqhilika.co.za/

M. Hill
Department of Zoology and Entomology, Rhodes University, P.O. Box 94, Grahamstown 6140, South Africa
e-mail: m.p.hill@ru.ac.za
URL: http://www.ru.ac.za/zoologyandentomology/staff/martinhill

Published online: 03 February 2012

ecosystem diversity and health, while providing background data useful for establishing and promoting honey bee conservation practices in the region.

Nest site selection is crucial to honey bee colony survival and reproductive success, making it an important behavior to study. Western honey bees typically nest in cavities, such as those found in cliffs, trees, manmade structures and underground (Crane, 1999). The selection of a good quality nest site is essential for a number of reasons. First, a nest site should be secure and easily defended (Steinhouse et al., 2005). Potential threats such as predation, parasitism, and harsh weather can disrupt, weaken, or even kill a honey bee colony (Morse and Flottum, 1997; Blaschon et al., 1999). Furthermore, a nest should be close to essential resources (Hansell, 1993; Steinhouse et al., 2005) to maximize foraging efficiency.

Nest site selection and availability can be affected by a number of factors, including resource availability, cavity size (Seeley, 1977), nest entrance orientation (Seeley and Morse, 1978), protection from the elements (Seeley and Morse, 1978), protection from predation (Kajobe and Roubik, 2006), and land use practices (Dietemann et al., 2009). For example, a land use practice such as 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 honey bees. Clearing land for agricultural use also may destroy potential ground cavity nesting sites. Urban settings on the other hand may provide a multitude of potential nesting sites to honey bees including cavities in roofs, walls, and underneath floorboards and in planted trees.

A honey bee colony's choice of an optimal nest site may optimize its strength and reproductive potential. If a nest is located close to adequate resources such as food and water, a colony may be more efficient at raising brood, storing foodstuffs, and regulating temperature. Nesting close to foraging resources has been modeled to predict bumblebee colony location and success (Suzuki et al., 2007). Foraging resources have also been shown to influence ant colony nest location (van Wilgenburg and Elgar, 2007). Additionally, a nest that is hard for predators to find or access would allow the colony to invest less energy and time in defense and absconding. Evasion of predators is important in ant (McGlynn et al., 2004) and stingless bee nesting choice (Kajobe and Roubik, 2006). Also, nest location could be important in colony thermoregulation as demonstrated in Argentine ants (Heller and Gordon, 2006). These factors may apply to honey bees as well.

In this study, we investigated various parameters associated with nest sites (independent of resource availability) of *A. m. capensis/A. m. scutellata* hybrids located in the Eastern Cape Province of South Africa, hypothesizing that these parameters would be related to colony strength. To address our hypothesis, we measured a number variables associated with honey bee nest sites and individual colony strength. Our long-term goal is to better understand the natural history of honey bees in South Africa, thus allowing us to outline conservation recommendations for honey bees in this region.

Methods and materials

Study area

We collected data from wild honey bee colonies nesting in Grahamstown, South Africa and on four farms and four game reserves near Grahamstown (33°18′37.50″S, 26°31′31.13″E, a small urban community in the Eastern Cape) in order to assess nesting behavior among different landscapes. Grahamstown and the surrounding vicinity are located in the Albany region of the Maputaland–Pondoland–Albany hotspot, a region that exhibits a convergence of the Albany Centre of Floristic Endemism and Cape Floristic Region biomes. 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). Grahamstown and its vicinity are considered to be in the hybrid zone of the Cape honey bee, *A. m. capensis* and *A. m. scutellata* (Hepburn and Radloff, 1998). Honey bees from colonies in the region were sampled and identified at an independent lab at the University of São Paulo, Brazil. Using morphometric tests, the bees were confirmed to be hybrids between *A. m. capensis* and *A. m. scutellata*.

The four reserves used in this project were Amakhala Game Reserve/Carnarvon Dale (33°29′45.07″S, 26° 7′24.05″E), Crown River Safari and Wildlife Reserve (33°24′33.49″S, 26°29′20.81″E), Emlanjeni Game Reserve (33°38′23.15″S, 26°35′22.51″E), and Kwandwe Game Reserve (33° 8′38.63″S, 26°32′19.00″E). Each reserve contained land that was converted from cattle and other livestock farms to reserves within the preceding 5 to 14 years. The four livestock farms used were Assegaai Trails (33°29′23.97″S, 26°35′2.85″E), Brentwood (33°28′25.78″S, 26° 9′28.21″E), Theo Harris's and Ezra Schoonbee's cattle farms (shared borders) (33°29′49.34″S, 26°27′44.82″E), and Hounslow (33°11′49.01″S, 26°25′20.86″E). All had been livestock farms for at least 15 years, with the farmers following farming practices typical of those in the area.

Locating honey bee colonies

Wild honey bee colonies were located in the eight study sites (four livestock farms and four game reserves) as well as in a single urban site (Grahamstown, South Africa). All colonies were located between September 2009 and March 2010. Some colonies were found by interviewing local landowners and their employees. Colonies in Grahamstown were located by searching and through interviews with homeowners and others who knew of existing colonies. Most of the remaining colonies were found using a bee-lining method modified from the one described in *The Bee Hunter* (Edgell, 1949) and subsequently used by others (Seeley and Morse, 1976; Seeley et al., 1982; Seeley, 1983; Visscher and Seeley, 1989). The method involves following the bee-line of foraging bees back to their colony from a food source. To establish bee lines to wild colonies, we baited feeding stations with a 1:3:3 mixture of honey:water:sugar, respectively, by volume. Feeding stations consisted of a 2 m tall iron rod with a plate on top and a plastic container affixed to the plate into which the bait was poured.

Feeding stations were placed throughout each study area so that some were close to cliffs, valleys, trees and open areas. Once the feeding stations were deployed, bee lines were established at each station and then followed away from the station to the wild nest. We were able to find ~90% of the colonies whose bee lines we followed. At times, the bee lines would occur over long distances and through areas of dense thicket, making them difficult to follow. During these instances, bee lines were reestablished 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. Colonies were also located by following foraging 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. A total of 94 colonies were located, with 42 in reserves, 32 on farms, and 20 in Grahamstown.

Nest site characteristics

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

1. GPS coordinates (to be able to relocate the colony for extraction)—recorded using a Garmin GPSmap 60CSx (Garmin International Inc., Olathe, KS) set to WGS 84 map datum,
2. nest type (building or other man-made structure, cliff, ground, or tree),
3. surrounding habitat (reserve, farm, or urban),
4. entrance orientation (compass direction that the nest entrance faced)—determined for true north,
5. height of the nest entrance from the ground (ground-nesting colonies were assigned a height of 0 m),
6. nest cavity volume—determined by extracting from cavities the nests of 19 colonies on farms, 18 colonies on reserves, and 4 colonies in Grahamstown.

   We estimated cavity volume (L) by observing the general shape of each nest cavity and measuring various dimensions to the nearest centimeter. Only the volume occupied by the comb was calculated for colonies that were located in open spaces such as in an attic or roof.

Colony dissection

Thirty-three colonies (17 from reserves and 16 from farms) of those located for determining nest site data were extracted from the cavity in which they nested and dissected to conduct colony strength readings. 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. All colonies were extracted between 7 May 2010 and 7 June 2010 to ensure that colony life cycles were similar for all colonies at the time of removal. This allowed a 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).

Removal of ground-nesting colonies was accomplished by opening the entrance to the colony using a chisel or pick if necessary. Efforts were made to prevent the earth from collapsing 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. Colonies nesting in cliffs were extracted by first removing the propolis covering the nest entrance and then using a “honey gathering stick” (made of fencing wire with a hook at the end) or a “Kwandwe staff” (a machete attached to the end of a long branch) to cut and remove the comb from the cavity ceiling. Access to colonies nesting in trees was accomplished using a machete, handsaw, and chisel. All combs from all colonies were stored in 20 L buckets. The buckets were placed in a freezer (−10°C) until ready to be measured.

Once the combs were removed from the cavity, clustering bees were collected to determine the number of bees in the nesting colonies. Bee clusters were collected from 19 of the extracted colonies (10 from reserves and 9 from farms) and placed into a cardboard 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. 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 then was determined. 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 us to determine an average weight per bee (g), estimate the number of bees in each colony (using the cluster weight), and determine the number of bees per liter in the nest cavity.

A transparent 500 cm^2 grid with vertical and horizontal lines every 1 cm was used to measure the total surface area (cm^2) of comb, honey, pollen, and brood (eggs, larvae, and pupae). These measurements were used to determine the proportion of comb that contained honey, brood, or pollen or that 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), 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 (Vaudo et al., 2011).

Statistical analyses

Nest entrance height (excluding colonies found in the ground) and cavity volume were compared between nesting types (building, cliff, ground, and tree) using a one-way ANOVA. In a second analysis, entrance height was assigned to one of the three categories: (1) entrances at or below ground level, (2) entrances >0 m but <3 m above ground, and (3) entrances ≥3 m above ground. Using Pearson's Chi-square test, the height categories then were compared by nesting types (building, cliff, and tree, Table 1) or when the data were pooled, to determine if colonies nested in cavities at a certain height more often than at other heights (Table 2).

Colony entrance orientations were mapped on a compass and examined for trends (Fig. 1). Nest entrance orientation was arranged and analyzed for 2 separate nest entrance comparisons, all based on "true" north:

Method 1: north versus east versus south versus west (north = entrances facing ≤45° and >315°, east = entrances facing >45° and ≤135°, south = entrances facing >135° and ≤225°, west = entrances facing >225° and ≤315°);

Method 2: northeast versus southeast versus southwest versus northwest (northeast = entrances facing ≥0° and <90°, southeast = entrances facing ≥90° and <180°, southwest = entrances facing ≥180° and <270°, northwest = entrances facing ≥270° and <360°).

Using Chi-square analysis, we determined whether colony entrance orientation was related to nesting type (Table 1), or when the data were pooled, whether colony entrances faced certain directions more often (Table 2).

Table 1 Nest site parameters compared for colonies nesting in the ground, buildings, cliffs, and trees

Parameter	Building (25)	Cliff (18)	Ground (33)	Tree (18)	ANOVA
Height (m) of nests	6.1 ± 0.9a (19)	6.5 ± 1.7a (11)	–	2.2 ± 1.4b (15)	$F_{2,42} = 5.3$; $P = 0.01$
Height category	1: 4	1: 4	–	1: 2	–
	2: 6	2: 3		2: 11	
	3: 25	3: 11		3: 5	
	$\chi^2(2) = 8.2$; $P = 0.02$	$\chi^2(2) = 6.3$; $P = 0.04$		$\chi^2(2) = 7$; $P = 0.03$	
Cavity volume (L)	76 ± 7.3a (6)	44.3 ± 6.7ab (6)	37.6 ± 6b (21)	36 ± 9.5b (8)	$F_{3,37} = 5.8$; $P < 0.01$
Entrance orientation (method 1)	North: 5	North: 2	North: 8	North: 3	
	East: 6	East: 7	East: 10	East: 4	
	South: 11	South: 5	South: 8	South: 3	
	West: 1	West: 4	West: 7	West: 7	
	$\chi^2(3) = 8.8$; $P = 0.03$	$\chi^2(3) = 2.9$; $P = 0.4$	$\chi^2(3) = 0.6$; $P = 0.9$	$\chi^2(3) = 2.5$; $P = 0.5$	
Entrance orientation (method 2)	NE: 5	NE: 0	NE: 10	NE: 2	
	SE: 13	SE: 10	SE: 8	SE: 5	
	SW: 3	SE: 2	SW: 8	SW: 6	
	NW: 2	NW: 6	NW: 7	NE: 4	
	$\chi^2(3) = 13$; $P < 0.01$	$\chi^2(3) = 13$; $P < 0.01$	$\chi^2(3) = 0.6$; $P = 0.9$	$\chi^2(3) = 2.1$; $P = 0.7$	

Data are mean ± SE (*N*) for ANOVA analyses and no. of colonies nesting in a given height category or no. of colonies with entrances facing a given direction. For χ^2 tests, *P* values ≤0.05 indicate that the data within the cell are not distributed randomly. For ANOVA analyses, row data followed by the same letter are not different at $\alpha = 0.05$. Nest entrance height categories are defined as: (1) entrances at or below ground level, (2) entrances >0 m but <3 m above ground, and (3) entrances ≥3 m above ground. Height category data are the number of colonies nesting in a given height category. Analyses are presented for entrance orientations considering true (rather than magnetic) compass directions. Entrance orientation data are the number of colonies with entrances facing a given direction

Table 2 Summary of nest site parameter data for honey bees nesting in the Eastern Cape, South Africa

Parameter	Colonies not nesting in manmade structures on reserves and farms	All colonies
Height (m) of nests (ground colonies excluded)	3.7 ± 1 (26)	4.6 ± 0.6 (48)
Height category	1: 36	1: 40
	2: 14	2: 23
	3: 12	3: 31
	$\chi^2(2) = 17.2$; $P < 0.01$	$\chi^2(2) = 4.6$; $P = 0.1$
Cavity volume (L)	38.6 ± 3.5 (35)	44.1 ± 3.8 (41)
Entrance orientation (method 1)	North: 12	North: 18
	East: 19	East: 27
	South: 16	South: 27
	West: 15	West: 19
	$\chi^2(3) = 1.6$; $P = 0.3$	$\chi^2(3) = 3.2$; $P = 0.36$
Entrance orientation (method 2)	NE: 11	NE: 17
	SE: 21	SE: 36
	SW: 14	SW: 19
	NW: 16	NW: 19
	$\chi^2(3) = 3.4$; $P = 0.3$	$\chi^2(3) = 10.4$; $P = 0.02$
Type	Cliff: 18	Building: 25
	Ground: 33	Cliff: 18
	Tree: 11	Ground: 33
	$\chi^2(2) = 12$; $P < 0.01$	Tree: 18
		$\chi^2(3) = 6.3$; $P = 0.1$

Data are mean ± SE (*N*) for height and cavity volume data. The number of colonies found in each nest type and each height category are included. For χ^2 tests, *P* values ≤0.05 indicate that the data within the cell are not distributed randomly. Nest entrance height categories are defines as: (1) entrances at or below ground level, (2) entrances >0 m but <3 m above ground, and (3) entrances ≥3 m above ground. Height category data are the number of colonies nesting in a given height category. Analyses are presented for entrance orientations considering true (rather than magnetic) compass directions. Entrance orientation data are the number of colonies with entrances facing a given direction. Analyses are presented for entrance orientations considering true (rather than magnetic) compass directions

The relationship between nest type ("building" excluded) and colony strength parameters was determined using a one-way ANOVA recognizing the following parameters as dependent variables: weight per bee (g); number of bees per colony; number of bees per liter of cavity volume; surface area (cm^2) of comb containing honey, brood, pollen, that was empty (nothing in cells), or filled (contained anything in cells); total comb area; and the proportion of comb that contained honey, brood, pollen, was empty, or was filled. Proportional data were arcsin square root transformed prior to analysis, although untransformed means are reported in "Results". The distribution of brood pattern ratings was compared within nesting types using Pearson's Chi-square test.

All nest site parameters were standardized so that the mean for each parameter equaled zero and MANOVA analyses were conducted to determine if nest type was correlated with:

1. weight per bee (g), number of bees per colony, and number of bees per liter cavity volume (cliff colonies were excluded because data were collected for only one colony),
2. surface area (cm^2) of comb containing brood, honey, pollen, that was filled, and total comb area,
3. the proportion of comb that contained brood, honey, pollen, and was filled.

All nest orientation data were analyzed using the statistical software package Oriana version 4 (Kovach Computing Services, 2011). All other analyses were conducted using the statistical software package JMP version 8.0 (SAS Institute, 2009). Data for pooled colony strength parameters for all extracted colonies is presented in Table 4 along with data collected from European honey bees (Seeley and Morse, 1976) and *A. m. scutellata* (Schneider and Blyther, 1988; McNally and Schneider, 1996).

Results

Nest site characteristics

The average nest entrance height of colonies not nesting in the ground was significantly higher for colonies nesting in buildings and cliffs than for colonies nesting in trees (Table 1). When analyzed by height category, colonies more frequently nested *above* ground in buildings, cliffs, and trees than at ground level (Table 1). The average cavity volume occupied by honey bee colonies was significantly

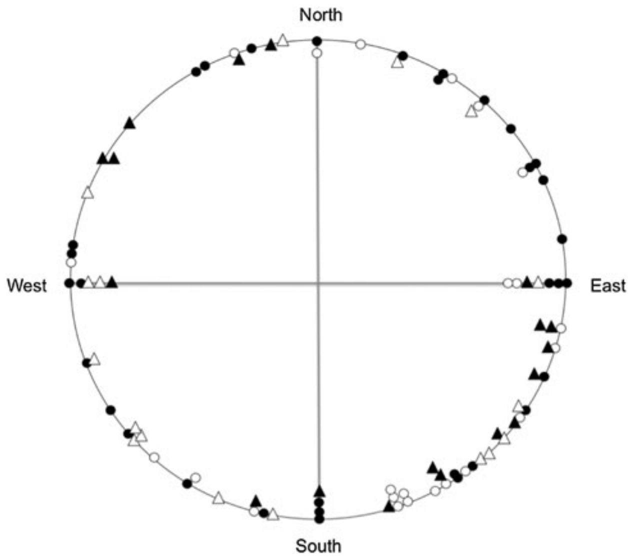

Fig. 1 The colony entrance orientations for honey bees nesting in the Eastern Cape, South Africa. *Black circles* indicate ground-nesting colonies. *White circles* indicate colonies nesting in manmade structures. *Black triangles* indicate cliff nesting colonies. *White triangles* indicate tree nesting colonies

larger in building cavities than ground and tree cavities, though cavity volume did not differ significantly between cliff, ground, and tree nests (Table 1). Nest entrance orientation was randomly distributed for colonies nesting in the ground or in trees, while colonies nesting in buildings and cliffs most often exhibited southeasterly facing entrances (Table 1; Fig. 1). When pooling entrance orientation data across all colonies, bees nested more often in cavities having southeasterly entrances (Table 2; Fig. 1). Pooled means of nest height, cavity volume, entrance orientation, and the number of colonies nesting in a particular cavity type on reserves, farms, and in Grahamstown (including and excluding colonies nesting in man-made structures) are reported in Table 2.

Colony strength

Nest type was significantly correlated with the surface area of honey, pollen, and total comb filled, and with the proportion of comb containing honey that was empty or that was filled (Table 3). Colonies nesting in cliffs contained more honey than colonies nesting in the ground, more pollen than colonies nesting in the ground or trees, had more comb area filled than colonies nesting in the ground or trees, had a higher proportion of pollen than colonies nesting in trees, and had a higher proportion of filled comb than colonies nesting in the ground (Table 3). Colonies nesting in trees had a larger proportion of their comb containing honey and filled comb than did colonies nesting in the ground (Table 3). No other colony strength parameters were significantly related to nest type. From MANOVA analyses, there was no observed relationship between nest type and weight per bee (g), number of bees per colony, and number of bees per liter cavity volume ($F_{1,15} = 0.09$; $P = 0.96$), or surface area (cm^2) of brood, honey, pollen, filled, and total comb ($F_{2,29} = 2$; $P = 0.06$). However, the MANOVA analysis did show that nest type was correlated with the proportion of comb that contained brood, honey, pollen, or that was filled ($F_{2,29} = 2$; $P < 0.01$), with colonies in cliffs using proportionately more of their comb than did colonies residing in the other nesting types (Table 3).

Discussion

Our study contributes to the understanding of the nesting behavior of honey bees in the Eastern Cape Province of South Africa. Nesting in the ground and in trees is a common trait of *A. m. scutellata* (Schneider and Blyther, 1988; McNally and Schneider, 1996) and other African races of bees (Hepburn and Radloff, 1998). Seeley and Morse (1978) found under controlled conditions that European honey bees around Ithaca, NY, USA nested in cavities 5 m above the ground more often than 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 fact that tree cavities or holes to access these cavities generally are closer to the ground while the cavities themselves extend upward. Regardless, we did not observe bees nesting consistently at any particular height.

Though we did not quantify nest site availability in the different locations, the distribution of nest sites inhabited by bees may indicate the relative nest site availability between study sites. For example, colonies in Grahamstown nested above the ground regularly and 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 trees that provide more nesting sites above the ground. In general, we found more honey bees nesting above ground than in ground cavities. Some species of stingless bees have been shown to do the same (Kajobe, 2007).

Beekeepers in the Northern hemisphere often prefer to face their colonies southward, presumably because the colonies forage more actively due to the consistent entrance exposure to the sun; Seeley and Morse (1978) found that feral colonies preferred southward facing entrances. Considering this information, we hypothesized that honey bees in the Eastern Cape would prefer to nest in cavities whose

Table 3 Colony strength parameters by nest type in the Eastern Cape, South Africa

Strength parameter	Ground	Tree	Cliff	ANOVA
Weight per bee (g)	0.1 ± 0.003a (11)	0.1 ± 0.004a (7)	–	$F_{1,16} = 0.04$; $P = 0.84$
Bees per colony	11,262 ± 1,640a (10)	12,048 ± 1,883a (7)	–	$F_{1,15} = 0.1$; $P = 0.76$
Bees per L cavity volume	439a ± 65a (10)	526 ± 191a (7)	–	$F_{2,15} = 0.2$; $P = 0.63$
Amount of brood (cm^2)	1,700 ± 235a (19)	1,201 ± 204a (7)	2,296 ± 492a (6)	$F_{2,29} = 2$; $P = 0.15$
Amount of honey (cm^2)	2,844 ± 450b (19)	4,211 ± 371ab (7)	5,785 ± 1,565a (6)	$F_{2,29} = 5.1$; $P = 0.03$
Amount of pollen (cm^2)	364 ± 65b (19)	237 ± 120b (7)	724 ± 130a (6)	$F_{2,29} = 4.2$; $P = 0.03$
Amount empty (cm^2)	3,764 ± 638a (19)	2,045 ± 393a (7)	2,769 ± 1,005a (6)	$F_{2,29} = 1.4$; $P = 0.27$
Amount filled (cm^2)	4,908 ± 607b (19)	5,649 ± 3,594b (7)	8,805 ± 1,549a (6)	$F_{2,29} = 4.9$; $P = 0.01$
Total comb (cm^2)	8,671 ± 1,080a (19)	7,694 ± 1,080a (7)	11,574 ± 1,659a (6)	$F_{2,29} = 1.6$; $P = 0.23$
Proportion 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 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 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 empty	0.42 ± 0.04a (19)	0.26 ± 0.04b (7)	0.24 ± 0.09b (6)	$F_{2,29} = 4.3$; $P = 0.02$
Brood pattern rating	1:[A]	1: 1	1:[A]	
	2: 5	2: 2	2: 1	
	3: 14	3: 4	3: 5	
	$\chi^2(1) = 4.3$; $P = 0.04$	$\chi^2(2) = 2$; $P = 0.37$	$\chi^2(1) = 2.7$; $P = 0.1$	

Data are mean ± SE (*N*) for ANOVA tests and no. of colonies assigned a given brood pattern rating for χ^2 analyses. Proportion data are proportion of comb containing a given variable. 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. 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)

[A] Data were excluded from analyses because χ^2 tests do not recognize “0” as a response

entrances more often faced north (since South Africa is in the southern hemisphere) or east. However, although colony entrances were found facing many directions (Fig. 1), there was a trend for colonies in this study to nest in cavities having a southerly and southeasterly orientation, especially in Grahamstown and when all of the data were pooled. Our results are consistent with data for *A. m. scutellata* in Botswana, whose colonies generally nested in cavities having south-facing nest entrances (Schneider and Blyther, 1988; McNally and Schneider, 1996).

Seeley and Morse (1976) reported that the volume of wild honey bee colony nest cavities around Ithaca, New York, USA was normally distributed around an average of 45 L. In choice tests, honey bees in New York preferred cavities that were greater than 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 colonies nested averaged ~39 L in volume. When including manmade structures, the average cavity volume was ~44 L. 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 a movable frame hive (Crane, 1999). The average volume of cavities in which bees nested in this study was larger than those reported by Schneider and Blyther (1988, ~17 L) and McNally and Schneider (1996, ~33 L) for *A. m. scutellata* colonies found in Botswana.

A relationship was observed between nest type and some colony strength parameters (Table 3). 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 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. Additionally, colonies nesting in cliffs may be more protected 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 (Kajobe and Roubik, 2006). The height of nests may be important for the health of bee colonies nesting in cliffs. Kajobe and Roubik (2006) found that stingless bee and honey bee nests closer to the ground were more likely to suffer predation than higher nests.

The data collected also permit us to compare the colony strength characteristics of the Eastern Cape colonies in

Table 4 Colony strength parameters for colonies sampled in our study, from the Okavango River Delta (McNally and Schneider 1996 or Schneider and Blyther 1988), and from New York State (Seeley and Morse 1976)

Parameter	Eastern Cape (*A. m. capensis*/*scutellata* hybrid)	Okavano (*A. m. scutellata*)	New York State (European honey bee)
Volume (L)	37.8 ± 3.6 (33); 37.4	44 ± 14 (38); 17	45 (8)[a]
Weight per bee (g)	0.983 ± 0.002 (19)	–	–
Bees per colony	12,060 ± 1,229 (18)	6,462 ± 1,336 (31)	18,804 ± 2,853 (5)
Bees per L cavity volume	484 ± 340 (18)	–	–
Amount brood (cm^2)	1,702 ± 179 (32)	–	–
Amount honey (cm^2)	3,649 ± 427 (33)	–	–
Amount pollen (cm^2)	395 ± 60 (33)	–	–
Amount (cm^2)	3,202 ± 427 (33)	–	–
Amount filled (cm^2)	5,695 ± 521 (33)	–	–
Total comb (cm^2)	8,896 ± 731 (33)	6,061 ± 484 (80)	23,400 ± 2,470 (8)
Proportion containing brood	0.22 ± 0.14 (32)	0.55 ± 0.03 (81)	0.25 ± 0.03 (8)
Proportion containing honey and pollen	0.43 ± 0.03 (33)	0.24 ± 0.02 (81)	0.55 ± 0.05 (8)
Proportion containing honey	0.39 ± 0.03 (33)	–	–
Proportion containing pollen	0.04 ± 0.01 (33)	–	–
Proportion empty	0.36 ± 0.03 (33)	0.22 ± 0.02 (81)	0.2 ± 0.03 (8)
Proportion filled	0.64 ± 0.03 (33)	0.78 ± 0.02 (81)	0.8 ± 0.03 (8)
Brood pattern rating	1: 1 2: 8 3: 23	–	–

Data are mean ± SE (*N*); median (where available)

[a] Data are median only

relation to those of feral European honey bee colonies in the United States and wild *A. m. scutellata* in Botswana. In general, European colonies had more bees and total comb area (Seeley and Morse, 1976) than did honey bee colonies sampled in our study (Table 4). On the other hand, *A. m. scutellata* had fewer bees and total comb (Schneider and Blyther, 1988, McNally and Schneider, 1996) than those sampled for this project (Table 4). The percentage of comb utilized for brood was similar between the European colonies and those in our study with ~25% of the comb utilized for brood in European colonies and ~22% of the comb utilized for brood in our sampled colonies. These values were much less than the percentage brood (~55%) found in *A. m. scutellata* colonies (Table 4). The amount of empty comb and the use of comb for honey and pollen storage differed for the three types of honey bees. 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. We found that honey bees nesting in the Eastern Cape 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).

There are a number of potential explanations for these results though we discuss only five 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 (abscond) throughout a season as resources become limited in a given habitat (Hepburn and Radloff, 1998) or due to predation, both of which can cause bees to construct less comb and store less food (McNally and Schneider, 1996). Second, the Eastern Cape and Okavango River Delta are semiarid environments (Schneider and Blyther, 1988) where flowering plants exist much of the year. Therefore, bees in our study and *A. m. scutellata* colonies may be pressured less to hoard honey or pollen. On the other hand, Seeley and Morse (1976) studied wild colonies in temperate New York, USA 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 flowering plants available year round, they can produce more swarms, thus experiencing population fluctuations over the year and limiting the maximum size of a colony (McNally and Schneider, 1996; Hepburn and Radloff, 1998). Fourth, the colonies in our study appeared to have an intermediate nesting biology between those of European and *A. m. scutellata* colonies. This may be an effect of the environmental conditions in each location. New York's climate is temperate, Botswana's is subtropical, and the Eastern Cape has a Mediterranean-type climate (Hepburn and Radloff, 1998). Finally, differences in nesting biology could be based on the season in which the colonies were sampled. While Seeley and Morse (1976) and

Schneider and Blyther (1988) sampled colonies in the summer and over a 12-month period respectively, we sampled colonies in autumn.

Though nest entrances in cliff and tree colonies typically do not have entrance obstructions as do those nesting in the ground (thorny bushes for example), most colonies nesting in cliffs and trees reduced their nest entrance to holes ~2–3 cm in diameter using propolis, consistent with Ellis and Hepburn (2003) and similar to what many species of stingless bees do (Roubik, 2006). This is especially true for colonies nesting in cliffs where propolis "walls" were constructed to enclose entire sides of colonies.

In conclusion, future research on honey bee nest site selection could be viewed at a larger scale using GIS technology to determine the effects of topography, canopy cover (Baum et al., 2005), vegetation biome and structure, proximity to water, etc. on nest site selection and colony strength. In addition, floral and nest site availability should be quantified and related to nest site selection. We believe that it is important to better understand the natural history of honey bees in South Africa and elsewhere, thus allowing one to outline conservation recommendations for honey bees globally.

Acknowledgments This project was made possible by the cooperation of the University of Florida (Gainesville, FL, USA) and Rhodes University (Grahamstown, South Africa). We are grateful to University of Florida and Rhodes University faculty (especially Professor Randall Hepburn), staff, and students for providing resources necessary for conducting the research. We thank General Motors of South Africa for the provision of a subsidized research 4 × 4 vehicle through Makana Meadery. We thank all the landowners, managers, employees of the study sites and Makana Meadery for allowing access and assistance during the field work phase of this project: Jennifer and Giles Gush, the Dell family, Mike Sparg, Hennie le Roux, Theo Harris, Ezra Schoonbee, Roger Hart, Charlene Bisset, Toast Rowan Seagers, Mirko Barnard, Coburs Delanga, Andy Ndyawe, Riaan Boucher, Phumlani Honi and Sindiswa Teyise. We also thank the laboratory of Dr. David deJong at the University of São, Paulo, Brazil for confirming the identity of the test honey bees.

References

Baum K.A., Rubink W.L., Pinto M.A. and Coulson R.N. 2005. Spatial and temporal distribution and nest site characteristics of feral honey bee (Hymenoptera: Apidae) colonies in a coastal prairie landscape. *Environ. Entomol.* **34**: 610-618

Blaschon B., Guttenberger H., Hrassnigg N. and Crailsheim K. 1999. Impact of bad weather on the development of the broodnest and pollen stores in a honeybee colony (Hymenoptera: Apidae). *Entomol. Gen.* **24**: 49-60

Crane E. 1999. *The World History of Beekeeping and Honey Hunting*. Gerald Duckworth & Co. Ltd., London

Dietemann V., Pirk C.W.W. and Crewe R. 2009. Is there a need for conservation of honeybees in Africa? *Apidologie* **40**: 285-295

Ellis J.D. and Hepburn H.R. 2003. A note on mapping propolis deposits in Cape honey bee (*Apis mellifera capensis*) colonies. *Afr. Entomol*. **11**: 122-124

Edgell G.H. 1949. *The Bee Hunter*. Harvard University Press, Cambridge

Hansell M.H. 1993. The ecological impact of animal nests and burrows. *Funct. Ecol.* **7**: 5-12

Heller N.E. and Gordon D.M. 2006. Seasonal spatial dynamics and causes of nest movement in colonies of the invasive Argentine ant (*Linepithema humile*). *Ecol. Entomol.* **31**: 499-510

Hepburn H.R. and Radloff S.E. 1998. *Honeybees of Africa*. Springer-Verlag, Berlin

Kajobe R. 2007. Nesting biology of equatorial Afrotropical stingless bees (Apidae; Meliponini) in Bwindi Impenetrable National Park, Uganda. *J. Apicult. Res*. **46**: 245-255

Kajobe R. and Roubik D.W. 2006. Honey-making bee colony abundance and predation by apes and humans in a Uganda forest reserve. *Biotropica* **38**: 210-218

Kovach Computing Services. 2011. Oriana Version 4 User's Manual. Kovach Computing Services, Pentraeth, Wales

Mangnall M.J. and Crowe T.M. 2003. The effects of agriculture on farmland bird assemblages on the Agulhas Plain, Western Cape, South Africa. *Afr. J. Ecol.* **3**: 266-276

McGlynn T.P., Carr R.A., Carson J.H. and Buma J. 2004. Frequent nest relocation in the ant *Aphaenogaster araneoides*: resources, competition, and natural enemies. *Oikos* **106**: 611-621

McNally L.C. and Schneider S.S. 1996. Spatial distribution and nesting biology of colonies of the African honey bee *Apis mellifera scutellata* (Hymenoptera: Apidae) in Botswana, Africa. *Environ Entomol.* **25**: 643-652

Morse R.A. and Flottum K. (Eds) 1997. *Honey Bee Pests, Predators, and Diseases*. A I Root Company, Medina

Roubik D.W. 2006. Stingless bee nesting biology. *Apidologie* **37**: 124-143

SAS Institute. 2009. JMP® 8 User Guide, 2nd ed. SAS Institute, Cary

Schneider S. and Blyther R. 1988. The habitat and nesting biology of the African honey bee *Apis mellifera scutellata* in the Okavango River Delta, Botswana, Africa. *Insect. Soc.* **35**: 167-181

Seeley T.D. 1977. Measurement of nest cavity volume by the honey bee (*Apis mellifera*). *Behav. Ecol. Sociobiol*. **2**: 201-227

Seeley T.D. 1983. The ecology of temperate and tropical honeybee societies. *Am. Sci*. **71**: 264-272

Seeley T.D. and Morse R.A. 1976. The nest of the honey bee (*Apis mellifera* L.). *Insect. Soc*. **23**: 495-512

Seeley T.D. and Morse R.A. 1978. Nest site selection by the honey bee, *Apis mellifera*. *Insect. Soc.* **25**: 323-337

Seeley T.D., Seeley R.H. and Akratanakul P. 1982. Colony defense strategies of the honeybees in Thailand. *Ecol. Monogr.* **52**: 42-63

Steinhouse I.J., Gilchrist H.G. and Montevecchi W.A. 2005. Factors affecting nest-site selection of Sabine's gulls in the Eastern Canadian Arctic. *Can. J. Zool.* **83**: 1240-1245

Suzuki Y., Kawaguchi L.G. and Toquenaga Y. 2007. Estimating nest locations of bumblebee *Bombus ardens* from flower quality and distribution. *Ecol. Res.* **22**: 220-227

van Wilgenburg E. and Elgar M.A. 2007. Colony structure and spatial distribution of food resources in the polydomous meat ant *Iridomyrmex purpureus*. *Insect. Soc.* **54**: 5-10

Vaudo A.D., Ellis J.D., Cambray G.A. and Hill M. 2011. The effects of land use on honey bee (*Apis mellifera*) population density and colony strength parameters in the Eastern Cape, South Africa. *J. Insect Conserv*. doi: 10.1007/s10841-011-9445-0 (published electronically in advance of print)

Victor J.E. and Dold A.P. 2003. Threatened plants of the Albany Centre of Floristic Endemism, South Africa. *S. Afr. J. Sci*. **99**: 437-446

Visscher P.K. and Seeley T.D. 1989. Bee-lining as a research technique in ecological studies of honey bees. *Am. Bee. J*. **129**: 536-539

Whitmore T.C. and Sayer J.A. (Eds) 1992. *Tropical Deforestation and Species Extinction.* Chapman & Hall, New York