

**A PHENOLOGICAL AND BIOCLIMATIC ANALYSIS OF HONEY YIELD IN
SOUTH AFRICA**

A thesis submitted in fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

of

RHODES UNIVERSITY

by

PETER MARK ILLGNER

November 2002

ACKNOWLEDGMENTS

I would like to thank my supervisor, Professor Randall Hepburn, for providing a stimulating intellectual environment and patience! I would also like to thank Martin Johansmeier who so generously provided the scale-hive records, Jeremy Baxter for statistical advice, Gillian McGregor for map production, my family, in-laws, friends and all the others who supported me in various ways over the years. I am particularly grateful to Lil Haigh for her patience and understanding and most of all to my wonderful wife for her unstinting support and my daughter Caitlin for her time!

ABSTRACT

This study has investigated the interaction between honeybees and their forage plants and the impact of selected climatic variables on honey production in South Africa. Twenty-seven scale-hive records from 25 localities have been used as a measure of colony honey reserves. At least 944 plant species are visited by honeybees in South Africa for their nectar and/or pollen, with more than half providing both rewards. The entire honeybee flora encompasses 532 genera and 137 families.

The flowering phenologies of the different reward categories of the indigenous forage plants are all significantly and positively correlated at the 0.05 level. Similarly, species offering both rewards are significantly and positively correlated with the flowering phenology of the null flora. The same results were obtained for correlations between the different reward categories of the exotic forage plants in South Africa.

Of the 30 species pairs which fulfilled the criteria for selection, 23 occurred in sympatry, 5 in allopatry and 2 in possible parapatry. There is evidence for both competition and facilitation within different indigenous species pairs.

The lack of geographical correlation in the intra-annual variation in honey stores and the near absence of any statistically significant ($p < 0.05$) honey related intra-annual intra-colonial correlations may indicate that the former is more important than the latter for the determination of the level of honey reserves within a colony.

Only one statistically significant correlation was found between either scale-hive record from the University of Pretoria Experimental Farm and any of the selected climatic variables. A one month lag period and/or possible seasonal effects were detected for each variable, with the exception of the duration of sunshine, in the autocorrelation analyses. A possible 12 month

seasonal period was also identified in the single series fourier analyses for a number of variables. Similarly, 12 months was also the most frequently recurring period in the cross-spectral results for the one scale-hive record (H42).

Any activities which have an impact on the landscape have the potential to affect honeybees and/or their forage plants. Honeybee crop or plant pollination may also enhance yields for commercial farmers and facilitate rural food security.

TABLE OF CONTENTS

Acknowledgments.....	ii
Abstract.....	iii
Contents.....	v
List of Figures.....	xi
List of Tables.....	xiii
 Chapter 1. Preface.....	 1
Chapter 2. Scale-hive records from South Africa.....	3
2.1. Introduction.....	3
2.2. Climate.....	4
2.3. Biomes.....	5
2.4. Conclusion.....	6
2.5. References.....	8
Chapter 3. Taxonomy and distribution of South African honeybee forage plants.....	11
3.1. Introduction.....	11
3.2. Methods.....	16
3.2.1. Nomenclature.....	16
3.2.2. Nectar.....	17
3.2.3. Distribution.....	17
3.3. Results.....	18
3.3.1. Floristic composition.....	18
3.3.2. Nectar sugar composition.....	24

3.3.3. Distribution.....	26
3.4. Discussion.....	29
3.5. References.....	32

Chapter 4. Trapping the light fantastic: the flowering phenology of South African honeybee

forage plants.....	45
4.1. Introduction.....	45
4.1.1. Physical environment.....	47
4.1.2. Biological environment: gene expression to community dynamics.....	52
4.1.3. Flowering phenology and the honeybee.....	59
4.1.4. Towards a theory of ultimate causation for honeybee forage plant flowering phenologies.....	61
4.2. Methods.....	62
4.3. Results.....	65
4.3.1. The null flora.....	65
4.3.2. Comparative analysis of reward phenologies.....	66
4.3.3. Comparative analysis of family phenologies.....	70
4.3.4. Comparative analysis of indigenous species pairs.....	74
4.3.5. <i>Eucalyptus</i> in South Africa.....	78
4.4. Discussion.....	81
4.4.1. Phylogenetic constraint.....	81
4.4.2. Pollinator-limitation.....	83
4.4.3. Exotic species flowering phenology.....	84
4.5. References.....	85

Chapter 5. Honeybees and land management in South Africa.....	93
---	----

5.1. Introduction.....	93
5.2. The impact of land use strategies on honeybees.....	94
5.3. Honeybee and plant conservation in South Africa.....	99
5.4. Honeybees in the service of man.....	102
5.4.1. Commercial crop pollination.....	102
5.4.2. Rural food security.....	104
5.5. Conclusion.....	106
5.6. References.....	107

Chapter 6. The geographical and intra-annual variation of honey reserves in South African

honeybee colonies.....	112
6.1. Introduction.....	112
6.1.1. The honeybee reproductive cycle.....	113
6.1.2. Honey storage: a global perspective.....	114
6.1.2.1. Queen traits.....	118
6.1.2.2. Worker traits.....	120
6.1.2.3. Colony size.....	122
6.1.2.4. Empty comb area.....	123
6.1.2.5. Do honey reserves affect the behaviour of nectar foragers?.....	124
6.2. Methods.....	124
6.2.1. Scale-hive records.....	124
6.2.2. Colony demography.....	127
6.3. Results.....	127
6.3.1. Scale-hive records.....	127
6.3.1.1. Site specific intra-annual variation and correlation.....	127

6.3.1.2. Biome specific intra-annual variation and correlation.....	134
6.3.1.3. Rainfall.....	139
6.3.1.4. Extreme hive weight variations for all records.....	141
6.3.2. Colony demography.....	142
6.3.2.1. Total comb area.....	143
6.3.2.2. Honey.....	144
6.3.2.3. Pollen.....	146
6.3.2.4. Worker brood.....	146
6.3.2.5. Drone brood.....	148
6.3.2.6. Queen cells.....	150
6.4. Discussion.....	151
6.4.1. Geographical variation.....	151
6.4.1.1. Geographical correlation of intra-annual variations in honey stores.....	151
6.4.1.2. The onset, duration and termination of the honey flow season.....	152
6.4.1.3. Intra-annual variation in the extremes for all records combined.....	153
6.4.1.4. Spatial variation in the magnitude of intra-annual changes in hive weight....	153
6.4.1.5. The implications of spatiotemporal variations in hive weight to commercial honey production.....	155
6.4.2. Colony demography.....	157
6.4.2.1. Total comb area.....	157
6.4.2.2. Honey reserves.....	157
6.4.2.3. Pollen stores.....	158
6.4.2.4. Worker and drone brood.....	159
6.4.2.5. Number of queen cells.....	161

6.5. References.....	162
----------------------	-----

Chapter 7. The influence of climate on honey reserves: a case study of two scale-hive records

from the University of Pretoria Experimental Farm.....	169
--	-----

7.1. Introduction.....	169
------------------------	-----

7.1.1. Air pressure (hPa).....	170
--------------------------------	-----

7.1.2. Cloud cover.....	170
-------------------------	-----

7.1.3. Duration of daily sunshine.....	171
--	-----

7.1.4. Evaporation.....	172
-------------------------	-----

7.1.5 Rainfall.....	172
---------------------	-----

7.1.6. Relative humidity (%).....	174
-----------------------------------	-----

7.1.7. Southern Oscillation Index (SOI).....	176
--	-----

7.1.8. Temperature (°C).....	176
------------------------------	-----

7.2. Methods.....	178
-------------------	-----

7.2.1. Descriptive statistics.....	179
------------------------------------	-----

7.2.2. Spearman Rank Order Correlations.....	179
--	-----

7.2.3. Time series analyses.....	180
----------------------------------	-----

7.2.3.1. Autocorrelation and cross-correlation.....	180
---	-----

7.2.3.2. Spectral analyses.....	180
---------------------------------	-----

7.3. Results.....	181
-------------------	-----

7.3.1. Scale-hive records (kg).....	181
-------------------------------------	-----

7.3.2. Air pressure (hPa) at 14h00.....	186
---	-----

7.3.3. Cloud cover (octas) at 14h00.....	187
--	-----

7.3.4. Daily sunshine (hours/day).....	189
--	-----

7.3.5. Evaporation (mm/day).....	190
----------------------------------	-----

7.3.6. Rainfall (mm/month).....	191
7.3.7. Relative humidity (%).....	193
7.3.8. Southern Oscillation Index (SOI).....	195
7.3.9. Temperature (°C).....	195
7.4. Discussion.....	197
7.5. References.....	201
Chapter 8. Conclusion.....	208
8.1. Introduction.....	208
8.2. Phylogeny of honeybee forage plants in South Africa.....	208
8.3. Flowering phenology of South African honeybee forage plants.....	210
8.4. Geographical variation in intra-annual changes in hive weight.....	215
8.5. Colony demography.....	217
8.6. The influence of climate on honey reserves: a case study of two scale-hive records from the University of Pretoria Experimental Farm.....	219
8.7. Conclusion.....	221
8.8. References.....	221
Appendix 2.A.....	222
Appendix 3.A.....	231
Appendix 6.A.....	263
Appendix 8A.....	275

LIST OF FIGURES

Figure 2.1. Distribution of scale-hive records in southern Africa.....	7
Figure 4.1. The null flora of indigenous honeybee forage plant species (n = 50).....	65
Figure 4.2. Flowering durations for the null flora.....	66
Figure 4.3. The flowering phenologies of indigenous honeybee forage plant species in South Africa according to reward category.....	67
Figure 4.4. The flowering phenologies of exotic honeybee forage plant species in South Africa according to reward category.....	68
Figure 4.5. The flowering phenologies of indigenous honeybee forage plants within the Asteraceae, Ericaceae and Fabaceae in South Africa.....	71
Figure 4.6. The flowering phenology of indigenous and exotic honeybee forage plant species within the Asteraceae in South Africa.....	72
Figure 4.7. The flowering phenologies of the indigenous and exotic honeybee forage plant species within the Fabaceae in South Africa.....	73

Figure 4.8. The flowering phenology of Eucalyptus within South Africa in relation to the flowering phenologies of the null, indigenous and exotic flora's.....	80
---	----

LIST OF TABLES

Table 3.1. A numerical summary of the honeybee forage plants of South Africa by reward (N = nectar source, P = pollen source, U = reward unknown).....	19
Table 3.2. Unresolved forage plant name changes. The scheme of nomenclature followed in each case is indicated in brackets after each set of alternatives.....	22
Table 3.3. A classification of South African honeybee forage plants according their nectar sugar composition (n = 81). (Based van Wyk, (1993), van Wyk <i>et al.</i> , (1993), Davis <i>et al.</i> (1994), Galetto <i>et al.</i> , (1994), Nicolson (1994), Barnes <i>et al.</i> (1995), Goldblatt <i>et al.</i> (1995, 1999), Davis (1997), Nicolson & van Wyk (1998), Goldblatt & Bernhard (1999)).....	25
Table 3.4. The centres of diversity for the 21 best represented indigenous honeybee forage plant genera in South Africa (after Gibbs Russel, 1987).....	28
Table 4.1. The flowering durations of indigenous and exotic honeybee forage plants in South Africa by reward category. I = indigenous species, E = exotic species, NP = source of nectar and pollen, N = source of nectar, P = source of pollen.....	69
Table 4.2. The flowering durations of indigenous and exotic honeybee forage plants in South Africa by family. I = indigenous, E = exotic, AST = Asteraceae, ERI = Ericaceae, FAB = Fabaceae, NULL = null flora.....	74

Table 4.3. Species pairs of congeneric honeybee forage plant species indigenous to South Africa.....	76
Table 4.4. Flowering duration and Spearman Rank Order Correlations for selected <i>Eucalyptus</i> species in South Africa and Western Australia.....	80
Table 5.1. Declared problem and honeybee forage plants in South Africa according to the Conservation of Agricultural Resources Act, 1983 (Act 43 of 1983)(Notice 2485 of 1999), Republic of South Africa. The plant species are listed alphabetically below in accordance with the biome in which the heaviest infestations can be found (<i>sensu</i> Richardson <i>et al.</i> , 1997)...	101
Table 5.2. The volume and value of commercial crops (Anonymous, 2001) pollinated by honeybees in South Africa. Only those crops for which honeybees are known to enhance yields are listed below (Crane & Walker, 1984).....	103
Table 5.3. A selection of fruit and seeds from honeybee forage plants utilised by poor rural communities in South Africa.....	105
Table 6.1. The pairwise correlation between scale-hive records according to <i>Procedure 1</i> ...	128
Table 6.2. The mean monthly weight gains and losses for selected scale-hive records (* = estimated mean monthly value - see text for technique).....	130

Table 6.3. The extent of correlation in the intra-annual variation in honey reserves at six selected localities (see Methods - <i>Procedure 2</i>) (n = 12).....	133
Table 6.4. The mean monthly hive weight changes in the savanna, grassland and fynbos biomes.....	136
Table 6.5. The extent of correlations of the intra-annual variations in hive weight of the three biomes; savanna, grassland and fynbos.....	139
Table 6.6. The maximum and minimum monthly hive weights associated with different rainfall classes.....	140
Table 6.7. The combined monthly extremes for all 27 scale-hive records.....	141
Table 6.8. The mean total comb area (cm ²) and percentage (%) of comb utilised in hives within the Andries Vosloo Kudu Reserve during 1992 and/or 1993.....	144
Table 6.9. The mean area (cm ²) covered by pollen, uncapped honey, capped honey and all honey comb in the hives within the Andries Vosloo Kudu Reserve in 1992 and/or 1993. The difference in the area (cm ²) covered by uncapped and capped honey is also indicated below.....	145
Table 6.10. The mean area (cm ²) of unsealed, sealed and total worker brood in hives within the Andries Vosloo Kudu Reserve in 1992 and/or 1993.....	148

Table 6.11. The mean area (cm ²) of drone comb, unsealed, sealed and total drone brood in hives within the Andries Vosloo Kudu Reserve in 1992 and/or 1993.....	150
Table 6.12. The mean number of queen cells in hives within the Andries Vosloo Kudu Reserve in 1992 and/or 1993.....	151
Table 7.1. Descriptive statistics for the changes in hive weight calculated from the two scale-hive records (H42 & H47) from the University of Pretoria Experimental Farm (n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).....	183
Table 7.2. The results of the single series fourier analyses carried out on the monthly changes in hive weight associated with the two scale-hive records (* = uneven series, see Methods for details).....	184
Table 7.3. The results of the cross-spectrum analyses on the monthly changes in hive weight associated with the two scale-hive records (¹ = repetitive periods within each scale-hive record are <u>underlined</u> , PF = Pretoria (Forum), SOI = Southern Oscillation Index (standardized), UP = University of Pretoria Experimental Farm, * = uneven series, see Methods for details).....	184
Table 7.4. The descriptive statistics for the mean monthly air pressure (hPa) at 14h00 for Pretoria (Forum)(n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).....	186

Table 7.5. The statistically significant Spearman Rank Order Correlations between the mean monthly air pressure (hPa) at 14h00 for Pretoria (Forum) and the other climatic variables investigated (except Pretoria (Forum))(PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).....187

Table 7.6. The descriptive statistics for the mean monthly cloud cover (octas) at 14h00 for the University of Pretoria Experimental Farm (n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).....188

Table 7.7. The statistically significant Spearman Rank Order Correlations between the mean monthly cloud cover (octas) at 14h00 for the University of Pretoria Experimental Farm and the other climatic variables investigated (except Pretoria (Forum))(PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).....188

Table 7.8. The descriptive statistics for the mean monthly daily sunshine (hours/day) for Pretoria (Forum)(n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).....189

Table 7.9. The statistically significant Spearman Rank Order Correlations between the mean monthly daily sunshine hours for Pretoria (Forum) and the other climatic variables investigated (except Pretoria (Forum))(PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).....190

Table 7.10. The descriptive statistics for the mean monthly evaporation (mm/day) for the University of Pretoria Experimental Farm (n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).....191

Table 7.11. The statistically significant Spearman Rank Order Correlations between the mean monthly daily evaporation for the University of Pretoria Experimental Farm and the other climatic variables investigated (except Pretoria (Forum))(PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).....191

Table 7.12. The descriptive statistics for the mean monthly rainfall (mm) for Pretoria (Forum) (PF) and the University of Pretoria Experimental Farm (UP)(n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).....192

Table 7.13. The statistically significant Spearman Rank Order Correlations between the mean monthly rainfall for the University of Pretoria Experimental Farm and the other climatic variables investigated (PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).....193

Table 7.14. The descriptive statistics for the mean monthly relative humidity (%) for the University of Pretoria Experimental Farm (n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).....194

Table 7.15. The statistically significant Spearman Rank Order Correlations between the mean monthly relative humidity for the University of Pretoria Experimental Farm and the other climatic variables investigated (except Pretoria (Forum))(PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).....194

Table 7.16. The descriptive statistics for the mean monthly SOI (standardized) (n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).....195

Table 7.17. The descriptive statistics for the mean monthly daily maxima and minima (°C) for the University of Pretoria Experimental Farm (n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).....196

Table 7.18. The statistically significant Spearman Rank Order Correlations between the mean monthly daily maxima and minima for the University of Pretoria Experimental Farm and the other climatic variables investigated (except Pretoria (Forum))(PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).....197

CHAPTER 1. PREFACE.

The climatic and botanical characteristics of the environment strongly influence the biology of the honeybee (*Apis mellifera*). The former also affects the flowering phenology and associated floral rewards of the honeybee forage plants. The climatic conditions within an area therefore have the potential to effect honeybees both directly and indirectly. This study investigates the influence climate and honeybee forage plants have on honey production in South Africa.

The study can be divided into two sections. The first has a botanical focus (Chapters 3-5), while the second considers the geographical variation in honey production and the potential climatic variables driving this variability (Chapters 6-7). The locations of known scale-hive records are shown in Chapter 2, where they have been placed within a biogeographical context.

Chapter 3 provides an analysis of the taxonomy and distribution of South African honeybee forage plants. To the author's knowledge the associated Appendix 3A provides the most comprehensive checklist of honeybee forage plants in South Africa. Both the floral reward categories and the flowering times have been indicated in Appendix 3A. The flowering phenologies of the honeybee forage plants are investigated in Chapter 4 within the context of both the floral rewards offered and their phylogenies. Where applicable, comparisons have been made between the indigenous and exotic honeybee floras in South Africa. In Chapter 5 the potential impacts of land management strategies on honeybees and *vice versa* have been reviewed. Issues such as plant conservation, commercial crop pollination and rural food security have all been discussed within this context.

The geographical and intra-annual variation in honey reserves within South Africa are investigated in Chapter 6. The spatial analyses of these honey reserves are based on a number

of scale-hive records obtained from the Plant Protection Research Institute in Pretoria. In addition, demographic data from colonies located in the Fish River valley have been used to examine fluctuations in the various components of the reproductive cycle and these components with each other. These components include the total comb area, the honey reserves, pollen stores, worker and drone brood and the number of queen cells.

Lastly, in Chapter 7, the influence of climate on honey reserves has been investigated, based on a case study of two scale-hive records from the University of Pretoria Experimental Farm. The climatic variables selected for this study include air pressure, cloud cover, duration of sunshine, evaporation, rainfall, relative humidity, the Southern Oscillation Index (SOI) and temperature.

A separate introduction and review of the relevant literature appears in each of the following chapters.

CHAPTER 2. SCALE-HIVE RECORDS FROM SOUTH AFRICA.

2.1. Introduction

A scale-hive and associated records should form an integral part of every beekeeper's ensemble of management tools. Scale-hives record changes in the weight of a hive over a selected time-period, preferably 24 hours. They have been used worldwide to monitor nectar flows, including countries such as Canada (Mitchener, 1955; Szabo, 1982 & 1996), Germany (Gerlach, 1985), South Africa (Schnettler, 1946; Johannsmeier, 1988), Tanzania (Smith, 1960), the United Kingdom (McLellan, 1977) and the United States (Hambleton, 1925; Munro, 1929; Jorgensen & Markham, 1946; Moffett & Parker, 1953). Changes in hive weight have been related to climatic variables (e.g. McLellan, 1977; Johannsmeier, 1988) and the flowering phenology of honeybee forage plants (e.g. Johannsmeier, 1988).

This chapter briefly outlines the biophysical environment in order to contextualize the ensuing chapters. The locations of 39 scale-hive records (see Appendix 2.A.) are illustrated in Figure 2.1, all but one of which, namely Beluluane (*c.* 25°55'S 32°24'E, 1939-1941) in Mozambique, are located in South Africa. The earliest four records from Morokwen(g) (*c.* 26°08'S 23°46'E, 1924-1930), Taylor's Siding/Halt (*c.* 29°41'S 30°11'E, 1927-1935), Duiwelskloof ("No.2", *c.* 23°43'S 30°08'E, 1929-1931) and Peach Farm (*c.* 28°39'S 31°29'E, 1929-1932) commenced in the 1920's. The honey yields reported by Garin (1931) for Morowen(g) have been assumed for the purposes of this study to refer to scale-hive data, although this has not been explicitly stated within the text. The longest scale-hive record came from the University of Pretoria Experimental Farm (*c.* 25°45'S 28°16'E, 1968-1991). A single scale appears to have been used at each location, with the exception of the University of

Pretoria Experimental Farm, Kalkfontein (c. 27°38'S 27°02'E, 1986-1990), near Kroonstad and Duiwelskloof No.2, where two were used simultaneously.

2.2. Climate

Climatic conditions in South Africa are extremely varied, with elevation exerting a significant effect over large areas of the interior. Low-lying areas are restricted to a narrow strip between the coast and the Great Escarpment, which reaches its maximum extent in the Natal Drakensberg (+3000 m above mean sea level). A series of step-like planation surfaces lie below the Great Escarpment, deeply dissected in places by river valleys, particularly along the eastern seaboard. Inland of the Great Escarpment river drainage is dominated by the Gariep (formerly Orange) in the south and the Limpopo in the north. An exception to the above occurs along the southern coast, roughly delimited by Cape Town in the west and Port Elizabeth in the east, where a series of fold mountains parallel to the coast provide an area of enhanced relief seaward of the Great Escarpment.

South Africa can be roughly divided into drier (< 500 mm *per annum*) western and wetter (> 500 mm *per annum*) eastern halves separated by the 26°E line of longitude. Most high rainfall (> 900 mm *per annum*) areas lie east of this great circle, such as the eastern seaboard and sections of the Great Escarpment (e.g. Natal Drakensberg). Additional areas of moderate (> 500 mm *per annum*) and high rainfall (> 900 mm *per annum*) occur along the southern and southwestern coastlines west of 26°E. Maximum annual rainfall may exceed 3500 mm (e.g. 3874 mm, Jonkershoek, 1950) or lie below 200 mm (e.g. 158 mm, Port Nolloth, 1925) (Schulze, 1965). Drier areas within South Africa tend to have a less predictable rainfall regime than wetter areas. Most rainfall in the country occurs in the summer, with the

exception of the southern and southwestern coastal areas where most rainfall occurs either all year round or in the winter respectively. Rainfall is usually associated with the passage of cold fronts or thunderstorms.

Mean annual air temperatures in South Africa are affected by latitude and moderated by altitude and proximity to the two bounding ocean currents, namely the cold Benguela current on the west coast and the warm Agulhas current on the east coast. Temperatures tend to increase equatorward, with the high-lying areas of the southern and eastern Great Escarpment, including the Drakensberg massif, roughly circumscribed by the 15°C isotherm for mean annual air temperature (Schulze, 1965). The effect of the two ocean currents mentioned above is well illustrated by the difference in value of the isotherms for mean annual air temperature associated with the corresponding areas of the west and east coasts at 30°S. The isotherm associated with the west coast (15°C) is 5°C cooler than the one for the east coast (20°C) (Schulze, 1965). Mean annual air temperatures in the region range from 23.3°C at Goodhouse on the Namibian border to 11.5°C at Mokhotlong in Lesotho. Isotherms for the intra-annual range in mean monthly air temperatures are greatest in the central interior (15°C) and least along the west (5.0°C) and east (7.5°C) coasts (Schulze, 1965). Marked drops in temperature are often associated with passing cold fronts while hot days can be associated with “föhn-like” “Berg” winds.

2.3. Biomes

The classification of vegetation communities within South Africa has been carried out a number of times, arguably the most notable treatments include those by White (1983), Acocks (1988), Rutherford & Westfall (1994) and Low & Rebelo (1996). The biome classification

system outlined in Low & Rebelo (1996) is closest to that shown in Figure 2.1. Scale-hive records are available for each of the seven biomes represented in Figure 2.1, with the exception of the forest biome for which none are known to exist. The succulent karoo (n=1) is the poorest represented and the savanna biome (n=15) the best represented of the remaining biomes. A more detailed analysis of the honeybee forage plants within these biomes and selected scale-hive records appears in Chapters 3-5 and Chapters 6-7 respectively.

2.4. Conclusion

The South African environment encompasses a wide variety of climatic conditions and habitats for honeybees. A number of scale-hive records have been produced over the past century representing a number of these environments. The manner in which the honeybees respond to these environmental conditions as expressed in part through these scale-hive records will be explored in forthcoming chapters.

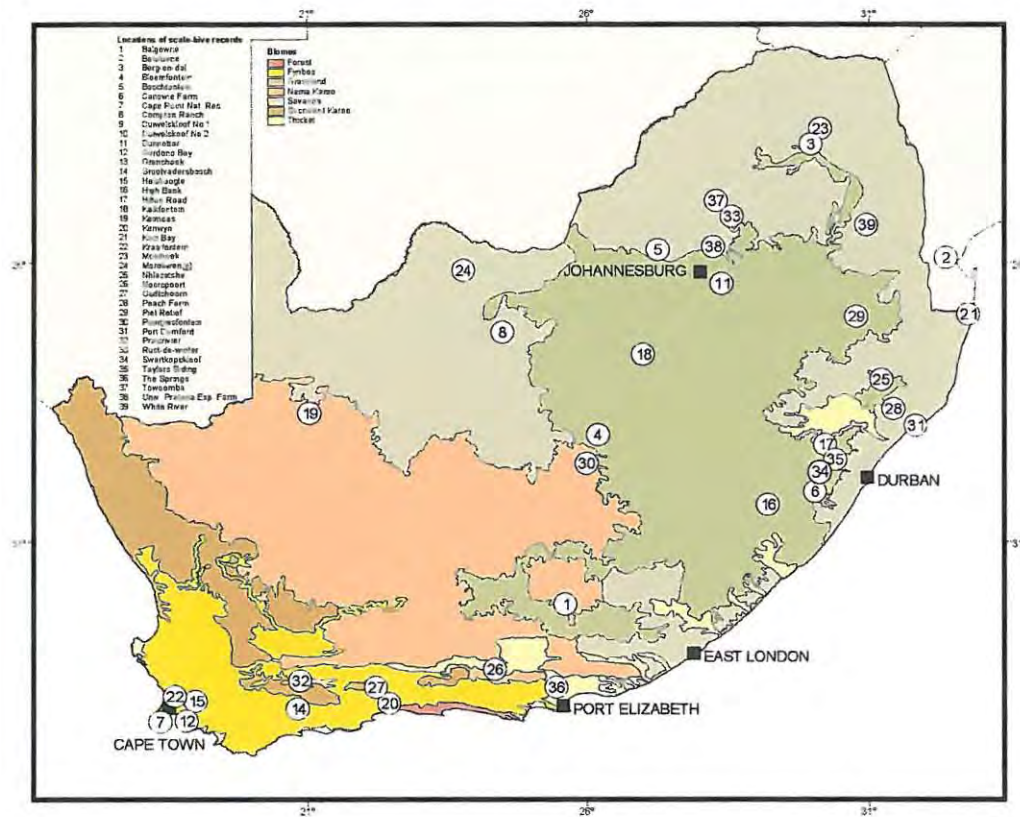


Figure 2.1 Distribution of scale-hive records in Southern Africa.

2.5. References

- Acocks, J.P.H. 1988. Veld types of South Africa. Third Edition. Memoirs of the Botanical Survey of South Africa No. 57, 146 pp..
- Garin, H. 1931. Morokwen (Bechuanaland) records. The South African Bee Journal, 6, 15-18.
- Gerlach, J. 1985. The dependence of honey-bee behaviour on weather - shown by the results of weighing bee-hives in the period of 1969 to 1978 in the region of the Beekeepers' Association of Hannover. International Journal of Biometeorology, 29, 67-85.
- Hambleton, J.I. 1925. The effect of weather upon the change in weight of a colony of bees during the honey flow. Department Bulletin No. 1339, United States Department of Agriculture, 51 pp..
- Johannsmeier, M.F. 1988. Beekeeping potential of native flora of South Africa. South African Bee Journal, 60, 98-108.
- Jorgensen, C. and Markham, F. 1946. Weather factors influencing honey production. Special Bulletin 340, Agricultural Experiment Station, Section of Horticulture, Michigan State College, East Lansing, 22 pp..
- Low, A.B. and Rebelo, A. (Eds). 1996. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria, 85 pp..

- McLellan, A.R. 1977. Honeybee colony weight as an index of honey production and nectar flow: a critical evaluation. *Journal of Applied Ecology*, 14, 401-408.
- Mitchener, A.V. 1955. Manitoba nectar flows 1924-1954, with particular reference to 1947-1954. *Journal of Economic Entomology*, 48, 514-518.
- Moffett, J.O. and Parker, R.L. 1953. Relation of weather factors to nectarflow in honey production. Technical Bulletin 74, Kansas Agricultural Experiment Station, Manhattan, Kansas, 27 pp..
- Munro, J.A. 1929. A study of the factors influencing the yield of honey during the main nectar flow. *Journal of Economic Entomology*, 22, 518-521.
- Rutherford, M.C. and Westfall, R.H. 1994. Biomes of southern Africa: an objective categorization. *Memoirs of the Botanical Survey of South Africa* No. 63, 94 pp..
- Schnettler, E.A. 1946. Honey production record. *The South African Bee Journal*, 21, 10.
- Schulze, B.R. 1965. Climate of South Africa. Part 8. General Survey. Weather Bureau, Department of Environmental Affairs, Republic of South Africa, WB 28, 330 pp..
- Smith, F.G. 1960. Beekeeping in the tropics. Longmans, London, 265 pp..

Szabo, T.I. 1982. Phenotypic correlations between colony traits in the honey bee. *American Bee Journal*, 122, 711-716.

Szabo, T.I. 1996. Scale colony records as indicators for nectar-producing plants in southern Ontario. *American Bee Journal*, 136, 733-736.

White, F. 1983. *The vegetation of Africa*. UNESCO, Paris, France.

CHAPTER 3. TAXONOMY AND DISTRIBUTION OF SOUTH AFRICAN HONEYBEE FORAGE PLANTS.

3.1. Introduction

Knowledge of the honeybee forage plants of any area can have significant economic benefits, not the least of which are the pollination services provided by the honeybee to commercial crops. This chapter documents the taxonomy and distribution of honeybee forage plants within South Africa. Where known, the nature of the rewards have also been indicated, namely nectar, pollen or both. An attempt has also been made in this chapter to characterise the nectar sugar composition of South African honeybee forage plants. An investigation of the floral morphology of the honeybee forage plants has not been carried out, although in a general sense this would be implicit within any taxonomic study.

Publications dedicated to the honeybee - forage plant axis in South Africa are modest, with the most significant in chronological order being those of Crisp (1957), Beyleveld (1968a&b), Looock (1983), Kennard (1988), Nicolson & W.-Worswick (1990), Eksteen & Johannsmeier (1991), Hepburn & Jacot-Guillarmod (1991), Johannsmeier (1975, 1984, 1988, 1995), and Johannsmeier & Allsopp (1995). In addition, Köttner (1991) has carried out a melissopalynological study of the Cape honeybee, *Apis mellifera capensis*. Two books on beekeeping also contain important information on honeybee forage plants, namely the works of May (1961) and Anderson *et al.* (1983). On a larger scale Hepburn & Radloff (1998) have reviewed the honeybee forage plants of the African continent. Very few if any floristic analyses of the potential co-evolutionary relationship between honeybees and their forage plants appears to have been carried out. The historical perception in the literature appears to be of

honeybees as consummate generalists, a view tested further on in this study. Whether this perception will withstand further scrutiny is debatable as Hepburn & Radloff (1998) have suggested the following with regard to the flowering phenologies of the African continent:

"In evolutionary terms the relationships between the honeybees and bee flora of Africa constitute a compelling example of diffuse co-evolution as defined by Futuyama (1986)." (Hepburn & Radloff, 1998, p.17)

Outside the apicultural field of study useful publications are available on the nectar sugar composition of the families Iridaceae (Goldblatt *et al.*, 1999) and Proteaceae (Mostert *et al.*, 1980; Cowling & Mitchell, 1981; van Wyk & Nicolson, 1995; Nicolson & van Wyk, 1998), the subfamily Alooideae within the Asphodelaceae (van Wyk *et al.*, 1993), the subfamily Papilionoideae within the Fabaceae (van Wyk, 1993) and the genera *Lapeirousia* (Goldblatt *et al.*, 1995), *Moraea* (Goldblatt & Bernhardt, 1999), *Erica* (Barnes *et al.*, 1995) and *Eucalyptus* (Nicolson, 1994). In addition, significant data is available on nectar volume and nectar sugar concentration within the family Iridaceae (Goldblatt *et al.*, 1995 & 1999; Goldblatt & Bernhardt, 1999), with a number of other publications covering various other species (e.g. Wiens & Rourke, 1978; Collins, 1983a,b,c; Louw & Nicolson, 1983; Nicolson & W.-Worswick, 1990; Brieschke, 1991; Nicolson, 1994). Very little additional quantitative data appears to be available with regard to the reward value of floral nectars in South Africa. The only apparent exceptions being the concentration of K and Na in various species reported by Nicolson & W.-Worswick (1990) and the concentration of protein (Mean = 1.2 ± 0.9 g/100 ml, Range = 0-3.3 g/100 ml) and free amino-acid (Mean = 0.7 ± 1.4 mg/100 ml, Range = 0-39 mg/100 ml) in the nectar of *Protea repens* by Mostert *et al.* (1980). No studies to the

author's knowledge have been done on the pH of floral nectars of the region, with the exception of Baker & Baker (1983) who report a low acidic pH (2.8) for *Strelitzia reginae*.

The extent of post-secretory changes in nectar composition facilitated by micro- and/or macro-organisms is also poorly documented. These changes may be significant as Mostert *et al.* (1980) reported a build-up of ethyl alcohol associated with the fermentation of sugars in the older inflorescences of *Protea repens* (Mean = 1.1 ± 0.8 g/l, Range 0-1.8 g/l). Further afield, Percival (1961) has speculated that intra- and interspecific differences in nectar sugar composition may be attributed to enzymes such as transfructosidase and transglucosidase in nectar. More recently and locally, Nicolson & van Wyk (1998) have proposed a proximate causal relationship between the conversion of sucrose to the hexose sugars fructose and glucose in the nectary. Nectar sugar composition is also known to vary with age (Percival, 1961 & 1965; Nicolson & van Wyk, 1998) and on an intraspecific level, geographic location (Percival, 1961) and ploidy (Davis *et al.*, 1994) although the taxonomic extent of either appears uncertain. Indeed, it is difficult to determine the taxonomic extent of any of the features affecting nectar sugar composition discussed above. In a survey of +850 nectars Percival (1961) found that only 61 (< 10%) had inconsistent nectar sugar compositions.

More recently, the intraspecific uniformity in nectar sugar composition has been reiterated by Free (1993). It is therefore tempting to assume that a relationship exists between nectar sugar composition and the pollination syndromes of flowering plants, however evidence in this regard is lacking for South Africa. No unequivocal support for an association of this nature could be found within the Proteaceae (Nicolson & van Wyk, 1998), the subfamilies Alooideae (Asphodelaceae) (van Wyk *et al.*, 1993) and Papilionoideae (Fabaceae) (van Wyk, 1993) or the genus *Erica* (Barnes *et al.*, 1995). Perhaps as van Wyk *et al.* (1993) have suggested for the Alooideae, nectar sugar composition is a better indicator of phylogeny than

co-evolutionary relationships with pollinators. A conclusion by Baker & Baker (1983) in this regard nearly 20 years ago appears as valid today as it was then, namely:

"...there may be some tendency to predispose members of a particular family to pollination by particular classes of pollinators by reason of nectar chemistry, but this can be out-weighed by adaptations in the morphological (and phenological) features of flowers and inflorescences." (Baker & Baker, 1983, p.138)

Nevertheless, Wykes (1952) reported that honeybees do have a preference for certain types of nectar sugar composition if concentration is kept constant. He found that when sugars were tested singly, sucrose was the most and fructose the least favoured nectar, with glucose of intermediate importance. In addition he discovered that an equiproportional mixture of the three sugars was favoured above all other single, binary or ternary combinations of the sugars in an assortment of ratios. However, Waller & Bachman (1981) found no evidence to support a preference by honeybees for one mixture of sugars over another, but agreed with Wykes (1952) that sucrose is preferred above all other sugars. They also found that nectar concentration can affect the relative preference of honeybees for fructose or glucose. At concentrations of 10%, 20% and 30% fructose is preferred, but at 40% and 50% glucose is collected in greater volumes. However, the sugar composition is possibly the least significant of the tripartite combination of features by which honeybees evaluate the quality of a nectar source. Free (1993) suggested the other two, concentration and volume were the most important factors governing the value of nectar to honeybees. Similarly, Crane (1990) proposed that nectar concentration is the most important criterion honeybees use to evaluate a resource, implying that volume is of lesser significance. Indeed, as Butler (1945) so succinctly

put it more than 50 years ago:

“Nectar concentration appears to be very largely the species determiner, nectar abundance the population determiner.” (Butler, 1945 p.11)

However, nectar concentration and/or volume may be affected by weather conditions, the age of both flowers and plants, the sex of flowers, ploidy and removal by pollinators (Butler, 1945; Oertel, 1946; Percival, 1965; Baker & Baker, 1983; Free, 1993; Galetto *et al.*, 1994; Nicolson, 1994). Nectar may also be reabsorbed by a species e.g. the forage plants *Brassica napus* (Búrquez & Corbet, 1991) and *Grevillea robusta* (Nicolson & van Wyk, 1998). Therefore, only nectar sugar composition, the attribute displaying the least amount of intraspecific variation is investigated further.

No work has been published to the author's knowledge which analyses the main characteristics of the pollen collected by honeybees within South Africa, with the exception of the research by Köttner (1991) which investigated the mineral and protein content. This is surprising given the well-known nature of the pollen morphology of the local flora (e.g. van Zinderen Bakker, 1953 & 1956, van Zinderen Bakker & Coetzee, 1959, etc). Köttner (1991) reported that the protein content of the main pollen plants was less than 20%, while the predominant elements in order of decreasing concentration were K, P, and Ca. However, in keeping with the main theme of this study, namely honey flow, the emphasis in this chapter is on the nectar rewards and more specifically as stated earlier, the nectar sugar composition.

3.2. Methods

The known floral rewards for South African honeybee forage plants listed in Appendix 3.A were obtained from the literature. However, as a generalization returning foragers with pollen loads (and not propolis) in their corbiculae may be regarded as pollen or pollen and nectar foragers, while the remainder would most likely be nectar foragers with a lesser number collecting only water (Free, 1993).

3.2.1. Nomenclature

A literature survey was conducted to obtain a list of the honeybee forage plants of South Africa. The main sources of information were May (1961), Anderson *et al.* (1983), Johannsmeier (1995), and Johannsmeier & Allsopp (1995). The nomenclature in this study follows Arnold & de Wet (1993) (AD - Appendix A) unless otherwise stated. Species not listed in Arnold & de Wet (1993) follow in order of decreasing precedence Flora Europaea (FE - Appendix A), W³TROPICOS of the Missouri Botanical Gardens, and the Index Kewensis entries within the International Plant Names Index (IPNI(IK) - Appendix A). The only exceptions to the above are the species (e.g. the genera *Eucalyptus*, *Grevillea*, *Hakea*, and *Melaleuca*), selected on an *ad hoc* basis, which follow the Australian Plant Names Index (APNI - Appendix A). Exotic species are indicated with an asterisk “*”. Any species listed as an exotic in Arnold & de Wet (1993) or not listed within it is assumed *ex silentio* to be an exotic within southern Africa. Problem plants listed within South Africa’s Conservation of Agricultural Resources Act, 1983 (Act 43 of 1983) (Notice 2485 of 1999) are marked in superscript within Appendix A. Likewise, indicators of bush encroachment are marked by a

“B”. Definitions of these plants are given within the “Methods” of Chapter 5.

3.2.2. Nectar

The sugar compositions of floral nectars produced by honeybee forage plants were obtained from published data, primarily van Wyk (1993) (Asphodelaceae), Barnes *et al.* (1995) (Ericaceae), van Wyk (1993) (Fabaceae), Goldblatt & Bernhardt (1999), Goldblatt *et al.* (1995,1999) (Iridaceae), Nicolson (1994) (Myrtaceae), and Nicolson & van Wyk (1998) (Proteaceae). Values indicated as trace amounts were taken as 0 e.g. Barnes *et al.* (1995). The ratios of sucrose to the hexose sugars, fructose and glucose, were then calculated for each species if not already available. These ratios were then assigned to one of the following four categories in order of decreasing sucrose content, > 0.999 (sucrose-dominant), 0.5 - 0.99 (sucrose-rich), 0.1 - 0.499 (hexose-rich), and < 0.1 (hexose-dominant) (Baker & Baker, 1983).

3.2.2. Distribution

Data on the worldwide distribution of indigenous genera were obtained from Goldblatt (1978). The southern African distribution of bee taxa within the fynbos, savanna, grassland, succulent Karoo, and Nama-Karoo biomes is in accordance with Gibbs Russel (1987). The conservation status of the honeybee forage plants were obtained from Hilton-Taylor (1996a & b).

3.3. Results

3.3.1. Floristic Composition

The complete list of the honeybee forage plants appears in Appendix 3.A. A summary of the numerical breakdown of the honeybee forage plants of South Africa in accordance with the different reward categories is presented in Table 3.1. A minimum of 137 families representing 532 genera have been reported for the country, of which at least 91 (66.42%) families and 241 (45.30%) genera are indigenous (Appendix 3.A). This is an underestimate of the total as it excludes genera which have been reported as bee plant taxa, but for which no species name was recorded in the original source or species that are known hybrids. At least 464 (excluding hybrids) (49.15%) of a minimum 944 (including hybrids) species of honeybee forage plant are indigenous to South Africa (Appendix 3.A).

Table 3.1. A numerical summary of the honeybee forage plants of South Africa by reward (N = nectar source, P = pollen source, U = reward unknown).

	N & P	N	P	U	Total
Indigenous					
Number of Families					91
Number of Genera (excl. sp., spp., hybrids)					241
Number of Species (excl. sp., spp., hybrids)	203	104	63	94	464
Exotic					
Number of Families					93
Number of Genera (excl. sp., spp.)					266
Number of Species (excl. sp., spp.)	330	58	74	18	480
Total					
Number of Families					137
Number of Genera					532
Number of Species	533	162	137	112	944

Most species ($n=533$, 56.46%) provide both nectar and pollen rewards to foraging honeybees. Far fewer plant species provide only nectar ($n=162$, 17.16%) or pollen ($n=137$, 14.51%). It is unclear what the nature of the reward is for 112 (11.86%) of the forage plants. Less than half ($n=203$, 43.75%) of the indigenous bee plant taxa are sources of both nectar and pollen, with 104 (22.41%) species utilised solely for nectar and 63 (13.58%) solely for pollen. The reward status of 94 (20.26%) indigenous species remains to be determined.

The best represented families (indigenous + exotic), with the numbers of genera in brackets, are the Asteraceae (58), Fabaceae (54), Mesembryanthemaceae (19), Rosaceae (17), Lamiaceae (15) and Myrtaceae (15). The largest families (indigenous + exotic), with the

numbers of species in brackets, are the Fabaceae (119), Myrtaceae (104), Asteraceae (96), Proteaceae (50) and Rosaceae (31). The five best represented indigenous genera are *Erica* (15), *Aloe* (14), *Pelargonium* (14), *Aspalathus* (13), and *Protea* (12). The Orchidaceae are the largest family not represented in the honeybee flora, with 439 species in 54 genera in southern Africa (Gibbs Russel, 1985). The largest genera on the subcontinent not recorded as forage plants in South Africa, with number of indigenous species and family in parentheses, are *Conophytum* (301, Mesembryanthemaceae), *Delosperma* (159, Mesembryanthemaceae), *Haworthia* (153, Asphodelaceae), *Restio* (113, Restionaceae), and *Stapelia* (88, Asclepiadaceae).

In addition, there are a number of plant species indigenous to southern Africa which remain to be reported as forage plants within South Africa, but have been reported as such elsewhere. These include, with reward indicated, *Aloe dichotoma* (Nectar & Pollen, Asphodelaceae), *Carissa macrocarpa* (Nectar, Apocynaceae), *Clematopsis scabiosifolia* (Pollen, Ranunculaceae), *Cleome gynandra* (Pollen, Capparaceae), *Cynodon dactylon* (Pollen, Poaceae), *Monechma genistifolium* (Nectar, Acanthaceae), *Petalidium linifolium* (Nectar, Acanthaceae), *Pteridium aquilinum* (Nectar, Dennstaedtiaceae), *Sesamum angustifolium* (Pollen, Pedaliaceae), *Sida cordifolia* (Pollen, Malvaceae), *Sporobolus pyramidalis* (Pollen, Poaceae), and *Waltheria indica* (Pollen, Sterculiaceae) (Smith, 1957; Percival, 1965; Crane & Walker, 1984; Free, 1993; Tribe & Johannsmeier, 1996). *Carissa*, *Clematopsis*, *Pteridium*, *Sesamum*, *Sida*, *Sporobolus*, and *Waltheria* would all be new generic records for South Africa. It is also interesting to note that *Ricinus communis*, a "Category 2" exotic plant invader in South Africa, comprised 31% of the pollen in one honey sample from Tengeru, Tanzania (Smith, 1957).

Nectar is not only collected from floral sources, but also extra-floral nectaries. In

South Africa there are a few records e.g. *Acacia terminalis* (petiole) (Voges, 1979). A number of nectar and pollen substitutes have also been reported in the South African literature. Honeybees reportedly collect sap (phloem) from burnt or cut sugar cane (*Saccharum officinarum*), the juice from bird or insect damaged grapes (*Vitis vinifera*), and manna from damaged areas on *Eucalyptus viminalis* plants caused by the eucalyptus snout beetle (Voges, 1979; Johannsmeier, 1981; Anderson *et al.*, 1983). Honeydew produced by the Black Pine Aphid (host: *Pinus* spp.) and Willow Aphid (host: *Salix babylonica*) has also been collected by honeybees in South Africa (Anderson *et al.*, 1983). Reported pollen substitutes include *Melampsora* sp. fungal spores, trichomes and maize dust (Johannsmeier, 1981).

During the compilation of the list of honeybee forage plants in Appendix A some problems arose related to the identification of a number of species. The following species have only tentatively been identified as honeybee forage plants, *Aspalathus flexuosa*, *Othonna filicaulis*, *Papaver somniferum*, *Viburnum sinensis* and *Yucca filamentosa* (Johannsmeier, 1995). Furthermore, it is uncertain whether Eksteen & Johannsmeier (1991) and May (1961) were referring to species within the genera *Oxygonum* and *Wisteria* respectively in the singular or plural. No species author name was obtainable for *Euphorbia veronica* or the hybrids, *Abutilon* x *hybridum*, *Cheiranthus* x *allionii*, *Cytisus* x *kewensis*, *Erica capensis* x *E. laeta*, *Gladiolus* x *hortulanus* and *Penstemon* x *spectabilis* (Anon., 1981; Johannsmeier, 1995). Foraging records with untraceable species names which possibly represent spelling errors include *Aspalathus filiformis* (possibly *A. filicaulis* Eckl. & Zeyh.), *Maytenus heteracantha* (possibly *M. heterophylla* (Eckl. & Zeyh.) N.K.B. Robson or *M. polyacantha* (Sond.) Marais) and *Westringia rosmarinifolia* (possibly *W. rosmariniformis* Sm., *W. rosmariniformis* Labill. ex Benth. or *W. rosmarinacea* Andr.) (Scharf, 1986; Challen & Scharf, 1987; Johannsmeier,

1995; Johannsmeier & Allsopp, 1995). *Lycium horridum* and *Olea laurifolia* have also been cited by Johannsmeier (1984) and Phillips (1928) respectively as honeybee forage plants, however neither of the apparently indigenous species is listed in Arnold & de Wet (1993). Lastly, the correct names of a number of forage plants which have undergone name changes remain unresolved, these species are listed in Table 3.2.. No species author names appear in the original text which would have made the final selection of the correct name possible.

Table 3.2. Unresolved forage plant name changes. The scheme of nomenclature followed in each case is indicated in brackets after each set of alternatives.

Species	Alternatives	Original Reference(s)
<i>Acacia giraffae</i>	<i>A. giraffae</i> Willd. = <i>A. erioloba</i> x <i>A. haematoxylon</i> ; <i>A. giraffae</i> sensu auct. mult., non <i>A. giraffae</i> Willd. = <i>A. erioloba</i> (Arnold & de Wet, 1993)	Beyleveld (1968b) Poynton (1973)
<i>Althaea rosea</i>	<i>A. rosea</i> (L.) Cav. = <i>Alcea rosea</i> L.; <i>A. rosea</i> auct.balcan., non (L.) Cav. = <i>Alcea setosa</i> (Boiss.) Alef.; <i>A. rosea</i> auct.plur., non (L.) Cav. = <i>Alcea pallida</i> (Willd.) Waldst. & Kit. (Flora Europaea)	Johannsmeier (1995) Johannsmeier & Allsopp (1995)
<i>Aspalathus elongata</i>	<i>A. elongata</i> E. Mey. a. <i>virgata</i> Benth. = <i>A. linguiloba</i> Dahlg.; <i>A. elongata</i> Eckl. & Zeyh. = <i>A. quinquefolia</i> L. (Arnold & de Wet, 1993)	

<i>Aspalathus thymifolia</i>	<i>A. thymifolia</i> L. = <i>A. cymbiformis</i> DC.; <i>A. thymifolia</i> L. a. <i>albiflora</i> (Eckl. & Zeyh.) Benth. = <i>A. hispida</i> Thunb. subsp. <i>albiflora</i> (Eckl. & Zeyh.) Dahlg. (Arnold & de Wet, 1993)	Taylor (1937) Johannsmeier (1995)
<i>Cheiranthus cheiri</i> L.	Listed as both accepted and as a synonym for <i>Erysimum cheiri</i> (L.) Crantz. (Flora Europaea)	Johannsmeier (1995)
<i>Cytisus albus</i>	<i>C. albus</i> (Lam.) Link, non Hacq. = <i>C. multiflorus</i> (L'Hér.) Sweet; <i>C. albus</i> Hacq. = <i>Chamaecytisus albus</i> (Hacq.) Rothm. (Flora Europaea)	Johannsmeier (1995)
<i>Erica mediterranea</i>	<i>E. mediterranea</i> L. = <i>E. herbacea</i> L.; <i>E. mediterranea</i> auct., non L. = <i>E. erigena</i> R.Ross (Flora Europaea)	Johannsmeier (1995)
<i>Rhus viminalis</i>	<i>R. viminalis</i> Ait. = <i>R. lancea</i> L. f.; <i>R. viminalis</i> sensu Schonl. et auct. mult. non Ait. nec Vahl = <i>R. pendulina</i> Jacq.; <i>R. viminalis</i> sensu Vahl non Ait. = <i>R. laevigata</i> L. (Arnold & de Wet, 1993)	Eksteen & Johannsmeier (1991) Johannsmeier (1995)

3.3.2. Nectar Sugar Composition

The nectar sugar compositions of 81 South African honeybee forage plants are presented in Table 3.3. Note that seven (8.64%) species are represented in more than one category, namely *Eucalyptus grandis*, *Protea burchellii*, *P. pruinosa*, *P. pudens*, *Trifolium repens*, *Virgillia oroboides* and *Watsonia meriana*. The overwhelming majority of species have nectar sugar compositions which are either hexose-dominant ($n = 41$, 50.62%) or sucrose-dominant ($n = 33$, 40.74%). Less than 10% of the species have nectar compositions which could be categorized as hexose-rich ($n = 7$, 8.64%) or sucrose-rich ($n = 7$, 8.64%). The nature of this apparently polarized distribution of nectar sugar compositions is considered further in the discussion.

Table 3.3. A classification of South African honeybee forage plants according to their nectar sugar composition (n = 81) (Based on van Wyk (1993), van Wyk *et al.* (1993), Davis *et al.* (1994), Galetto *et al.* (1994), Nicolson (1994), Barnes *et al.* (1995), Goldblatt *et al.* (1995,1999), Davis (1997), Nicolson & van Wyk (1998), Goldblatt & Bernhardt (1999)).

Species	# Species
Hexose-dominant (Sucrose / Glucose + Fructose < 0.1) <i>Aloe arborescens</i> , <i>Aloe castanea</i> , <i>Aloe greatheadii</i> , <i>Aloe bracteata</i> , <i>Brabejum stellatifolium</i> , <i>Brassica napus</i> , <i>Chasmanthe floribunda</i> , <i>Corymbia ficifolia</i> , <i>Erica bauera</i> , <i>Erica glandulosa</i> , <i>Erica sphaeroidea</i> , <i>Erythrina caffra</i> , <i>Erythrina crista-galli</i> , <i>Erythrina lysistemon</i> , <i>Eucalyptus calophylla</i> , <i>Eucalyptus grandis</i> , <i>Eucalyptus robusta</i> , <i>Faurea saligna</i> , <i>Leucospermum catherinae</i> , <i>Leucospermum conocarpodendron</i> , <i>Leucospermum cordifolium</i> , <i>Leucospermum cuneiform</i> , <i>Leucospermum erubescens</i> , <i>Leucospermum glabrum</i> , <i>Leucospermum reflexum</i> , <i>Macadamia integrifolia</i> , <i>Mimetes cucullatus</i> , <i>Mimetes hirtus</i> , <i>Moraea bifida</i> , <i>Moraea collina</i> , <i>Moraea ochroleuca</i> , <i>Moraea reflexa</i> , <i>Protea aurea</i> , <i>Protea caffra</i> , <i>Protea compacta</i> , <i>Protea eximia</i> , <i>Protea mundii</i> , <i>Protea nitida</i> , <i>Protea repens</i> , <i>Schotia afra</i> , <i>Sutherlandia frutescens</i> .	41
Hexose-rich (Sucrose / Glucose + Fructose = 0.1 - 0.499) <i>Erica sitiens</i> , <i>Eucalyptus gomphocephala</i> , <i>Eucalyptus grandis</i> , <i>Eucalyptus sideroxylon</i> , <i>Grevillea robusta</i> , <i>Protea obtusifolia</i> , <i>Protea pudens</i> .	7

Sucrose-rich (Sucrose / Glucose + Fructose = 0.5 - 0.99) <i>Eucalyptus cladocalyx</i> , <i>Protea burchellii</i> , <i>Protea humiflora</i> , <i>Protea pruinosa</i> , <i>Trifolium repens</i> , <i>Virgillia oroboides</i> , <i>Watsonia meriana</i> .	7
Sucrose-dominant (Sucrose / Glucose + Fructose > 0.999) <i>Bauhinia galpinii</i> , <i>Bolusanthus speciosus</i> , <i>Calpurnia aurea</i> , <i>Cyclopia maculata</i> , <i>Erica densifolia</i> , <i>Erica discolor</i> , <i>Erica perspicua</i> , <i>Erica versicolor</i> , <i>Erica vestita</i> , <i>Eucalyptus globulus</i> , <i>Eucalyptus lehmannii</i> , <i>Eucalyptus macrocarpa</i> , <i>Grevillea bipinnatifida</i> , <i>Grevillea juniperina</i> , <i>Grevillea lavandulacea</i> , <i>Grevillea rosmarinifolia</i> , <i>Lapeirousia exilis</i> , <i>Lapeirousia plicata</i> , <i>Lebeckia sericea</i> , <i>Leucospermum mundii</i> , <i>Leucospermum oleifolium</i> , <i>Leucospermum prostratum</i> , <i>Paranomus reflexus</i> , <i>Podalyria calyptrata</i> , <i>Protea burchellii</i> , <i>Protea pruinosa</i> , <i>Protea pudens</i> , <i>Psoralea pinnata</i> , <i>Pyrostegia venusta</i> , <i>Sophora japonica</i> , <i>Trifolium repens</i> , <i>Virgillia oroboides</i> , <i>Watsonia meriana</i> .	33

3.3.3. Distribution

The overwhelming majority (>80%) of indigenous forage plant families are cosmopolitan or pantropic in nature, including the families Aizoaceae, Asteraceae, Ericaceae and Iridaceae.

Only the Strelitziaceae could possibly be considered Palaeotropic in distribution if placed within the Musaceae. The Selaginaceae and Melianthaceae have African-Madagascan and African distributions respectively, while the Dipsacaceae, Neuradaceae, Pedaliaceae and

Vahliaceae are dispersed throughout Africa-Eurasia. One family, the Hydrophyllaceae is found within Africa and the New World. The remaining six families either have an austral distribution (Africa-Australasia-South America), namely the Cunoniaceae, Haemodoraceae, Proteaceae and Restionaceae or are endemic to southern Africa, namely the Bruniaceae and Greyiaceae. A detailed analysis of indigenous genera has not been carried out, but it is interesting to note that genera with worldwide distributions such as *Euphorbia* (11 species) and *Senecio* (7 species) are well-represented as are those with much more limited geographical ranges such as *Agathosma* (6 species) and *Aspalathus* (13 species). The latter two genera are endemic to southern Africa.

The 21 best represented indigenous genera are not evenly spread throughout the different biomes in southern Africa (Table 3.4.). More than half ($n = 13$) have their centre of diversity within the fynbos, with the rest centred within the savanna ($n = 6$), grassland ($n = 2$), succulent karoo ($n = 1$), and Nama-karoo ($n = 1$) biomes. The only exception is *Aloe*, which has no centre of diversity. Note that *Asclepias* (savanna, grassland), *Heliophila* (fynbos, succulent karoo), *Lycium* (savanna, Nama-karoo), and *Rhus* (savanna, grassland) are centred on two biomes.

Table 3.4. The centres of diversity for the 21 best represented indigenous honeybee forage plant genera in South Africa (after Gibbs Russel, 1987).

Fynbos <i>Agathosma, Aspalathus, Crassula, Erica, Felicia, Heliophila, Hermannia, Leucospermum, Oxalis, Pelargonium, Protea, Senecio, Ursinia.</i>
Savanna <i>Acacia, Asclepias, Diospyros, Euphorbia, Lycium, Rhus.</i>
Grassland <i>Asclepias, Rhus.</i>
Succulent Karoo <i>Heliophila</i>
Nama-Karoo <i>Lycium.</i>
None <i>Aloe.</i>

Only seven species of honeybee forage plants indigenous to southern Africa merit urgent attention from conservationists. *Podalyria microphylla* is probably extinct in the wild, while *Protea pudens* is listed as endangered (Hilton-Taylor, 1996a&b). *Erica bauera*, *Leucadendron daphnoides*, *Mimetes hirtus*, *Otholobium fruticans*, *Paranomus reflexus* and *Podalyria sericea* are considered vulnerable (Hilton-Taylor, 1996a&b).

3.4. Discussion

Individual flowering plants are sessile organisms dependent on a suite of abiotic edaphic and climatic parameters for their survival. In contrast, reproduction and spatially oriented gene flow often require animal mediated pollination and seed dispersal. Globally, honeybees are arguably the most widespread and prolific pollinators of all, visiting *c.* 40, 000 plant species for sustenance (Crane, 1990). Their value to commercial crop cultivation and importance to angiosperms, seed predators and frugivores within temperate and tropical areas is therefore considerable. More than 40% ($n = 91$) of the angiosperm plant families within southern Africa have at least one species visited by honeybees in South Africa (Arnold & de Wet, 1993). Hepburn & Radloff (1998) have speculated whether the pervasive presence of honeybee plant genera on the African continent can not, at least in part, be attributed to the honeybees themselves. Whether the same conclusion is applicable to southern Africa awaits further investigation. Only 10.82% ($n = 241$) of the regional flowering plant genera and 2.20% ($n = 464$) of the species have been reported as honeybee forage plants (Appendix 3.A)(Arnold & de Wet, 1993). More than anything else this emphasises the lack of research which has been carried out on the indigenous bee plant taxa of South Africa. For example, more than 50 species of grasses have been recorded as forage plants in Kenya (Hepburn & Radloff, 1998

citing Bogdan, 1962), but only one species (*Paspalum distichum*) and probably another four genera (*Antheophora*, *Cynodon*, *Hyparrhenia* and *Urochloa*) in South Africa, yet there are reports of grass pollen constituting more than 30% of pollen loads per day in the former Transvaal (Hepburn & Radloff, 1998). Additional anecdotal accounts of foraging on grasses can be found in Field (1933) and Semple (1950). Field (1933) reported obtaining a honey flow off the grasses for at least 3 “seasons”, however it is unclear whether this came from honeydew or extra-floral nectaries.

In the absence of a detailed analysis it would appear from the results obtained in this study that nectar sugar compositions are of very limited value as indicators of forage plant attractiveness to honeybees. The nectars are either sucrose- or hexose-dominated, although the evolutionary significance to honeybees remains unclear. This supports the view held by others (van Wyk, 1993; van Wyk *et al.*, 1993, Barnes *et al.*, 1995) that ascribing nectar sugar compositions to pollination syndromes as proposed by Baker & Baker (1983) may not be particularly informative. Besides the nectar characteristics, honeybees alone are known to be attracted to flowers as individuals or following recruitment in the hive, according to their colour, shape and size (Kevan & Baker, 1984; Robacker & Erickson, 1984; Crane, 1990). Nevertheless, it is interesting to note that Freeman *et al.* (1991) found a similar distribution of nectar sugar compositions in a survey of 62 species from southeast Asia. It appears that the nectar sugar compositions are better indicators of phylogeny than adaptation to particular pollination regimes as alluded to previously by a number of investigators (van Wyk, 1993; van Wyk *et al.*, 1993; Barnes *et al.*, 1995; Nicolson & van Wyk, 1998). However, this assertion needs to be tested as some species appear to display geographical variation in their nectar sugar compositions. For example, *Eucalyptus grandis* was found to be hexose-dominant in South

Africa (Nicolson, 1994), but hexose-rich in Australia (Davis, 1997).

One could have anticipated from the review of nectar sugar preferences of honeybees earlier that the nectar rewards secreted by their forage plants would have been mostly sucrose-rich or sucrose-dominated. The fact that they appear to have no obvious bias or even a slight preference for hexose-dominated sugars seems to indicate a minor role for sugar composition in the hierarchy of characters honeybees use to evaluate the quality of a nectar reward.

Indirect support for this position can be found in the nectar composition of the genera, *Faurea* and *Protea*, both of which can have significant compliments of xylose, a sugar unattractive to honeybees (Allsopp *et al.*, 1998; Nicolson & van Wyk, 1998). Xylose has been known to comprise up to 27 % and 32% of the sugars from *Faurea saligna* and *Protea caffra* nectar respectively, both of which are known to be associated with honey flows (Anderson *et al.*, 1983; Nicolson & van Wyk, 1998). The adaptive significance of xylose to *Faurea* and *Protea* species is unclear. Allsopp *et al.* (1998) have suggested that the xylose may decrease the nutritional quality of the nectar and hence increase the foraging times of pollinators. This could in turn facilitate cross-pollination. However, van Wyk & Nicolson (1995) speculated a few years earlier that “...the presence of xylose in nectar seems unrelated to pollination syndromes and may be due to enzymatic activities in the plants rather than direct selection” (p.152).

At a familial level the results of this study do not contradict the suggestion by Hepburn & Radloff (1998) that pollination may have contributed to the successful dispersal of honeybee forage plants within Africa. The vast majority of South African honeybee forage plant families have a cosmopolitan or pantropic affinity. However, a different picture emerges if the honeybee forage plants are analysed by habitat. More than half (N = 13, 61.90%) of the 21

best represented honeybee plant genera have centres of diversity located within the fynbos biome. The savanna (n = 6, 28.57%) and grassland (n = 2, 9.52%) biomes are the two next best represented habitats. The two most likely explanations are that this distribution reflects the levels of species diversity within the different biomes or that it is indicative of investigative effort. Both explanations have some merit, as the fynbos is renowned for its species diversity, but also remains the best described of all the biomes from a honeybee forage plant perspective. Further research is required to ascertain the relative importance of the different biomes within South Africa. The success of honeybees as pollinators of the local flora is probably borne out by the very small percentage of honeybee forage plants which appear on the Red Data List of southern African plants (Hilton-Taylor, 1996a&b).

3.5. References

- Allsopp, M.H., Nicolson, S.W. and Jackson, S. 1998. Xylose as a nectar sugar: the response of Cape honeybees, *Apis mellifera capensis* Eschscholtz (Hymenoptera: Apidae). African Entomology, 6, 317-323.
- Anderson, R.H., Buys, B. and Johannismeier, M.F. 1983. Beekeeping in South Africa. Bulletin 394, Department of Agricultural Technical Services, Pretoria, 207 pp..
- Anon., 1981. Research being carried out by the Plant Protection Research Institute. South African Bee Journal, 53, 4-16.

Arnold, T.H. and de Wet, B.C. (Eds).1993. Plants of southern Africa: names and distribution. Memoirs of the Botanical Survey of South Africa No. 62, 825 pp.

Baker, H.G. and Baker, I. 1983. Floral nectar sugar constituents in relation to pollinator type. Chapter 5. In Handbook of Experimental Pollination Biology, Jones, C.E. and Little, R.J. (Eds), Van Nostrand Reinhold, New York, p. 117-141.

Barnes, K., Nicolson, S.W. and van Wyk, B.-E. 1995. Nectar sugar composition in *Erica*. Biochemical Systematics and Ecology, 23, 419-423.

Beylerveld, G.P. 1968a. Nectar and pollen producing trees and plants of the Transvaal. South African Bee Journal, 40, 10-11.

Beylerveld, G.P. 1968b. Detailed list of nectar and pollen producing plants of economic importance in the Transvaal. South African Bee Journal, 40, 13-14.

Bogdan, A.V. 1962. Grass pollination by bees in Kenya. Proceedings of Linnean Society of London, 173, 57-60.

Brieschke, H. 1991. Brutbiologische und nahrungsökologische untersuchungen am kleinen halsbandnektarvogel (*Panaeola chalybea*) und am großen halsbandnektarvogel (*Panaeola afra*) im freiland (Südafrika) und im labor. PhD Thesis, Johann Wolfgang Goethe-Universität in Frankfurt am Main.

Búrquez, A. and Corbet, S.A. 1991. Do flowers reabsorb nectar? *Functional Ecology*, 5, 369-379.

Butler, C.G. 1945. The influence of various physical and biological factors of the environment on honeybee activity. An examination of the relationship between activity and nectar concentration and abundance. *Journal of Experimental Biology*, 21, 5-12.

Challen, M. and Scharf, H. 1987. Beekeeping in the Eastern Cape. *South African Bee Journal*, 59, 74-77.

Coetzee, J.H. and Giliomee, J.H. 1985. Insects in association with the inflorescence of *Protea repens* (L.) (Proteaceae) and their role in pollination. *Journal of the Entomological Society of Southern Africa*, 48, 303-314.

Collins, B.G. 1983a. A first approximation of the energetic of Cape sugarbirds (*Promerops cafer*) and orange-breasted sunbirds (*Nectarinia violacea*). *South African Journal of Zoology*, 18, 363-369.

Collins, B.G. 1983b. Pollination of *Mimetes hirtus* (Proteaceae) by Cape sugarbirds and orange-breasted sunbirds. *Journal of South African Botany*, 49, 125-142.

Collins, B.G. 1983c. Seasonal variations in the energetics of territorial Cape sugarbirds. *Ostrich*, 54, 121-125.

Cowling, R.M. and Mitchell, D.T. 1981. Sugar composition, total nitrogen and accumulation of C-₁₄ assimilates in floral nectaries of *Protea* species. *Journal of South African Botany*, 47, 743-750.

Crane, E. 1990. Bees and beekeeping: science, practice and world resources. Heinemann Newnes, Oxford, 614 pp..

Crane, E. and Walker, P. 1984. Pollination directory for world crops. International Bee Research Association, London, 183 pp..

Crisp, W.F. 1957. About South African honey flora. *South African Bee Journal*, 32, 12-13.

Davis, A.R. 1997. Influence of floral visitation on nectar-sugar composition and nectary surface changes in *Eucalyptus*. *Apidologie*, 28, 27-42.

Davis, A.R., Sawhney, V.K., Fowke, L.C. and Low, N.H. 1994. Floral nectar secretion and ploidy in *Brassica rapa* and *B. napus* (Brassicaceae). I. Nectary size and nectar carbohydrate production and composition. *Apidologie*, 25, 602-614.

Eksteen, J.K. and Johannsmeier, M.F. 1991. Oor bye en byeplante van die Noord-Kaap. *South African Bee Journal*, 63, 128-136.

Field, A.N. 1933. Notes from all quarters. *The South African Bee Journal*, 8, 5-6.

- Free, J.B. 1993. Insect pollination of crops. Second Edition. Academic Press, London, 684 pp..
- Freeman, C.E. Worthington, R.D. and Jackson, M.S. 1991. Floral nectar sugar compositions of some south and southeast Asian species. *Biotropica*, 23, 568-574.
- Futuyma, D.J. 1986. Evolutionary Biology. Second Edition. Sinauer, Sunderland, Massachusetts, U.S.A..
- Galetto, L., Bernardello, L.M. and Juliani, H.R. 1994. Characteristics of secretion of nectar in *Pyrostegia venusta* (Ker-Gawl.) Miers (Bignoniaceae). *New Phytologist*, 127, 465-471.
- Gibbs Russel, G.E. 1985. Analysis of the size and composition of the southern African flora. *Bothalia* 15, 613-629.
- Gibbs Russel, G.E. 1987. Preliminary floristic analysis of the major biomes in southern Africa. *Bothalia*, 17, 213-227.
- Goldblatt, P. 1978. An analysis of the flora of southern Africa: its characteristics, relationships, and origins. *Annals of the Missouri Botanical Garden*, 65, 369-436.
- Goldblatt, P. and Bernhardt, P. 1999. Pollination of *Moraea* species (Iridaceae) with a staminal column. *Annals of the Missouri Botanical Garden*, 86, 47-56.

- Goldblatt, P., Manning, J.C. and Bernhardt, P. 1995. Pollination biology of *Lapeirousia* subgenus *Lapeirousia* (Iridaceae) in southern Africa; floral divergence and adaptation for long-tongued fly pollination. *Annals of the Missouri Botanical Garden*, 82, 517-534.
- Goldblatt, P., Manning, J.C. and Bernhardt, P. 1999. Evidence of bird pollination in Iridaceae of southern Africa. *Adansonia*, série 3, 21, 25-40.
- Hattingh, V. and Giliomee, J.H. 1989. Pollination of certain *Leucadendron* species (Proteaceae). *South African Journal of Botany*, 55, 387-393.
- Hepburn, H.R. and Jacot Guillarmod, A. 1991. The Cape honeybee and the fynbos biome. *South African Journal of Science*, 87, 70-73.
- Hepburn, H.R. and Radloff, S.E. 1998. *Honeybees of Africa*. Springer, Berlin, 370 pp..
- Hilton-Taylor, C. 1996a. Red Data List of southern African plants. *Strelitzia*, 4, 117 pp..
- Hilton-Taylor, C. 1996b. Red Data List of southern African plants. 1. Corrections and additions. *Bothalia*, 26, 177-182.
- Hoffman, M.T. 1988. The pollination ecology of *Aloe ferox* Mill.. *South African Journal of Botany*, 54, 345-350.

Johannsmeier, M.F. 1975. Commercial beekeeping in the Transvaal in relation to honeyplants. Proceedings I Congress of the Entomological Society of Southern Africa, 181-184.

Johannsmeier, M.F. 1981. Corbicular loads of the African honeybee. South African Bee Journal, 53, 3-6.

Johannsmeier, M.F. 1984. A "new" honey plant of the potato family: *Lycium*. South African Bee Journal, 56, 108-112.

Johannsmeier, M.F. 1988. Beekeeping potential of native flora of South Africa. South African Bee Journal, 60, 98-108.

Johannsmeier, M.F. 1995. Beeplants of the south-western Cape: nectar and pollen sources of honeybees. Department of Agriculture, Pretoria, 59 pp..

Johannsmeier, M. and Allsopp, M. 1995. Beeplants for South African suburban gardens. South African Bee Journal, 67, 70-75.

Kennard, R. 1988. "Hlalwane" in Natal. South African Bee Journal, 60, 122-125.

Kevan, P.G. and Baker, H.G. 1984. Insects on flowers. Chapter 20. In Ecological Entomology, Huffaker, C.B. and Rabb, R.L. (Eds), John Wiley & Sons, New York, p. 607-631.

Köttner, M. 1991. *Apis mellifera capensis* Escholtz; Bienenhaltung, Pollenfallenversuche und pollenanalytische Untersuchungen. Diplomarbeit, Universität Hohenheim, 90 pp.

Lear, E. 1995. Cover photo. South African Bee Journal, 67, 69.

Lear, E.N. 1996a. Cover photo. South African Bee Journal, 68, 67.

Lear, E.N. 1996b. Cover photo. South African Bee Journal, 68, 99.

Le Roux, P.J. 1985. The need for selection and breeding of non-commercial tree species. South African Forestry Journal, 135, 81-85.

Loock, E.E.M. 1983. Eucalypts suitable for honey production. South African Bee Journal, 55, 42-46.

Louw, G.N. and Nicolson, S.W. 1983. Thermal, energetic and nutritional considerations in the foraging and reproduction of the carpenter bee *Xylocopa capitata*. Journal of the Entomological Society of Southern Africa, 46, 227-240.

Manning, J. and Goldblatt, P. 1999. Busy bodies: the power of pollinators. Africa - Environment & Wildlife, 7, 50-57.

May, A.F. 1961. Beekeeping in southern Africa. Haum, Cape Town, 210 pp.

- McDonald, D.J. and van der Walt, J.J.A. 1992. Observations on the pollination of *Pelargonium tricolor*, section *Campylia* (Geraniaceae). South African Journal of Botany, 58, 386-392.
- Mostert, D.P., Siegfried, W.R. and Louw, G.N. 1980. Protea nectar and satellite fauna in relation to the food requirements and pollinating role of the Cape Sugarbird. South African Journal of Science, 76, 409-412.
- Nicolson, S.W. 1994. *Eucalyptus* nectar: production, availability, composition and osmotic consequences for the larva of the eucalypt fly, *Drosophila flavohirta*. South African Journal of Science, 90, 75-79.
- Nicolson, S.W. and van Wyk, B.-E. 1998. Nectar sugars in Proteaceae: patterns and processes. Australian Journal of Botany, 46, 489-504.
- Nicolson, S.W. and W.-Worswick, P.V. 1990. Sodium and potassium concentrations in floral nectars in relation to foraging by honeybees. South African Journal of Zoology, 25, 93-96.
- Oertel, E. 1946. Effect of temperature and relative humidity on sugar concentration of nectar. Journal of Economic Entomology, 39, 513-515.
- Percival, M.S. 1961. Types of nectar in angiosperms. New Phytologist, 60, 235-281.
- Percival, M. 1965. Floral Biology. Pergamon Press, Oxford.

Phillips, J.F.V. 1925. *Platylophus trifolius* D. Don: a contribution to its ecology. The South African Journal of Science, 22, 144-160.

Phillips, J.F.V. 1927. *Ekebergia capensis* Sparrm. ("Essenhout") in the Knysna region: a preliminary ecological note. South African Journal of Science, 24, 216-224.

Phillips, J.F.V. 1928. *Olea laurifolia* Lam. ("Ironwood"): an introduction to its ecology. Transactions of the Royal Society of South Africa, 16, 169-190.

Pooley, E. 1998. A field guide to wild flowers KwaZulu-Natal and the eastern region. Natal Flora Publications Trust, 630 pp..

Poynton, R.J. 1973. 200 selected indigenous and exotic species: how to recognise and grow them. In Our Green Heritage: The South African Book of Trees, Immelman W.F.E., Wicht, C.L. and Ackerman, D.P. (eds), Tafelberg, Cape Town, 75-256.

Retief, E. and Herman, P.P.J. 1997. Plants of the northern provinces of South Africa: keys and diagnostic characters. Strelitzia 6, 1-681.

Robacker, D.C. and Erickson, E.H., Jr. 1984. A bioassay for comparing attractiveness of plants to honeybees. Journal of Apicultural Research, 23, 199-203.

Scharf, H.T. 1986. Honey Dawn Bee Farm. South African Bee Journal, 58, 133-134.

- Semple, G.A. 1950. Some impressions of South African beekeeping. *The South African Bee Journal*, 25, 13-17.
- Smith, F.G. 1957. Bee botany in East Africa. *East African Agricultural Journal*, 23, 119-126.
- Steiner, K.E. 1990. The *Diascia* (Scrophulariaceae) window: an orientation cue for oil-collecting bees. *Botanical Journal of the Linnean Society*, 102, 175-195.
- Stirton, C.H. 1977a. The pollination of *Canavalia virosa* by Xylocopid and Megachilid bees. *Bothalia*, 12, 225-227.
- Stirton, C.H. 1977b. Broad-spectrum pollination of *Plectranthus neochilus*. *Bothalia*, 12, 229-230.
- Struck, M. 1994. Flowers and their insect visitors in the arid winter rainfall region of southern Africa: observations on permanent plots. Insect visitation behaviour. *Journal of Arid Environments*, 28, 51-74.
- Struck, M. 1997. Floral divergence and convergence in the genus *Pelargonium* (Geraniaceae) in southern Africa: ecological and evolutionary considerations. *Plant Systematics and Evolution*, 208, 71-97.
- Taylor, F. 1937. Times and intensities of South African honey flows. *South African Bee Journal*, 12, 4-5.

Tribe, G.D. and Johannsmeier, M.F. 1996. Bees and quiver trees. South African Bee Journal, 68, 111-115.

Van Steenis, C.G.G.J. 1978. Gregarious flowering in the monocarpic genus *Isoglossa* (Acanthaceae). Bothalia, 12, 553.

Van Wyk, B.-E. 1993. Nectar sugar composition in southern African Papilionoideae (Fabaceae). Biochemical Systematics and Ecology, 21, 271-277.

Van Wyk, B.-E. and Nicolson, S.W. 1995. Xylose is a major nectar sugar in *Protea* and *Faurea*. South African Journal of Science, 91, 151-153.

Van Wyk, B.-E., Whitehead, C.S., Glen, H.F., Hardy, D.S., van Jaarsveld, E.J. and Smith, G.F. 1993. Nectar sugar composition in the subfamily Alooideae (Asphodelaceae). Biochemical Systematics and Ecology, 21, 249-253.

Van Zinderen Bakker, E.M. 1953. South African pollen grains and spores. Part I. A.A. Balkema, Amsterdam, 88 pp.

Van Zinderen Bakker, E.M. 1956. South African pollen grains and spores. Part II. A.A. Balkema, Amsterdam, 132 pp.

Van Zinderen Bakker, E.M. and Coetzee, J.A. 1959. South African pollen grains and spores. Part III. A.A. Balkema, Amsterdam, 200 pp.

Voges, K. 1979. Honey from sugarcane. South African Bee Journal, 51, 18-19.

Waller, G.D. and Bachman, W.W. 1981. Use of honey-sac load and dance characteristics of worker honeybees to determine their sugar preferences. Journal of Apicultural Research, 20, 23-27.

Wiens, D. and Rourke, J.P. 1978. Rodent pollination in southern African *Protea* spp.. Nature, 276, 71-73.

Wise, A. 1985. Wheelchair beekeeping. South African Bee Journal, 57, 6, 135-137.

Wykes, G.R. 1952. The preferences of honeybees for solutions of various sugars which occur in nectar. Journal of Experimental Biology, 29, 4, 511-519.

Zietsman, P.C. 1993. Pollination in *Pelargonium dolomiticum* Knuth (Geraniaceae). South African Journal of Botany, 59, 2, 259-264.

Zietsman, P.C. 1998. Pollination biology of *Cotyledon orbiculata* L. var *dactyloopsis* Toelken (Crassulaceae). Navorsinge van die Nasionale Museum, Bloemfontein, 14, 4, 81-96.

CHAPTER 4. TRAPPING THE LIGHT FANTASTIC: THE FLOWERING PHENOLOGY OF SOUTH AFRICAN HONEYBEE FORAGE PLANTS.

“Come and trip it, as you go,

On the light fantastic toe;”

(*L'Allegro*, John Milton, 1645)

4.1. Introduction

Originally meant as a reference to a jovial dance by John Milton, the words may with latitude, aptly describe the relationship between honeybees and their food plants. Honeybees famously perform a dance within their nest cavity to convey to nestmates the location and quality of nectar and pollen sources (Crane, 1990), with trapped light often acting as a trigger for flowering (Taiz & Zeiger, 1991). Both the proximate and ultimate factors (*sensu* Bawa, 1983) associated with flowering phenologies from the individual to the community level are reviewed in this chapter. The emphasis is on the latter with the results presented in this study discussed in terms of their evolutionary significance for the forage plants. An important caveat of the synthesis to follow is that only the response of flowering times to environmental stimuli are considered, whereas under field conditions plants may react to a particular agent of selection in a number of different ways.

The efficacy of zoophilic sexual reproduction in terrestrial plants is dependent on the duration, frequency and timing of flowering events. The gene flow within a population is regulated by the degree of pollination success and extent of seed dispersal. In this chapter the flowering

phenologies of the honeybee forage plants listed in Appendix 3.A are characterised and an attempt is made to identify some of the potential underlying processes which may have influenced the development of the flowering regimes. As generalist foragers which occur year round throughout South Africa, honeybees can be expected to play a vital role in the survival of obligate outcrossers and/or to have indirectly mediated their widespread dispersal within the country (Hepburn & Radloff, 1995). However, clearly demonstrating an evolutionary link between this trait and flowering time in the honeybee flora of South Africa is more problematical. Worker honeybees may live under ideal conditions for a few months and queens on rare occasions longer than three years, but trees may survive for centuries (Tyson, 1986; Free, 1993; Hepburn & Radloff, 1998).

One would therefore anticipate that honeybees and annuals adjust more rapidly to environmental change than supra-annually flowering trees and monocarpic species. Lastly, while this study is predominantly concerned with the timing of intra-annual flowering events, it would be amiss not to emphasize the importance of longer time scales as a means to interpret the evolution of flowering patterns in honeybee forage plants. For example, some species may have relict flowering regimes adapted to past climatic conditions. Friedel *et al.* (1994) have speculated that flowering in some *Acacia* species in central Australia appears ill-adapted to present climatic conditions and may reflect their areas of origin. However, this interpretation for *growth phases* in some fynbos species has been disputed by Pierce (1984). A measure of caution is therefore required when making inferences of this nature.

There are four basic types of flowering strategy which a plant species can adopt, namely (in order of increasing expected total duration), big bang, multiple bang, cornucopian and steady-state (Proctor *et al.*, 1996). Big bang displays are expected to last days, similarly the multiple bang strategy, only repeated a number of times, the cornucopian style lasts in

excess of two weeks and the steady-state flowering regime up to a few months (Proctor *et al.*, 1996). Other differences include limited flower production during episodes of steady-state flowering and an absence of food rewards during multiple-bang events (Proctor *et al.*, 1996). Struck (1994) reported that honeybees foraged preferentially on shrubs with a cornucopian flowering strategy or substantial aggregations of annuals in Namaqualand. If facilitated pollination occurs between species they could be expected to show limited dispersion in their flowering regimes (Rathcke & Lacey, 1985). A positively skewed distribution of the flowering regime has been attributed to an environmental stimulus (Rathcke & Lacey, 1985).

The flowering strategy of a plant species may be viewed as an evolutionary response to the availability of pollinators within the limits imposed by exogenous (e.g. climate) and endogenous (e.g. phylogenetic constraint) factors (Kochmer & Handel, 1986). Flowering may be further restricted directly by herbivory and/or indirectly via seed dispersal. Very few phenological studies appear to have been carried out on the flowering regimes of indigenous South African plants, nevertheless some of the trends evident within local species and further afield are reviewed below.

4.1.1. Physical Environment

Flowering can take place in the absence of an external stimulus (autonomous induction), but often requires one (Taiz & Zeiger, 1991). Photoperiod, rainfall and temperature appear to be the most important aspects of the physical environment affecting the flowering phenology of a species (Bawa, 1983; Vince-Prue, 1983; Pierce, 1984; Rathcke & Lacey, 1985; Smith-Ramírez & Armesto, 1994). Aspect, fire, irradiance, humidity and nutrients have also been associated with flowering, but will not be reviewed in this chapter (Phillips, 1926; Jackson,

1966; Rathcke & Lacey, 1985; le Maitre & Midgley, 1992; Milton, 1992; Smith-Ramírez & Armesto, 1994; Wright & van Schaik, 1994; Esler, 1999).

An extensive review of photoperiodism is beyond the scope of this chapter, nevertheless it would be germane to outline its most salient features with regard to flowering. Daylength is detected mainly by the leaves and flowering evoked within the lateral or apical meristems (Vince-Prue, 1983; Bernier, 1988). Daylength, or more precisely the duration of darkness determines the time of flowering in plants. Species that flower when the length of darkness falls below a critical threshold are termed long-day plants (LDP), while the reverse applies to short-day plants (SDP). Flowering in day-neutral plants is not affected by photoperiod (Taiz & Zeiger, 1991). Ambiphotoperiodic plants flower in response to short or long nights, but not to those of mid-duration (Vince-Prue, 1983; Taiz & Zeiger, 1991). In contrast, intermediate-day plants (IDP) only flower when the duration of darkness lies between an upper and lower limit (Vince-Prue, 1983, Taiz & Zeiger, 1991). Thermoperiodism is also exhibited by some plant species which grow best at different temperatures during the day and night respectively (Mohr & Schopfer, 1995).

Flowering triggered by low temperatures (vernalization) is well-known in plants. The shoot apices, leaves and roots may all be receptive to temperature stimuli (Bernier, 1988; Taiz & Zeiger, 1991). The age at which a plant becomes responsive to low temperature varies from species to species. For example, flowering may be induced early on within the seeds of some species, but only much later in others (Taiz & Zeiger, 1991; Mohr & Schopfer, 1995). There are also inter- and intraspecific differences in sensitivity to the duration of these low temperature treatments (Taiz & Zeiger, 1991). If temperatures do not fall below a critical

threshold flowering may be delayed or absent altogether, while elevated temperatures may reverse the effects of vernalization (e.g. *Cheiranthus cheiri*) (Bernier, 1988; Taiz & Zeiger, 1991). To complicate matters further, long nights may act *in lieu* of apical vernalization in certain species (e.g. *Campanula medium*, Campanulaceae), while in others both vernalization and photoperiod may act in concert to govern a flowering regime (Taiz & Zeiger, 1991).

Devernalization may also occur in the carrot (*Daucus carota*) during exposure to short days (Bernier, 1988). In the SDP *Pharbitis* sp. one varietal (Violet) flowers during long days when subjected to low temperatures, elevated irradiance levels or inadequate nutrition (Bernier, 1988). Similarly, the LDP *Silene* sp. will commence flowering during SD if exposed to high or low temperatures or elevated quantities of CO₂ (Bernier, 1988). A response to the gaseous environment has also been reported for Chicory (*Cichorium intybus*), where vernalization may be substituted by ethylene and anaerobiosis (Bernier, 1988). Lastly, and perhaps counter-intuitively, high temperatures may stimulate flowering in some species which require vernalization (e.g. *Scrophularia alata*) (Bernier, 1988). Flowering stimuli may also operate additively, initiating a floral response in plants at lower levels than if they acted in isolation (Bernier, 1988). Phillips (1926) has reported that flowering on the northern sides of trees may precede by "several weeks" that on the southern sides (e.g. *Virgilia oroboides*). This he attributed to more light and greater temperatures equatorward. Flowering in the Karoo shrub, *Osteospermum sinuatum* is also reputedly effected by temperature with flowering intensity greater for plants cultivated at 17°C than 27°C (Milton, 1992).

The start of flowering for a particular species can be determined using an empirical approach, where the cumulative degree-days are calculated (Reader, 1983, Frenguelli & Bricchi, 1998). The number of degrees per day above a predetermined growth threshold are summed from a particular date (e.g. 1 January in the northern hemisphere) to the flowering

event. The cumulative degree-day concept may explain in part why some plant communities have a positive correlation between mean monthly temperatures and flowering, such as the temperate rain forests on the eastern side of Chiloé Island, Chile (Smith-Ramírez & Armesto, 1994). It also enabled Frenguelli & Bricchi (1998) to suggest for *Alnus* sp. that the extent of autumn chilling is negatively correlated with the amount of heat necessary for “pollination”, which in the context of their study refers to pollen release, but taken here as an approximation of flowering time. Schemske *et al.* (1978) however found the technique less effective in predicting flowering times within seven herbaceous species near Urbana, Illinois.

In South Africa both high and low temperatures have been associated with flowering in the Knysna forests (Phillips, 1926). Esler (1999) has speculated that temperature could effect both pollination and flowering. As a corollary it would be interesting to determine whether the optimal foraging temperatures for honeybees are correlated in any way with thermal flowering cues in their forage plants.

Rainfall has been widely recognized for its influence on the flowering phenologies of many species and plant communities. Rainfall affects plants via the soil moisture content, which is in turn an expression of the subtle interplay between a number of other soil characteristics such as its mineralogy, granulometry and thermal regime. The importance of rainfall to flowering has been recognised in both desert (Ackerman & Bamberg, 1974) and tropical environments (Rathcke & Lacey, 1985), while on a continental scale flowering is coincident or nearly so, with rainfall in Africa (Hepburn & Radloff, 1995). In contrast, Smith-Ramírez & Armesto (1994) in the study on Chiloé Island, Chile, reported a negative correlation between monthly rainfall and flowering. A rise and fall in moisture stress have both been associated with flowering (Rathcke & Lacey, 1985; Bernier, 1988). Moisture stress and

rainfall may not always act in isolation of one another. In coffee (*Coffea arabica* var. *typica*) rainfall needs to be preceded by an interval of moisture stress to initiate flowering in dormant buds (Alvim, 1960). Phillips (1926), in an early paper on the Knysna forests, suggested limited periods of both anomalously wet and dry conditions may be associated with flowering. In tropical trees a drop in moisture stress levels may be caused by rainfall or leaf abscission (Rathcke & Lacey, 1985). Flowering in desert annuals has also been attributed to falling moisture stress levels (Rathcke & Lacey, 1985), however Fox (1990) was of the opinion that no unequivocal data to support drought related flowering in mesic or xeric annuals existed. A drop in soil moisture might retard the onset of flowering, while its availability could affect the nectar and pollen rewards on offer (Fox, 1990). The assimilation and transport of carbohydrates, transport of nutrients and microsporogenesis are all retarded by moisture stress (Fox, 1990).

Moisture stress has an effect on some Namaqualand ephemerals such as the honeybee forage plants *Dimorphotheca sinuata* and *Senecio arenarius* (Steyn *et al.*, 1996a). In *D. sinuata* moisture stress hastens the onset of flowering for seeds planted from May to July, but retards it in individuals grown from April. In all four treatments it also reduces the time to the flowering climax, but diminishes its extent (Steyn *et al.*, 1996a). The duration of flowering appears to be markedly more limited in moisture stressed plants grown from June and July (Steyn *et al.*, 1996a). The effects of moisture stress are somewhat more equivocal for *S. arenarius*, where it delays the start of flowering in seeds grown from April, has no effect on those grown from June and advances flowering in seeds planted in May and July (Steyn *et al.*, 1996a). The interval between planting and the flowering climax was unaffected by moisture stress for the April and May treatments, but reduced for the June and July treatments (Steyn *et al.*, 1996a). It would appear from earlier studies quoted by Steyn *et al.* (1996a) that in the



absence of moisture stress flowering is governed by photoperiod and temperature.

In the arid Karoo *Osteospermum sinuatum* flowers in response to rain during spring, autumn and winter, with the intensity of flowering positively correlated with the rainfall during the preceding 12 weeks (Milton, 1992). Another honeybee forage plant from the Karoo, *Lycium cinereum*, also flowers after rainfall (Milton, 1992), while flowering in a third, *Mesembrythemum crystallinum*, occurs when moisture stress prevents growth (Esler, 1999).

4.1.2. Biological Environment: Gene Expression to Community Dynamics

Intraplant characteristics and plant-animal interactions are both known to influence flowering times in plants. A short description of the salient features of both are given below. Genes, plant size and plant age are all known to affect flowering and will be discussed first. This is followed by an overview of the modifying effects of herbivory and the role pollinators might have played in determining the pattern of flowering within plant communities. The physiological and hormonal aspects of flowering and plant-plant interactions are beyond the scope of this study, for further information see Bernier (1988), Taiz & Zeiger (1991) and Milton (1992).

Genes undoubtedly influence the expression of many flowering traits such as flower colour, size and phenology (Bannister, 1978). For example, in some species diploids flower earlier than their polyploid offspring (Rathcke & Lacey, 1985). Flowering times are genetically related in some species to frost tolerance, germination, aspects of plant size and a facet of reproduction (Rathcke & Lacey, 1985). However, the flowering trait under genetic control most pertinent to this study is the geographic variation of flowering time. The examples

described below serve to outline the most important trends associated with the trait. The honeybee forage plants *Calluna vulgaris* and *Erica cinerea* both display latitudinal variation in their flowering times within Britain. Plants from northerly sites flowering earlier than those from the south when grown at the same location (Bannister, 1978). Bannister (1978) also reported geographic trends associated with longitude and altitude (e.g. *Erica cinerea*). Plants from the west and higher altitudes flowering before those from the east and lower altitudes. The most important factor governing these trends in *C. vulgaris* and *E. cinerea* appears to have been the mean annual maximum temperature, with one exception, when in one year the mean annual minimum temperature was of greater significance for *E. cinerea* (Bannister, 1978).

Phillips (1926), Hepburn & Jacot Guillarmod (1991) and Johnson (1993) have all noted longitudinal differences in flowering times within the southern temperate areas of South Africa. Phillips (1926) reported that the honeybee forage plants *Apodytes dimidiata*, *Brachylaena neriifolia*, *Cunonia capensis*, *Nuxia floribunda*, and *Platylophus trifolius* all have a propensity to flower first in the west within the “George-Knysna-Zitzikama (*sic*)” area. He noted a marginal decrease in temperature from east to west within the area during summer and winter, but did not explicitly attribute the change in flowering times to the variation. In their investigation of the fynbos biome Hepburn & Jacot Guillarmod (1991) found the flowering peak in the northwest preceded that in the east of the region by approximately two months (West - September, East - November).

Similarly, Johnson (1993) divided the Cape Floral Kingdom roughly in half and also found that flowering peaked in the west earlier than the east. Only Phillips (1926) appears to have recorded an altitudinal flowering cline in South Africa. Flowering in the mountains lagged behind that on the coast by up to a few months in the Knysna region. Temperature and

relative humidity increased slightly between the coast and mountains, but rainfall increased substantially, by at least 500mm (Phillips, 1926). *Heterotheca subaxillaris* is known to display ecotypic variation in flowering phenology attuned to regional variations in the rainfall regime (Burk, 1966). It remains to be seen whether the altitudinal flowering cline in the Knysna forests is due to environmental and/or genetic causes. Similarly, proteoids within the fynbos biome from low elevations flower earlier than congenics from higher up (Pierce, 1984).

Plants flower on reaching a critical size or age, with the former possibly of greater significance than the latter (Taiz & Zeiger, 1991). For example, older plants have a greater inclination to flower than younger plants that have reached maturity (Taiz & Zeiger, 1991). Bannister (1978) found that more mature and hence taller, *Calluna vulgaris* plants, generally flowered earlier than younger individuals. The growth strategy of a species is also of significance as determinate growth appears to be associated with predictable environments and indeterminate growth with unpredictable ones (Rathcke & Lacey, 1985). Rathcke & Lacey (1985) have suggested that this may enable plants pursuing an indeterminate growth strategy to flower all year round within the seasonal tropics. Flowering and growth occurs simultaneously in the honeybee forage plants *Paranomus bracteolaris* and *Protea nitida* on nutrient deficient soils in the fynbos biome (Pierce, 1984). Flowering is more drawn out in *Protea repens* with bud development in December of the first year preceding evocation at the end of the second year, with plants only in full flower the following autumn (Pierce, 1984). Johnson (1993) has suggested that growth and flowering may be “uncoupled” in some genera, such as *Gladiolus* in which synanthous species flower in spring, while hysteroanthous species can flower in autumn. He also reported that dicotyledons flower longer than monocotyledons, which he attributed to morphological limitations.

Flowering times in some species may also be determined by the germination date and be largely unaffected by external environmental conditions (Rathcke & Lacey, 1985). Factors which govern successful germination could therefore indirectly affect the onset of flowering in a particular species (Rathcke & Lacey, 1985). Johnson (1993) has proposed that dispersal of seeds and germination are correlated with the flowering regime of the Amaryllidaceae in the absence of seed dormancy. In South Africa the genus *Isoglossa* may reflect a link of this nature. For example, *Isoglossa ciliata*, *I. eckloniana* and *I. woodii* are all monocarpic honeybee forage plants in South Africa which flower at approximately 10, 7-10 and 7-10 year intervals respectively (Henkel *et al.*, 1936; Bayer, 1938; van Steenis, 1978; Kennard, 1988; Pooley, 1998). *Isoglossa* has flowered in the years (species & location in brackets) 1893 (*Isoglossa* sp., Tugela Valley?), 1903 (*I. eckloniana*, Tugela Valley), 1913 (*I. eckloniana*, Tugela Valley), 1933 (*I. eckloniana*, Tugela Valley), 1943 (*I. eckloniana*, Tugela Valley), 1948 (*I. eckloniana*, Umkomaas Valley), 1953 (*I. eckloniana*, Tugela Valley), 1957 (*I. ciliata*, St. Lucia), 1958 (*I. eckloniana*, Umkomaas Valley), 1960 (*I. eckloniana*, Tugela Valley), 1968 (*I. eckloniana*, Umkomaas Valley), 1970 (*I. eckloniana*, Tugela Valley), 1974 (*I. eckloniana*, Umkomaas Valley), and 1988 (*I. eckloniana*, Umkomaas Valley) ("Aerial", 1943; van Steenis, 1978; Kennard, 1988).

Bannister (1978) found that intraspecific differences in growth form were associated with a variation in flowering time within *C. vulgaris* and *Erica cinerea*. Erect or larger individuals flowering later than individuals growing lower down. This he attributed to the relatively higher temperatures at ground level. However, prostrate forms of *C. vulgaris* and *E. cinerea* generally came from northern and western coastal areas (Bannister, 1978). The extent to which the latitudinal and longitudinal trends discussed earlier may be attributed to these growth form differences does not appear to have been investigated.

Categorical trends in the flowering phenologies of different growth forms have also been identified. Rathcke & Lacey (1985) suggested flowering in “short-lived herbs” was governed by photoperiod, in certain “perennial herbs” and “temperate woody species” by temperature and that in selected “tropical trees” rainfall may serve to harmonize events. Furthermore, they suggested that trees within “the seasonal neotropics” generally flowered in the dry season, with “herbs and shrubs” flowering during the wet season (Rathcke & Lacey, 1985). A flowering climax is reputed to be absent from “aseasonal tropical forests”, although multiple intra-annual flowering by a species may be evident (Rathcke & Lacey, 1985). Species within the understory of tropical forests are inclined to pursue a steady-state flowering strategy, while trees often flower *en masse* during the dry season (Rathcke & Lacey, 1985). In North America herbaceous species may flower early before the canopy of the deciduous forests closes over (Schemske *et al.*, 1978). Flowering within the tree flora of the United Kingdom reaches a climax in May, preceding flowering maxima within the shrubs (June) and herbs (July) (Rathcke & Lacey, 1985). Different life forms also display different flowering phenologies in the Jonkershoek valley within the fynbos biome (Kruger, 1981). In Namaqualand non-succulent shrubs flower more profusely in wetter years, but the succulents in drier ones (Esler, 1999).

The genotypes and phenotypes extant within a plant community to a greater or lesser extent reflect the history of natural selection of its constituent members. Past competition for pollinators has been invoked in particular to describe flowering patterns within plant communities. The strength of this interpretation is dependent on the degree to which a plant is dependent on cross-pollination, assumes plants are of equal attractiveness to the common pollinator(s) and that fertilisation has been pollinator-limited in the past. Pollinator mediated

selection on the flowering times of species has been reported for both tropical and temperate areas (Mosquin, 1971; Pojar, 1974; Waser & Real, 1979). Plants which share pollinators are expected to have divergent flowering times if in competition for their services or if interspecific pollination occurs resulting in a decrease in reproductive success (Rathcke & Lacey, 1985). For example, early flowering in *Solidago graminifolia* can result in reduced seed set if it coincides with flowering in other honeybee forage plants in Michigan (Rathcke & Lacey, 1985). It has also been suggested that interspecific differences in the flowering time of sympatric *Eucalyptus* species have evolved to limit introgression between congenics (Pierce, 1984). Divergent flowering times have also been suggested as one possible explanation for the rarity of hybridization within the Mesembryanthemaceae in the wild, as hybrids are easily raised under cultivation (Ihlenfeldt, 1994). The dispersed nature of interspecific flowering times within the genus *Erica* could also be indicative of pollinator-limitation (Pierce, 1984). Nevertheless, the potential effects of pollination and phylogenetic constraint appear to be virtually indistinguishable (Esler, 1999).

In contrast, if facilitation is taking place plants could be expected to have co-incident flowering times or flowering times which closely follow one another (Frankie *et al.*, 1983). It may conceivably be advantageous for rare species with the same general morphology to flower at the same time and hence create a greater display to attract pollinators or for a species with a lower reward status to morphologically mimic and closely follow the flowering of a species with better quality rewards on offer. Nevertheless, the concept is contentious and needs to be viewed with circumspection. For example, species which share co-incident flowering times may alter the quality of their rewards or differ in the time the rewards are offered during the day to reduce competition for pollinators. Species with overlapping flowering times may also switch pollinators. For example, some previously insect-pollinated *Leucadendron* species are

now wind-pollinated (Pierce, 1984).

In addition, facultative outcrossers may rely more heavily on the selfing pathway to compensate for a lower visitation rate due to competition for pollinators. It is interesting to note in this regard that the duration of flowering is inclined to be shorter in species capable of self-pollination (Rathcke & Lacey, 1985). As a corollary this may indicate that self-incompatible species increase the duration of flowering to increase their chances of pollination (Rathcke & Lacey, 1985). A spatial or temporal dearth of resources necessary for seed development may also lead to prolonged flowering (Rathcke & Lacey, 1985). Rathcke & Lacey (1985) have speculated that protracted flowering “...*may reflect unpredictable or sparse resources (or)... a lack of seasonal differences in resource or pollinator availability*” (p.188). Site specific inter-annual differences in flowering time and spatial variation in the suite of pollinators and competitors for pollination only serve to further confound the interpretation of flowering regimes (Rathcke & Lacey, 1985). Lastly, and perhaps most importantly, it is difficult to determine whether the number of plant species in flower at any one time governs the number of pollinators extant or vice versa (Rathcke & Lacey, 1985).

Other plant-animal interactions which may have played a role in the evolution of a species' flowering time, include foliar herbivory and seed predation (Brody, 1997; Strauss, 1997). Foliar herbivory is thought to effect amongst other floral characters, flower size, flower number, pollen production and pollen quality (Strauss, 1997). Foliar herbivory therefore has the potential to reduce the attractiveness and quality of rewards on offer to honeybees. Phillips (1926) noted that “damaged” (e.g. burnt, diseased) trees flowered more profusely than undamaged ones. Similarly, grazing in the Karoo appears to have negatively affected flowering in the honeybee forage plant *Osteospermum sinuatum* (Milton, 1992). However, it is difficult

to determine whether this was due to foliar herbivory and/or florivory in their study, nevertheless foliar herbivore-limited flowering has been reported for some species such as *Galenia fruticosa* (Esler, 1999).

Pierce (1984) has speculated that myrmecochorous plants within the fynbos need to find a balance between the availability of seeds for dispersal, pollination by avian nectarivores and the need to avoid seed predation by rodents and other granivores. All these forces of selection must to a greater or lesser extent restrict the flowering phenology of a species. Interspecific differences in the time of flower production and fruit availability in the sympatric and myrmecochorous *Agathosma stenopetala* and *A. apiculata* have been attributed to past competition for agents of pollination and dispersal (Pierce, 1984).

4.1.3. Flowering Phenology and the Honeybee

This section is not meant to be a thorough examination of the life cycle of the honeybee, but merely to highlight some of the potential evolutionary links between the honeybee and the flowering phenology of their forage plants. The reproductive cycle of a honeybee colony is intimately related to the flowering phenology of the honeybee forage plants in its vicinity. The reproductive cycle encompasses a number of important events within the colony which to a greater or lesser extent are influenced by forage conditions. These include, worker, drone and queen brood-rearing, storage of pollen and nectar and reproductive swarming. During dearth periods colonies may also abscond to more profitable foraging areas. This event therefore represents a facultative response by the colony to the quality of local resources. It may or may not be associated with a seasonal return event. For the purposes of this study only the former will be regarded as migration. Absconding is here defined as a response to both foraging and

nesting conditions, such as damage to the nest cavity or pest attack. Absconding in this sense is therefore not strictly related to the reproductive cycle of honeybees.

Flowering regimes can be expected to have the greatest impact on brood-rearing, swarming and migration. Colonies from the temperate northern hemisphere tend to anticipate the arrival of spring by increasing the intensity of brood-rearing prior to the flowering peak, whereas colonies from southern Africa display “follow-flow” brood-rearing (Hepburn & Jacot Guillarmod, 1991; Hepburn & Radloff, 1998). A term first coined by Hepburn (1992) to describe the lag between peak flowering and the brood-rearing maximum within colonies from the region. Regional variations in the brood rhythm (*sensu* Hepburn & Radloff, 1998) within temperate and tropical areas appear in harmony with the flowering phenologies of the local flora (Hepburn, 1992; Hepburn & Radloff, 1998). The brood rhythms adapted to the local flowering regime appear to be fixed within the genes of each population (Hepburn, 1992; Hepburn & Radloff, 1998). Brood-rearing in temperate colonies is dependent on pollen *stores*, whereas in tropical colonies it is dependent on pollen *income* (Hepburn & Radloff, 1998). This accounts for the follow-flow brood-rearing evident within southern Africa. Brood-rearing, swarming and the flowering phenology of honeybee forage plants are correlated in sub-equatorial Africa (Hepburn & Radloff, 1998). In the fynbos biome swarming is associated with the flowering peak and migration with a seasonal dearth (Hepburn & Jacot Guillarmod, 1991). Swarming has been attributed to elevated pollen income in southern Africa (Hepburn, 1993). In South Africa both return mountain migrations (e.g. Paarl mountains) and supra-annual resource related movements (e.g. *Isoglossa* sp. flow) have been reported (“Aerial”, 1943; Francis, 1963; Kennard, 1988).

4.1.4. Towards a theory of ultimate causation for honeybee forage plant flowering phenologies

Characterization of the flowering phenology of honeybee forage plants in South Africa has been restricted to the data available in Appendix 3.A. As such no attempt has been made to quantify the potential effect life form may have on the flowering regimes of these plants, although there is some evidence from elsewhere that this may indeed occur. Kochmer & Handel (1986) found that in the Carolinas, U.S.A., trees flowered before shrubs which in turn flowered before herbaceous plants and vines. In view of the limitations of the dataset, the remainder of the chapter will concentrate on the evidence for phylogenetic constraint and competition for pollination within the honeybee flora.

The definition of phylogenetic constraint used by Kochmer & Handel (1986) has been adopted in this chapter, namely:

“...properties shared by the members of a monophyletic group by virtue of their common ancestry, and which limit the response of these taxa to directional selection.”

(Kochmer & Handel, 1986 p.304)

The effects of pollinator-limitation on the divergence of flowering times has already been reviewed above and hence will not be discussed further. In addition, for the purposes of this chapter, honeybees are assumed to be omnipresent spatially and temporally throughout South Africa, with the possible exception of the higher lying areas of the Drakensberg mountains. It is further assumed that colonies respond to local floral resource availability *via* in- or out-migration to more favourable conditions with the upper limits to colony density determined by

the availability of nesting sites.

Phylogenetic constraint and pollinator mediated divergence in flowering times are probably not mutually exclusive if evident at all, but are treated as such in this chapter to facilitate the analysis of the flowering phenologies. If taxonomic affinity matters one could make the following predictions:

- Families with different phylogenies should have different flowering regimes;
- Families should flower in the same order independent of geographical location;
- Interspecific synchronicity of flowering times within a family should be evident irrespective of geographic origin.

If closely related species compete for pollination services one could expect the following:

- Temporal divergence in the peak flowering times of sympatric congeneric species pairs offering the same rewards;
- Temporal dispersal of flowering peaks and/or increased flowering duration in families with significant interspecific competition for pollination.

The methods used to test these predictions are described in the section below.

4.2. Methods

The data used in the statistical analyses were obtained from Appendix 3.A. The flowering times and mean duration of flowering for indigenous and exotic species were then calculated separately for the different reward categories, namely sources of nectar and pollen, sources of both and the total. The total included species for which the reward category was unspecified in

Appendix 3.A. To determine whether the species within the different reward categories flower at similar times the flowering frequencies for each month were subjected to a Spearman Rank Order Correlation analysis (STATISTICA 6.0).

Two different methods were adopted to assess the taxonomic differences in flowering phenologies. One tested the inter-familial differences in flowering regimes, while the other determined the extent of correlation between congeneric species pairs. The families used in the first analysis were selected by determining which families had flowering data for ten or more indigenous species which offered both nectar and pollen as rewards. Comparative datasets of exotic flora were then obtained by determining which of these families met the same numerical and reward criteria mentioned above. A null flora was also created to determine whether the flowering times within a family were arranged at random. A similar approach using null floras was adopted by Kochmer & Handel (1986) to investigate phylogenetic constraint in the flowering times of the floras of the Carolinas in the U.S.A. and Honshu in Japan. In this study the null flora represented a sample of species selected from Appendix 3A according to the following protocol. Only indigenous sources of nectar and pollen were taken into account. By excluding other reward categories potential sources of variation in the flowering regime attributable to them were eliminated from the null flora. The species were then sorted alphabetically by their specific epithet, with every group of five species at 20 species intervals included within the null flora (e.g. numbers 50, 51, 52, 53, 54, 70, 71, 72, 73, 74 etc.). It would appear highly improbable that species selected according to these criteria would reflect their phylogeny in any way and the flowering times to be sufficiently random for the purposes of this study. The duration of flowering for the indigenous families and the null flora were tested for normality (Shapiro-Wilk's W test) and the skewness and kurtosis calculated. Directional, disruptive and stabilizing selection could all be expected to have an effect on the

distribution of biological character traits. For example, directional and stabilizing selection could be expected to increase the skewness and the kurtosis of a distribution respectively.

The genus, *Eucalyptus*, was also selected for analysis as it arguably represents the single most important source of nectar in South Africa and has considerable potential to disrupt the pollination of indigenous flora. It is highly attractive to honeybees, is widespread throughout the country and is part of countrywide afforestation schemes. Only *Eucalyptus* species offering both nectar and pollen as rewards were considered for analysis. Similarities between the flowering regimes were determined using the same correlation technique described earlier for the reward category analysis.

In the second method utilising congeneric species pairs, only those indigenous species offering both nectar and pollen rewards were considered. Obviously only genera with more than one listed species were taken into account, while the number of species was further reduced by excluding all those without an illustrated distribution in Coates Palgrave (1977). The latter criterion was necessary to determine whether species currently occurred in sympatry or allopatry. Lastly, the species of *Eucalyptus* which appear both in Appendix 3.A and Western Australia's Department of Agriculture publication on "Honey Plants" (Smith, 1969) are compared to determine the extent, if any, of phenotypic elasticity in flowering times and duration. Spearman Rank Order Correlations (Spearman's R) (STATISTICA 6.0) were again used to determine the extent of the relatedness between the pairs.

4.3. Results

4.3.1. The null flora

The flowering phenology of the null flora is weakly bimodal (Figure 4.1). The null flora displays a flowering peak in October, the austral spring, with a second minor peak in March. The least number of species were in flower during May, early winter in the southern hemisphere.

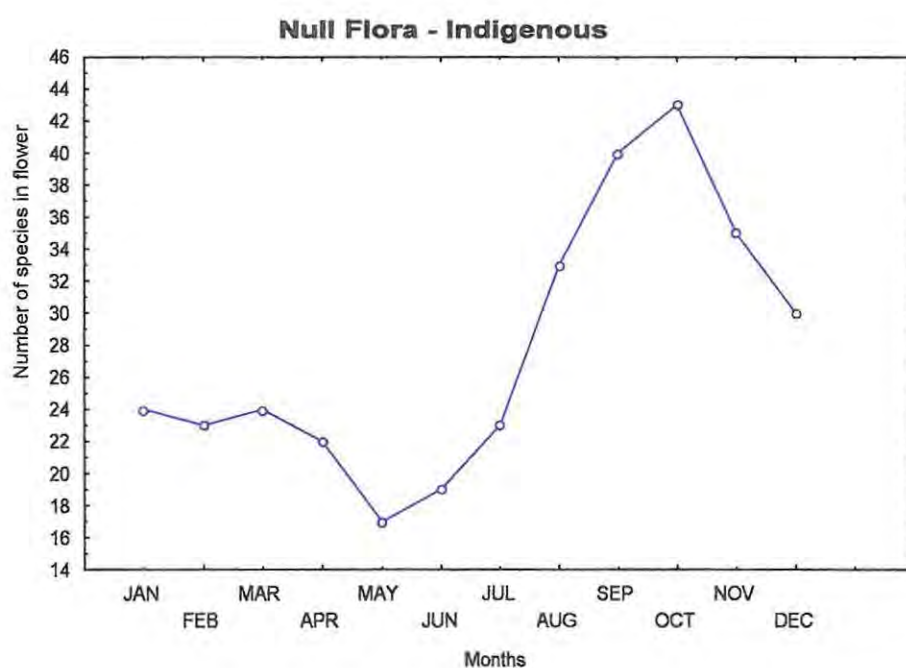


Figure 4.1. The null flora of indigenous honeybee forage plant species ($n = 50$).

Flowering lasted on average seven months (mean duration of flowering, $\bar{x} = 6.7$ months) for the null species. However, the distribution of flowering durations for the null flora differed significantly from normality at the 0.05 level (Shapiro-Wilk's W test = 0.9246, $p = 0.0035$), was positively skewed (0.2914) and platykurtic (-1.0393). This indicates that most species

probably flower for shorter periods, with the large number of species flowering throughout the year boosting the average calculated duration of the flowering period (Figure 4.2).

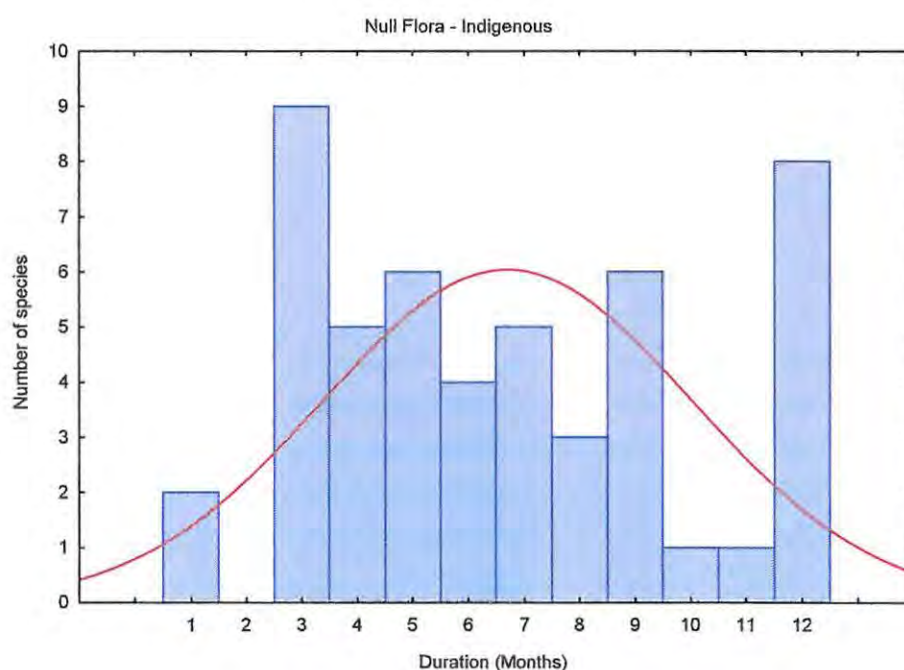


Figure 4.2. Flowering durations for the null flora.

4.3.2. Comparative analysis of reward phenologies

The flowering phenologies of the three reward categories for indigenous honeybee forage plants (Figure 4.3) are broadly similar (0.05 level), with the flowering peak in the indigenous nectar flora (September) preceding that of the indigenous pollen flora (November) by two months (Indigenous Nectar & Pollen vs Indigenous Nectar, Spearman $R = 0.7047$, $p = 0.0105$; Indigenous Nectar & Pollen vs Indigenous Pollen, Spearman $R = 0.8728$, $p = 0.0002$; Indigenous Nectar vs Indigenous Pollen, Spearman $R = 0.6402$, $p = 0.0249$). Indigenous species offering both a nectar and pollen reward flower most profusely at an intermediate time (October). The flowering low occurs in March for species offering nectar rewards, but from

May to June in those species offering pollen or both rewards. The flowering regimes of the null flora and indigenous plants offering both rewards are significantly correlated at the 0.01 level (Spearman $R = 0.9789$, $p < 0.0001$).

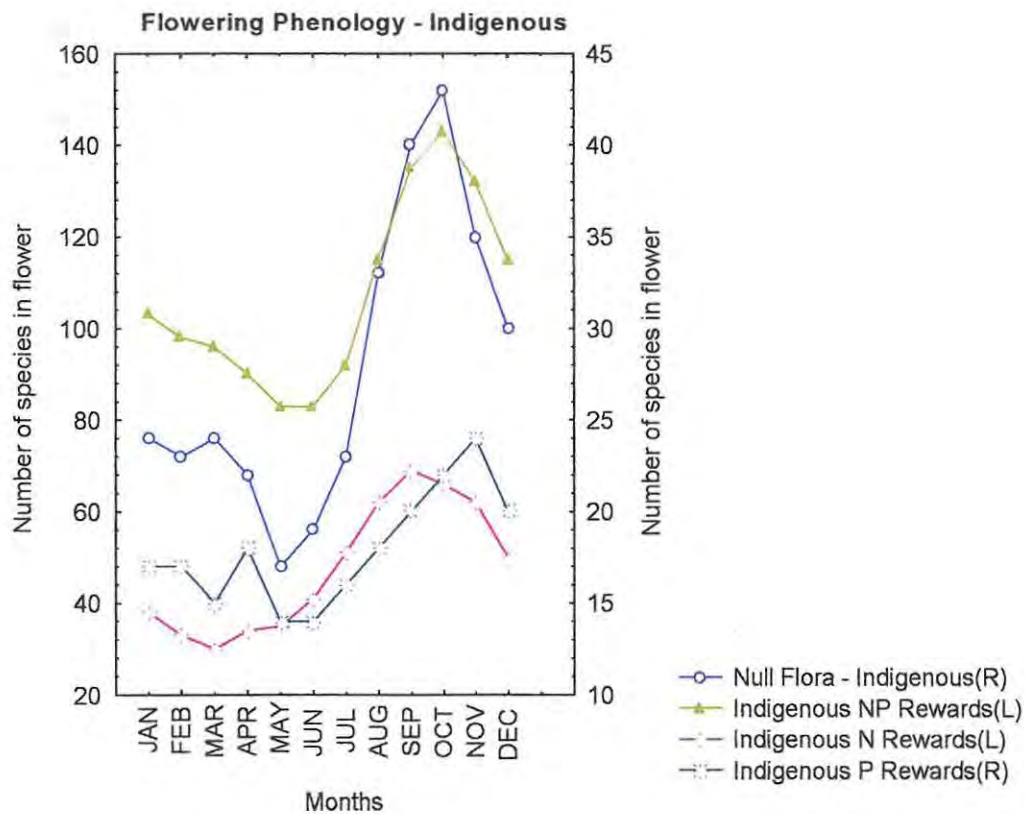


Figure 4.3. The flowering phenologies of indigenous honeybee forage plant species in South Africa according to reward category.

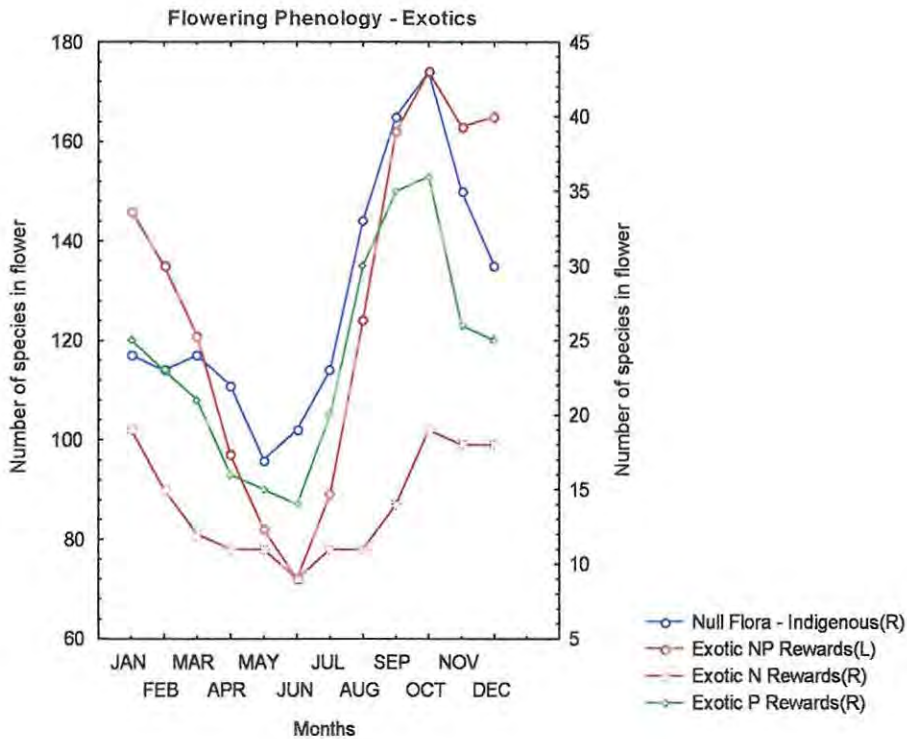


Figure 4.4. The flowering phenologies of exotic honeybee forage plant species in South Africa according to reward category.

The exotic species reward categories have a highly synchronous flowering regime (Exotic Nectar & Pollen vs Exotic Nectar, Spearman $R = 0.8931$, $p = 0.0001$; Exotic Nectar & Pollen vs Exotic Pollen, Spearman $R = 0.8722$, $p = 0.0002$; Exotic Nectar vs Exotic Pollen, Spearman $R = 0.6907$, $p = 0.0129$). All the reward categories for the exotic species flower at their peak in the same month (October) during early summer. However, for the exotic species only offering a nectar reward the same number of species are in flower during October and January (Figure 4.4). The correlation between the flowering phenologies of the null flora and the flowering phenologies of species offering both nectar and pollen (Spearman $R = 0.8667$, p

= 0.0003) are significant at the 0.01 level.

The mean durations and selected distribution measures of the flowering periods for the various reward categories appear in Table 4.1. Indigenous sources of nectar and pollen flower for the longest time (\bar{x} = 6.9 months) and the exotic sources of pollen for the shortest (\bar{x} = 5.4 months). For every category indigenous plants flower on average longer than the exotic species. None of the categories have normally distributed flowering durations at the 0.05 level of significance, but indigenous pollen plants are marginally so at the 0.01 level of significance. All the distributions for flowering duration are positively skewed and platykurtic. The indigenous nectar plants are the least skewed and have the greatest negative kurtosis value, whereas the exotic nectar plants are at the opposite extremes (Table 4.1).

Table 4.1. The flowering durations of indigenous and exotic honeybee forage plants in South Africa by reward category. I = Indigenous species, E = exotic species, NP = source of nectar and pollen, N = source of nectar, P = source of pollen.

	I NP	I N	I P	I T	E NP	E N	E P	E T
No. Species	186	84	35	346	259	28	53	345
Duration								
Mean Monthly	6.9	6.8	6.1	6.8	5.9	6.0	5.4	5.9
Normality (Shapiro-Wilk's W test)	0.92216 p<0.0001	0.9170 p<0.0001	0.9183 p<0.0128	0.9220 p<0.0001	0.8995 p<0.0001	0.8388 p<0.0006	0.8793 p<0.0001	0.8999 p<0.0001
Skewness	0.3185	0.2530	0.5384	0.2755	0.6230	0.8529	0.7315	0.6205
Kurtosis	-1.0148	-1.1507	-0.7428	-1.0997	-0.7663	-0.6620	-0.7070	-0.7868

4.3.3. Comparative analysis of family phenologies

Only three indigenous families met the selection criteria described in the methods, namely the Asteraceae, Ericaceae and Fabaceae. The flowering phenologies for the indigenous Asteraceae and Fabaceae have similar unimodal distributions and are significantly correlated at the 0.01 level of significance (Spearman $R = 0.8972$, $p = 0.0001$) (Figure 4.5). The indigenous Ericaceae have a quite different distribution, being distinctly bimodal and correlated with neither of the above families (Ericaceae vs Asteraceae, Spearman $R = -0.3848$, $p = 0.2168$; Ericaceae vs Fabaceae, Spearman $R = -0.2250$, $p = 0.4820$). The synchronous flowering regimes of the Asteraceae and Fabaceae are well correlated (0.01 level of significance) with the null flora (Null Flora vs Asteraceae, Spearman $R = 0.9577$, $p < 0.0001$; Null Flora vs Fabaceae, Spearman $R = 0.9273$, $p < 0.0001$).

Flowering reaches a peak in the indigenous Asteraceae during September-October and a low in May (Figure 4.5). The Fabaceae flower most profusely in October with a reciprocal low from April to June (Figure 4.5). The Ericaceae have a primary flowering mode in April and a secondary one in October-November, with an antimode in August.

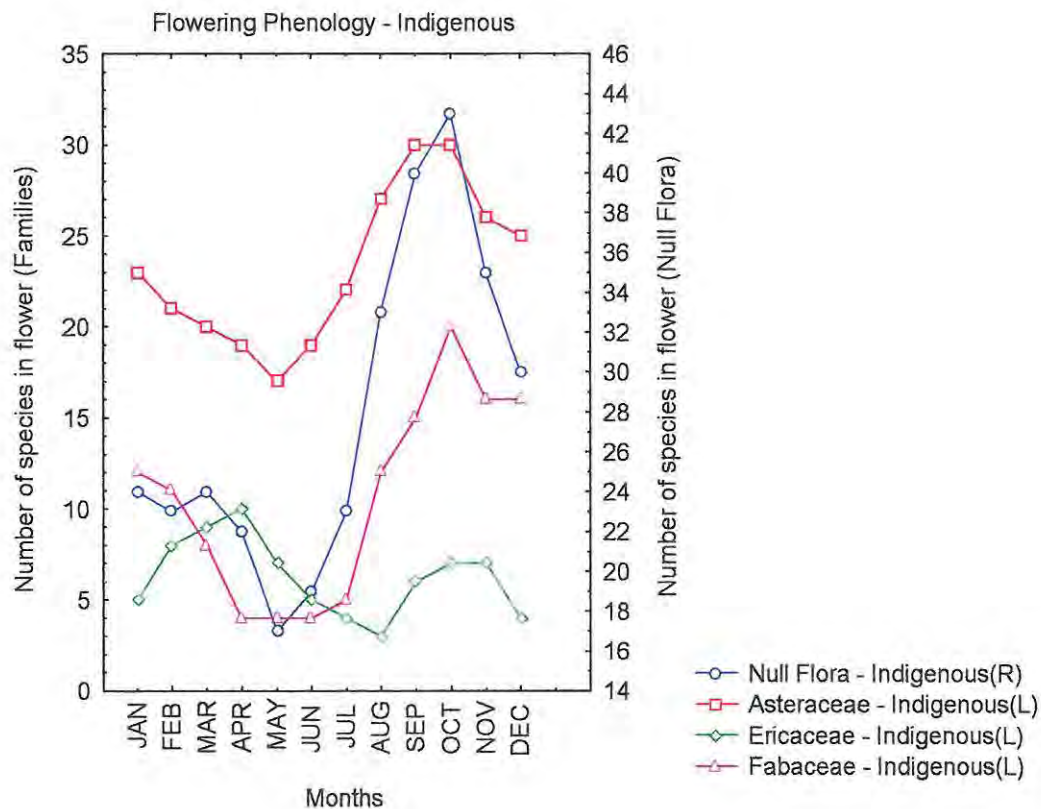


Figure 4.5. The flowering phenologies of indigenous honeybee forage plants within the Asteraceae, Ericaceae and Fabaceae in South Africa.

Flowering in the exotic Asteraceae is quite different to that in the indigenous Asteraceae (Spearman $R = 0.0231$, $p = 0.9433$) (Figure 4.6), reaching a high in December and falling to a low from June to August. The exotic Asteraceae also differ distinctly from the null flora with regard to flowering phenology (Spearman $R = 0.1631$, $p = 0.6125$). In contrast, the exotic Fabaceae flower synchronously with the local Fabaceae (Spearman $R = 0.9222$, $p < 0.0001$) (Figure 4.7) and the null flora (Spearman $R = 0.9701$, $p < 0.0001$) (Figure 4.7). They reach a flowering climax in October and a low in May (Figure 4.7).

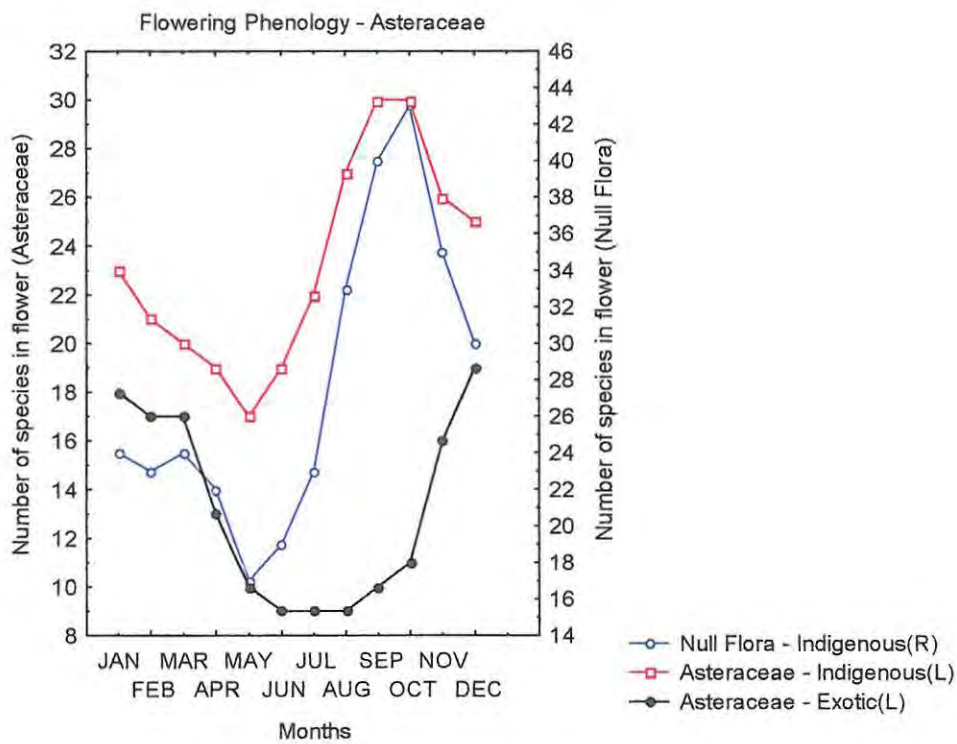


Figure 4.6. The flowering phenology of indigenous and exotic honeybee forage plant species within the Asteraceae in South Africa.

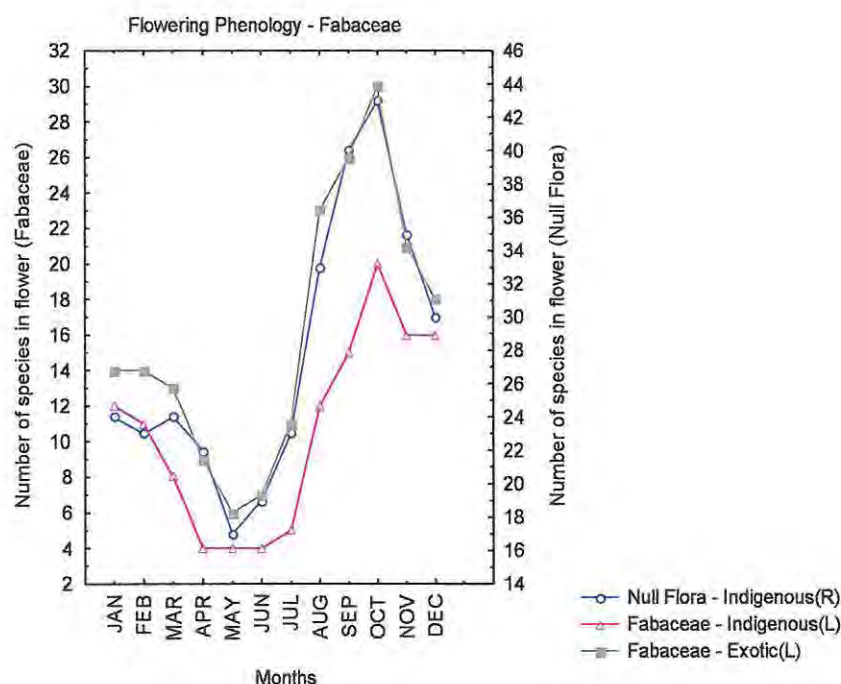


Figure 4.7. The flowering phenologies of the indigenous and exotic honeybee forage plant species within the Fabaceae in South Africa.

The average duration of flowering for the three indigenous families and two corresponding exotic families are indicated in Table 4.2. below. Indigenous Asteraceae ($\bar{x} = 7.8$ months) flower on average for the longest and exotic Fabaceae ($\bar{x} = 5.2$ months) for the shortest time period. The indigenous species of Asteraceae and Fabaceae ($\bar{x} = 5.8$ months) flower on average for longer periods than their exotic counterparts. The indigenous Asteraceae and Ericaceae ($\bar{x} = 6.8$ months) flower for longer, but the indigenous Fabaceae for shorter periods than the null flora ($\bar{x} = 6.7$ months).

The Shapiro-Wilk's (W) test for normality indicates that the flowering durations of the indigenous Ericaceae and Fabaceae are normally distributed, while the indigenous Asteraceae are not. The distributions for the indigenous Asteraceae and Ericaceae are negatively skewed and platykurtic, whereas the distribution of flowering durations for the Fabaceae is positively

skewed and leptokurtic (Table 4.2).

Table 4.2. The flowering durations of indigenous and exotic honeybee forage plants in South Africa by family. I = Indigenous, E = Exotic, AST = Asteraceae, ERI = Ericaceae, FAB = Fabaceae, NULL = Null flora.

	AST-I	AST-E	ERI-I	FAB-I	FAB-E	NULL-I
No. Species	36	24	11	22	37	50
Duration						
Mean Monthly	7.8	6.6	6.8	5.8	5.2	6.7
Normality	0.8180		0.9593	0.9364		0.9246
(Shapiro-Wilk's W test)	p<0.0001		p<0.7630	p<0.1664		p<0.0035
Skewness	-0.0389		-0.2477	0.7482		0.2914
Kurtosis	-1.7435		-0.9405	0.4300		-1.0393

4.3.4. Comparative analysis of indigenous species pairs

It was possible to arrange thirty pairs of congeneric honeybee forage plant species indigenous to South Africa following the protocol outlined in the methods (Table 4.3). Twenty-three of these species pairs occurred in sympatry and five in allopatry (Table 4.3). Two of the species pairs were difficult to classify into either group and are listed as parapatric in the table below (i.e. *Aloe arborescens*-*Aloe ferox* and *Schotia afra*-*Schotia brachypetala*). Where overlap is possible in the *Aloe arborescens*-*Aloe ferox* pairing *Aloe arborescens* appears to be restricted to the coastal areas and immediate hinterland, whereas *Aloe ferox* appears to occupy an area

further inland. *Schotia afra* and *Schotia brachypetala* may co-occur along the central Transkeian coast, but at best the extent of overlap would appear to be minimal.

Nine of the species pairs had significantly correlated (Spearman R, 0.05 level) flowering phenologies. This excluded the three species pairs where there was complete overlap of flowering times (i.e. *Acacia karroo* - *Acacia sieberiana*, *Aloe arborescens* - *Aloe marlothii* and *Protea caffra* - *Protea repens*) or the three other species pairs where one of the species flowered all year round (i.e. *Dombeya burgessiae* - *Dombeya rotundifolia*, *Protea caffra* - *Protea obtusifolia* and *Protea obtusifolia* - *Protea repens*)(Table 4.3). Both of the pairs occurring in parapatry were positively correlated, likewise four of the pairs which occur in allopatry (i.e. *Aloe ferox* - *Aloe marlothii*, *Protea caffra* - *Protea obtusifolia*, *Protea obtusifolia* - *Protea repens* and *Schotia afra* - *Schotia capitata*), while species occurring in sympatry were represented by both positively and negatively correlated pairings. The former are represented by *Acacia caffra* - *Acacia mellifera*, *Acacia erioloba* - *Acacia mellifera*, *Acacia karroo* - *Acacia sieberiana*, *Aloe arborescens* - *Aloe marlothii*, *Combretum apiculatum* - *Combretum zeyheri*, *Dombeya burgessiae* - *Dombeya zeyheri* and *Protea obtusifolia* - *Protea repens* while the latter are represented by *Crassula arborescens* - *Crassula ovata* and *Euclea racemosa* - *Euclea tomentosa*.

The duration of flowering within each of the pairings is often markedly different. In 21 of the pairings the species flowering for a shorter duration only flowered for 75% or less as long as the longer flowering species. In the *Combretum apiculatum* - *Combretum zeyheri* species pair *Combretum zeyheri* flowers for one month less than *Combretum apiculatum*, while the species with the pairings *Acacia karroo* - *Acacia sieberiana*, *Aloe arborescens* - *Aloe marlothii*, *Crassula arborescens* - *Crassula ovata* and *Protea caffra* - *Protea repens* all flower for the same duration.

Table 4.3. Species pairs of congeneric honeybee forage plant species indigenous to South Africa ("-" = no value produced by STATISTICA 6.0 for the Spearman Rank Order correlations).

Family	Species Pair	Distribution	Duration (Months)	Spearman R
Fabaceae	<i>Acacia caffra</i>	Sympatric	7	0.3780
	<i>Acacia erioloba</i>		2	p = 0.2258
Fabaceae	<i>Acacia caffra</i>	Sympatric	7	0.5071
	<i>Acacia karroo</i>		6	p = 0.0924
Fabaceae	<i>Acacia caffra</i>	Sympatric	7	0.5976
	<i>Acacia mellifera</i>		4	p = 0.0402
Fabaceae	<i>Acacia caffra</i>	Sympatric	7	0.5071
	<i>Acacia sieberiana</i>		6	p = 0.0924
Fabaceae	<i>Acacia erioloba</i>	Sympatric	2	0.0000
	<i>Acacia karroo</i>		6	p = 1.0000
Fabaceae	<i>Acacia erioloba</i>	Sympatric	2	0.6325
	<i>Acacia mellifera</i>		4	p = 0.0273
Fabaceae	<i>Acacia erioloba</i>	Sympatric	2	0.0000
	<i>Acacia sieberiana</i>		6	p = 1.0000
Fabaceae	<i>Acacia karroo</i>	Sympatric	6	0.0000
	<i>Acacia mellifera</i>		4	p = 1.0000
Fabaceae	<i>Acacia karroo</i>	Sympatric	6	1.0000
	<i>Acacia sieberiana</i>		6	p = -
Fabaceae	<i>Acacia mellifera</i>	Sympatric	4	0.0000
	<i>Acacia sieberiana</i>		6	p = 1.0000

Asphodelaceae	<i>Aloe arborescens</i>	Parapatric	4	0.5976
	<i>Aloe ferox</i>		7	p = 0.0402
Asphodelaceae	<i>Aloe arborescens</i>	Sympatric	4	1.0000
	<i>Aloe marlothii</i>		4	p = -
Asphodelaceae	<i>Aloe ferox</i>	Allopatric	7	0.5976
	<i>Aloe marlothii</i>		4	p = 0.0402
Asteraceae	<i>Brachylaena discolor</i>	Allopatric	3	-0.4880
	<i>Brachylaena neriifolia</i>		5	p = 0.1075
Loganiaceae	<i>Buddleja salina</i>	Sympatric	10	-0.4472
	<i>Buddleja salviifolia</i>		6	0.1449
Combretaceae	<i>Combretum appiculatum</i>	Sympatric	6	0.8452
	<i>Combretum zeyheri</i>		5	p = 0.0005
Crassulaceae	<i>Crassula arborescens</i>	Sympatric	5	-0.7143
	<i>Crassula ovata</i>		5	p = 0.0091
Ebenaceae	<i>Diospyros glabra</i>	Sympatric	3	0.3333
	<i>Diospyros whyteana</i>		9	p = 0.2897
Sterculiaceae	<i>Dombeya burgessiae</i>	Sympatric	12	-
	<i>Dombeya rotundifolia</i>		5	p = -
Ebenaceae	<i>Euclea racemosa</i>	Sympatric	7	-0.8367
	<i>Euclea tomentosa</i>		4	p = 0.0007
Euphorbiaceae	<i>Euphorbia tetragona</i>	Sympatric	4	0.4264
	<i>Euphorbia triangularis</i>		1	p = 0.1669
Greyiaceae	<i>Greyia radlkoferi</i>	Sympatric	6	-0.1925
	<i>Greyia sutherlandii</i>		9	0.5490
Proteaceae	<i>Protea caffra</i>	Allopatric	12	-
	<i>Protea obtusifolia</i>		9	p = -

Proteaceae	<i>Protea caffra</i>	Allopatric	12	-
	<i>Protea repens</i>		12	p = -
Proteaceae	<i>Protea obtusifolia</i>	Sympatric	9	-
	<i>Protea repens</i>		12	p = -
Fabaceae	<i>Pterocarpus angolensis</i>	Sympatric	5	0.1690
	<i>Pterocarpus rotundifolius</i>		6	0.5995
Anacardiaceae	<i>Rhus lancea</i>	Sympatric	8	0.0000
	<i>Rhus lucida</i>		9	p = 1.0000
Fabaceae	<i>Schotia afra</i>	Parapatric	6	0.7071
	<i>Schotia brachypetala</i>		4	p = 0.0101
Fabaceae	<i>Schotia afra</i>	Allopatric	6	0.7071
	<i>Schotia capitata</i>		8	p = 0.0101
Fabaceae	<i>Schotia brachypetala</i>	Sympatric	4	0.5000
	<i>Schotia capitata</i>		8	p = 0.0979

4.3.5. *Eucalyptus* in South Africa

More *Eucalyptus* species offering a reward of nectar and pollen in South Africa are in flower during December than any other month, with the least number of species in flower in June.

The flowering peak in the *Eucalyptus* lags that for the indigenous honeybee flora (all rewards) by two months and the flowering low by a month (Figure 4.8). The same association is evident between the *Eucalyptus* and the null flora (Figure 4.8). There is no significant correlation (Spearman R, 0.05 level of significance) between the flowering phenology of the *Eucalyptus* species and either the indigenous honeybee forage plants (all rewards) or the null flora. The

Eucalyptus flower on average for 7.9 months per annum. The distribution of the flowering durations deviates significantly from normal (Shapiro-Wilk's test, $W = 0.9329$, $p = 0.0029$) at the 0.01 level of significance. The distribution is positively skewed (0.1936) and platykurtic (-1.0618).

Eucalyptus cornuta, *E. calophylla*, *E. gomphocephala*, *E. platypus*, *E. salubris* and *E. torquata* were selected using the criteria described in the methods to test the geographic variation of flowering time within the genus. The flowering times in half were significant (Spearman R, 0.05 level of significance) (i.e. *E. calophylla*, *E. salubris* and *E. torquata*), while in the other half they were not (i.e. *E. cornuta*, *E. gomphocephala* and *E. platypus*) (Table 4.4). In all the species above flowering was longer in South Africa than Western Australia, with the exception of *E. platypus* which flowered for longer in Australia (Table 4.4).

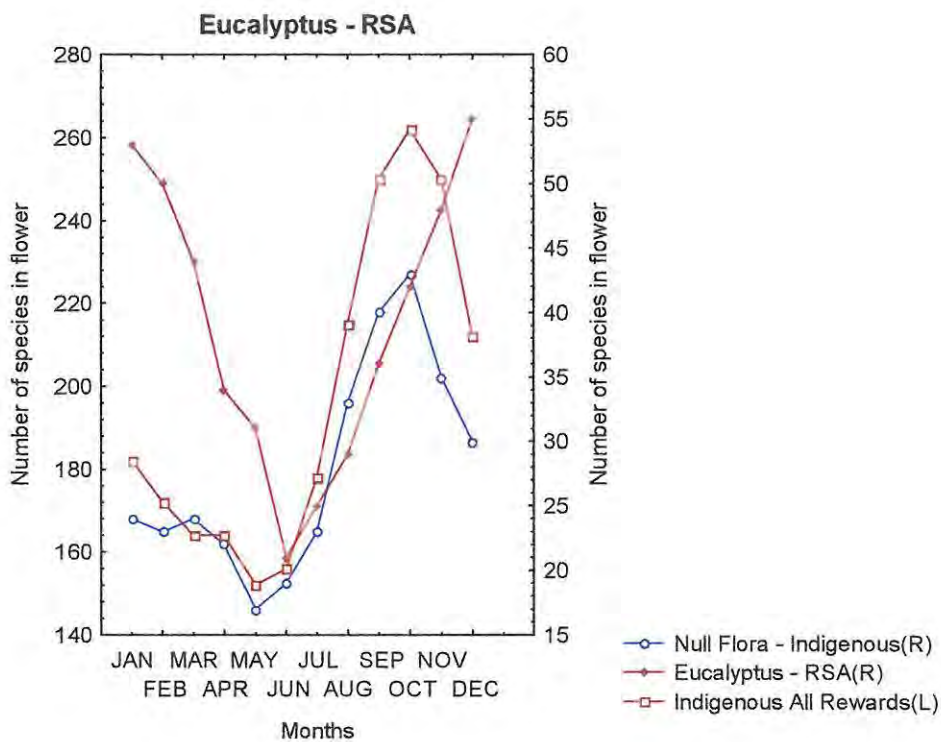


Figure 4.8. The flowering phenology of *Eucalyptus* within South Africa in relation to the flowering phenologies of the null, indigenous and exotic flora's.

Table 4.4. Flowering duration and Spearman Rank Order Correlations for selected *Eucalyptus* species in South Africa and Western Australia.

Family	Species	Distribution	Duration	Spearman R
Myrtaceae	<i>E. cornuta</i>	South Africa	9	0.3333
		Western Australia	3	(p = 0.2897)
	<i>E. calophylla</i>	South Africa	6	0.7071
		Western Australia	4	(p = 0.0101)
	<i>E. gomphocephala</i>	South Africa	10	0.3162
		Western Australia	4	(p = 0.3166)

	<i>E. platypus</i>	South Africa	4	0.1250
		Western Australia	8	(p = 0.6987)
	<i>E. salubris</i>	South Africa	6	0.7071
		Western Australia	4	(p = 0.0101)
	<i>E. torquata</i>	South Africa	6	0.8452
		Western Australia	5	(p = 0.0005)

4.4. Discussion

4.4.1. Phylogenetic constraint

Evidence for phylogenetic constraint appears limited at the family level. With only three families used in the analysis, conclusions can at best be regarded as tentative. One could have anticipated that if phylogeny strongly affected family flowering times that they would differ significantly from the null flora and perhaps each other. The indigenous Asteraceae and Fabaceae both have highly significant correlations (0.01 level of significance) with the null flora suggesting flowering times within the family are arranged at random. The indigenous Ericaceae are not correlated with the null flora and may indeed have flowering phenologies constrained by phylogeny. As additional evidence for the hypothesis of phylogenetic constraint one would anticipate that the exotic species of Asteraceae and Fabaceae flower at the same time as the indigenous species. In the Fabaceae the species of different geographical origin are highly correlated (0.01 level of significance) contradicting the evidence for randomized flowering times presented earlier. However, there is no correlation between the Asteraceae of different geographical origin which does provide further support for the hypothesis. Given the

equivocal nature of these results further research is required on larger datasets and more families of honeybee forage plants to determine the extent if any of phylogenetic constraint in the flowering phenology of indigenous South African honeybee forage plants. This could indicate that honeybees select from the different families species that have similar flowering phenologies. Alternatively, it could merely be an effect of selection by honeybees for another floral trait such as reward quality.

An analysis of the flowering durations of the Asteraceae and Fabaceae yielded results consistent with those obtained for the intra-annual flowering regimes discussed above. The flowering durations for the indigenous Fabaceae were leptokurtic and normally distributed which is indicative of stabilizing selection. In contrast, the flowering durations for the indigenous Asteraceae had a negatively skewed and platykurtic distribution. It is notable that Rathcke & Lacey (1985) reported that self-compatible species tended to have shorter flowering durations. The possibility that these floral traits may all be linked needs to be investigated further. It is not inconceivable that self-compatibility within the Fabaceae has facilitated the stabilizing selection in these floral traits.

The different reward categories (nectar, pollen, nectar & pollen) appear to have had little influence on the intra-annual flowering regimes or flowering durations of either the indigenous or exotic honeybee forage plants. The intra-annual flowering regimes of the three reward categories are significantly correlated (0.05 level) with each other for both the indigenous and exotic honeybee forage plants, while the forage plants offering both rewards (*i.e.* nectar & pollen) of either geographical origin are significantly correlated with the null flora. None of the reward categories for either the indigenous or exotic forage plants had normal distributions for flowering duration. All of these distributions were platykurtic and hence widely dispersed.

4.4.2. Pollinator-limitation

If indigenous honeybee forage plant species compete for honeybee pollination one would expect sympatric congeneric species pairs to be negatively correlated or to have different flowering durations. One could also expect that allopatric species pairs have positively correlated flowering regimes or if geographic separation has postdated a sympatric state for them to have divergent flowering times. No correlation could be expected if some trait other than flowering was of greater importance to the honeybees. Only half of the species pairs have highly coincident flowering regimes (Table 4.3) which would seem to suggest that flowering times are not particularly important to honeybees.

Only two of the nine correlated species pairs, both occurring in sympatry, have a statistically significant negative correlation (0.05 level of significance), namely *Crassula arborescens* - *Crassula ovata* and *Euclea racemosa* - *Euclea tomentosa*. This is consistent with the competition hypothesis, especially in the case of the former where flowering occurs for the same duration (5 months). Five of the remaining species pairs with positive correlations have flowering durations with one species flowering for only 50%-60% of the other, which again would be consistent with the competition hypothesis. The exception to the above are the *Acacia karroo* - *Acacia sieberiana*, *Aloe arborescens* - *Aloe marlothii* and *Combretum apiculatum* - *Combretum zeyheri* species pairs which are positively correlated, occur in sympatry and flower for similar durations. This could indicate flowering facilitation between the species, an adaptive response in another floral trait, that competition for pollination by honeybees is sub-optimal or that sufficient pollination is carried out by other pollinators.

It would therefore appear that competition for pollination within the indigenous honeybee flora has not been an important factor in the evolution of flowering time. This could

either be due to the efficacy of promiscuous honeybee pollination, their cosmopolitan distribution, catholic tastes or a combination of the aforementioned. Alternatively, visitation by generalist foragers such as honeybees probably implies that many other potential pollinators are also able to access the floral rewards on offer and hence carry out pollination of the plants.

4.4.3. Exotic species flowering phenology

The relationship between the honeybees and their exotic honeybee forage plants in South Africa is a double-edged sword. The honeybees could potentially facilitate the spread of invasive alien vegetation via pollination and/or preferentially visit exotic species at the expense of local honeybee forage plants. However, some exotic species, most notably the *Eucalyptus*, are of major importance to commercial beekeeping in the country. The flowering phenologies of exotic honeybee forage plant species are significantly positively correlated with the local honeybee flora (Spearman $R = 0.8647$, $p = 0.0003$). This suggests they have the potential to significantly disrupt the pollination of local flora.

Significant positive correlations occur between the plants offering nectar and pollen and only pollen as a reward, but not for the species acting solely as a source of nectar. The positive correlation between the indigenous and exotic Fabaceae (Spearman $R = 0.9222$, $p < 0.0001$) indicates that the competition may also be evident at the family level. *Eucalyptus* may provide particularly strong competition to the indigenous Fabaceae (Spearman $R = 0.5972$, $p = 0.0403$). The flowering phenology of *Eucalyptus* in South Africa appears to differ from that in Western Australia. The most important difference, particularly within the context of the potential threat to the pollination of the indigenous flora, is the extended duration of flowering in five of the six species examined in this study. The threat posed by exotic vegetation to the

pollination of local flora awaits further examination.

The genus *Apis* has been present since at least the mid-Oligocene (Michener, 2000). It is not inconceivable therefore that *Apis mellifera* has played a role in the evolution of the flowering phenologies of at least some of its forage plants or that the plants have played a role in the evolution of the honeybee reproductive cycle. However, if any of these links exist within the South African flora they have not been established convincingly in this study. Nevertheless, the relationship between honeybees and exotic forage plants in particular needs to be explored further.

4.5. References

Ackerman, T.L. and Bamberg, S.A. 1974. Phenological studies in the Mojave desert at Rock Valley (Nevada Test Site). In Phenology and seasonality modelling, Lieth, H. (Ed), Chapman & Hall Limited, London, Springer-Verlag, Berlin, 215-226.

“Aerial”. 1943. Natal’s ten-year honey phenomenon: the uhlalwane shrub. The South African Bee Journal, 18, 8-10.

Alvim, P. de T. 1960. Moisture stress as a requirement for flowering of coffee. Science, 132, 354.

Bannister, P. 1978. Flowering and shoot extension in heath plants of different geographical origin. Journal of Ecology, 66, 117-131.

Bawa, K.S. 1983. Patterns of flowering in tropical plants. In Handbook of Experimental Pollination Biology, Jones, C.E. and Little, R.J. (Eds), Van Nostrand Reinhold, New York, p. 394-410.

Bayer, A.W. 1938. An account of the plant ecology of the coastbelt and midlands of Zululand. Annals of the Natal Museum, 8, 371-454.

Bernier, G. 1988. The control of floral evocation and morphogenesis. Annual Review of Plant Physiology and Plant Molecular Biology, 39, 175-219.

Brody, A.K. 1997. Effects of pollinators, herbivores, and seed predators on flowering phenology. Ecology, 78, 1624-1631.

Burk, C.J. 1966. Rainfall periodicity as a major factor in the flowering of races of camphorweed (*Heterotheca subaxillaris*). American Journal of Botany, 53, 933-936.

Coates Palgrave, K. 1977. Trees of southern Africa. First Edition. C. Struik Publishers, Cape Town, 959 pp..

Crane, E. 1990. Bees and beekeeping: science, practice and world resources. Heinemann Newnes, Oxford, 614 pp..

Esler, K.J. 1999. Plant reproductive ecology. Chapter 8. In Dean, W.R.J. and Milton, S.J. (Eds), The Karoo: ecological patterns and processes, Cambridge University Press, p.123-144.

- Fox, G.A. 1990. Drought and the evolution of flowering time in desert annuals. *American Journal of Botany*, 77, 1508-1518.
- Francis, W.F.N. 1963. Cape beekeeper's phenomenal success with mountain swarms. *The South African Bee Journal*, 35, 2.
- Frankie, G.W., Haber, W.A., Opler, P.A. and Bawa, K.S. 1983. Characteristics and organization of the large bee pollination system in the Costa Rican dry forest. In *Handbook of Experimental Pollination Biology*, Jones, C.E. and Little, R.J. (Eds), Van Nostrand Reinhold, New York, p.411-447.
- Free, J.B. 1993. *Insect pollination of crops*. 2nd Edition. Academic Press, London, 684 pp..
- Frenguelli, G. and Bricchi, E. 1998. The use of the pheno-climatic model for forecasting the pollination of some arboreal taxa. *Aerobiologia*, 14, 39-44.
- Friedel, M.H., Nelson, D.J., Sparrow, A.D., Kinloch, J.E., and Maconochie, J.R. 1994. Flowering and fruiting of arid zone species of *Acacia* in central Australia. *Journal of Arid Environments*, 27, 221-239.
- Henkel, J.S., Ballenden, S. StC. and Bayer, A.W. 1936. An account of the plant ecology of the Dukuduku Forest Reserve and adjoining areas of the Zululand Coast Belt. *Annals of the Natal Museum*, 8, 95-125.

Hepburn, H.R. 1992. "Follow-flow" brood rearing in *capensis* and *scutellata*. South African Bee Journal, 64, 104-109.

Hepburn, H.R. 1993. Swarming, absconding and migration in southern African bees. South African Bee Journal, 65, 61-66.

Hepburn, H.R. and Jacot Guillarmod, A. 1991. The Cape honeybee and the fynbos biome. South African Journal of Science, 87, 70-73.

Hepburn, H.R. and Radloff, S.E. 1995. First approximation to a phenology of the honeybees (*Apis mellifera*) and flora of Africa. Oecologia, 101, 265-273.

Hepburn, H.R. and Radloff, S.E. 1998. Honeybees of Africa. Springer, Berlin, 370 pp..

Ihlenfeldt, H.-D. 1994. Diversification in an arid world: The Mesembryanthemaceae. Annual Review of Ecology and Systematics, 25, 521-546.

Jackson, M.T. 1966. Effects of microclimate on spring flowering phenology. Ecology, 47, 407-415.

Johnson, S.D. 1993. Climatic and phylogenetic determinants of flowering seasonality in the Cape flora. Journal of Ecology, 81, 567-572.

Kennard, R. 1988. "Hlalwane" in Natal. South African Bee Journal, 60, 122-125.

- Kochmer, J.P. and Handel, S.N. 1986. Constraints and competition in the evolution of flowering phenology. *Ecological Monographs*, 56, 303-325.
- Kruger, F.J. 1981. Seasonal growth and flowering rhythms: South African Heathlands. Chapter 1. In *Heathlands and related shrublands of the world B. Analytical studies*, Specht, R.L. (Ed), Elsevier, Amsterdam, 1-4.
- le Maitre, D.C. and Midgley, J.J. 1992. Plant reproductive ecology. In *Fynbos: nutrients, fire and diversity*, Cowling, R.M. (Ed), Oxford University Press, Cape Town, 135-174.
- Michener, C.D. 2000. *The bees of the world*. The Johns Hopkins University Press, Baltimore, 913 pp..
- Milton, S.J. 1992. Effects of rainfall, competition and grazing on flowering of *Osteospermum sinuatum* (Asteraceae) in arid Karoo rangeland. *Journal of the Grassland Society of Southern Africa*, 9, 158-164.
- Mohr, H. and Schopfer, P. 1995. *Plant Physiology*. Springer.
- Mosquin, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos*, 22, 398-402.
- Phillips, J.F.V. 1926. General biology of the flowers, fruits, and young regeneration of the more important species of the Knysna forests. *South African Journal of Science*, 23, 366-417.

- Pierce, S.M. 1984. A synthesis of plant phenology in the Fynbos Biome. South African National Scientific Programmes Report, 88, 57 pp..
- Pojar, J. 1974. Reproductive dynamics of four plant communities of southwestern British Columbia. *Canadian Journal of Botany*, 52, 1819-1834.
- Pooley, E. 1998. A field guide to wild flowers KwaZulu-Natal and the eastern region. Natal Flora Publications Trust, 630 pp..
- Proctor, M., Yeo, P. and Lack, A. 1996. The natural history of pollination. Harper Collins Publishers, London, 479 pp..
- Rathcke, B. and Lacey, E.P. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics*, 16, 179-214.
- Reader, R.J. 1983. Using heatsum models to account for geographic variation in the floral phenology of two ericaceous shrubs. *Journal of Biogeography*, 10, 47-64.
- Schemske, D.W., Willson, M.F., Melampy, M.N., Miller, L.J., Verner, L., Schemske, K.M. and Best, L.B. 1978. Flowering ecology of some spring woodland herbs. *Ecology*, 59, 351-366.
- Smith, F.G. 1969. Honey plants in Western Australia. Bulletin No. 3618, Department of Agriculture of Western Australia, South Perth, 78 pp..

Smith-Ramírez, C. and Armesto, J.J. 1994. Flowering and fruiting patterns in the temperate rainforest of Chiloé, Chile - ecologies and climatic constraints. *Journal of Ecology*, 82, 353-365.

Steyn, H.M., van Rooyen, N., van Rooyen, M.W. and Theron, G.K. 1996a. The phenology of Namaqualand ephemeral species. The effect of water stress. *Journal of Arid Environments*, 33, 49-62.

Strauss, S.Y. 1997. Floral characters link herbivores, pollinators, and plant fitness. *Ecology*, 78, 1640-1645.

Struck, M. 1994. Flowers and their insect visitors in the arid winter rainfall region of southern Africa: observations on permanent plots. Insect visitation behaviour. *Journal of Arid Environments*, 28, 51-74.

Taiz, L. and Zeiger, E. 1991. *Plant Physiology*. Benjamin Cummings, Menlo Park, 565 pp..

Tyson, P.D. 1986. *Climatic change and variability in southern Africa*. Oxford University Press, Cape Town, 220 pp..

van Steenis, C.G.G.J. 1978. Gregarious flowering in the monocarpic genus *Isoglossa* (Acanthaceae). *Bothalia*, 12, 553.

Vince-Prue, D. 1983. Photomorphogenesis and flowering. Chapter 18. In *Encyclopedia of Plant Physiology, Photomorphogenesis, New Series Volume 16B*, Shropshire, W. and Mohr, H. (Eds), Springer-Verlag, Berlin, 457-490.

Waser, N.M. and Real, L.A. 1979. Effective mutualism between sequentially flowering plant species. *Nature*, 281, 670-672.

Wright, S.J. and van Schaik, C.P. 1994. Light and the phenology of tropical trees. *The American Naturalist*, 143, 192-199.

CHAPTER 5. HONEYBEES AND LAND MANAGEMENT IN SOUTH AFRICA

"Pollinators are key to global sustainable terrestrial productivity. They are a bellwether for environmental stress as individuals and as colonies." (Kevan, 1999 p. 386)

5.1. Introduction

The reproductive successes of the honeybee and its forage plants are subtly interfused. As a consequence any land use strategy which impacts on the composition or flowering phenology of a plant community has the potential to affect the reproductive cycle of a colony and hence the honey yield. As generalist foragers and pollinators honeybees may in turn enhance the fruit set and seed production of their food plants and by inference their relative reproductive success in the plant community.

In this chapter the honeybee - forage plant axis is explored from two different perspectives, namely the effect of land use strategies on the honeybee and the reciprocal effect of honeybees on their forage plants. Man forms the central theme of each of the sections discussed in turn below. Even though honeybees are clearly important to the pollination of the indigenous flora and hence indirectly to the fruit set of many species, these links or those to the dependent frugivores are not explored in this study. The chapter is divided into three sections, the first considering the effect of land use strategies such as grazing and fire on honeybees. The second section investigates the potential of honeybees to act as instruments of plant conservation, while the last highlights the importance honeybee pollination may have for commercial crop production and rural food security.

5.2. The impact of land use strategies on honeybees

Habitat destruction can influence pollinators in a number of ways, including the loss of food plants, mating or nesting sites (Kevan, 1999). In this chapter only the impacts on sources of pollen and nectar are considered. Habitat modification in South Africa is most likely to result from alien plant invasions, bush clearing, fire, monoculture, overgrazing, and urbanization. In addition, flower harvesting in the fynbos biome probably degrades the quality of honeybee forage within that region. The threat posed by alien plant invasions to the local flora is discussed in the section on plant conservation. These invasions need not always have a negative impact on honeybee populations as evidenced by the importance of *Eucalyptus* spp. to local beekeepers (Lear, 1990).

Less bush clearing probably occurs today than in the past, but extensive areas have been cleared in some regions for pastures and crop production. In periurban and rural areas some honeybee forage plants are also used for fuel and building materials. For example, in the Eastern Cape, *Acacia karroo*, *Ehretia rigida*, *Euclea undulata*, *Harpehphyllum caffrum*, *Olea europaea*, *Schotia afra*, *Scutia myrtina*, *Sideroxylon inerme* and *Trichilia dregeana* are used for fuel, while *Acacia karroo* and *Trichilia dregeana* are used for building material (Briers & Powell, 1996; van Eck *et al.*, 1997).

Grazing and browsing management strategies have the potential to greatly influence the quality of forage in many areas of the country, with the exception of the indigenous forests. No distinction is made between communal and commercial grazing activities in this chapter. The focus will be restricted to the general impacts of grazing on plant species composition and not the potential differences which may arise under these two management strategies. Goats and sheep appear to have the greatest direct impact on the indigenous

vegetation, while cattle play an indirect role in habitat modification. Over the last 25 years the number of cattle (1975/76 = 8.8 million, 2000/01 = 13.5 million) and goats (1975 = 2.315 million, 1999 = 2.325 million) have increased, while the number of sheep (1975 = 30.989 million, 1999 = 25.235 million) have decreased within South Africa (National Department of Agriculture, 2001). According to Smit & Rethman (1992):

“Since the introduction of domestic livestock, large areas of natural veld in South Africa have undergone radical changes, and continue to do so (Aucamp, 1990). In most cases these changes are detrimental as they result in lower grazing capacity, soil erosion and general degradation of the environment.” (Smit & Rethman, 1992 p.76)

The advent of sedentary European grazing and browsing practices in South Africa has in all likelihood led to large scale changes in the state of honeybee forage conditions as well. As grazers cattle can indirectly affect the abundance of honeybee forage plant species. For example, at Towoomba Research Station (24°25'S 28°21'E), within Sourish Mixed Bushveld, an increase in the density of aloes (*Aloe transvaalensis*) was attributed to increased grazing pressure (Smit & Rethman, 1992). No grazing can lead to the same effect if grasses become “moribund”; likewise the absence of fire (Smit & Rethman, 1992).

Owen-Smith & Danckwerts (1997) have suggested that goats can hinder regrowth of *Portulacaria afra* and can have a greater impact on it than indigenous browsers. There is also some indication that browsing may restrict flower production in *Rhigozum obovatum* in the karoo (Milton & Dean, 1988). It is unclear to what extent this may be the result of foraging by goats, sheep or both. The flower:fruit ratio was lower in farmland than the neighbouring road verges, which they suggested could be indicative of a more limited floral display by plants in

the former areas (Milton & Dean, 1988). This would be consistent with the observations made by Struck (1994), who reported that honeybees prefer shrubs with a cornucopian flowering strategy within the Goegab Nature Reserve, Namaqualand. Sheep may also limit flowering in *Osteospermum sinuatum* (Milton, 1992), although it is difficult to ascertain whether this is an effect of florivory, foliar herbivory or both.

“Fire can be viewed as a large generalist herbivore, sometimes competing, sometimes replacing and sometimes facilitating vertebrate herbivores.” (Bond, 1997 p.421)

Fire has the potential to influence species composition in plant communities and hence affect the quality of honeybee forage within a given area. In South Africa the fynbos, grassland and savanna biomes are fire-adapted, while the forests and karoo biomes, where fires are less frequent, are probably not (Edwards, 1984). In moister areas fire frequency is largely a function of “ignition events” with fuel loads less significant, while in drier regions (rainfall < 650 mm *per annum*) it is dependent on the quantity of grass fuel available and hence largely restricted to wetter periods (Bond, 1997). Hot, dry weather in particular creates favourable conditions for veld fires within the fynbos and grassland biomes (Bond, 1997). Fire has been used as a land management tool for centuries in South Africa, with the practice already evident by the time the first Europeans settled in the southwestern Cape in 1652 (Edwards, 1984). Between 1959/1960 and 1977/1978 at least 65% (i.e. 3020 of 4668 fires) of fires on State Forest land were attributed to man (Edwards, 1984). Man-made fires have a different seasonality to lightning initiated veld fires (Bond, 1997) and have in all likelihood significantly increased the frequency with which fires occur in the landscape. However, in certain circumstances man may restrict the frequency with which fires occur in the landscape if grazing livestock have reduced the fuel

load in the grass layer. Naturally occurring veld fires have been attributed to lightning and rockfalls, with the former probably the cause of the vast majority of these events (Bond, 1997).

On an individual level fire may trigger flowering and seed germination and determine the frequency of flowering by honeybee forage plants. Plants may adopt a number of strategies to survive fires within the landscape, including tolerance and evasion in both space and time (Frost, 1984). Species within the fynbos biome may evade fires by growing in moist (e.g. *Cunonia capensis*) or rocky locations (e.g. *Heeria argentea*) (Frost, 1984). Termitaria in the savanna biome may also act as refugia from fire for some honeybee forage plants (e.g. *Schotia brachypetala*) (Frost, 1984). Post-fire recovery of plant species may be facilitated by resprouting dormant buds and/or seed germination (Frost, 1984). Growth in the dormant buds is initiated when apical meristems are destroyed (Frost, 1984). However, as suggested by Frost (1984), defoliation may also be occasioned by frost, drought, herbivores or pathogens, which makes a coevolutionary link between fire and resprouting dormant buds doubtful.

Species without the ability to resprout are known as obligate reseeders (e.g. the honeybee forage plants *Apodytes dimidiata*, *Ekebergia capensis*, *Trema orientalis* and *Virgilia oroboides*) (Frost, 1984). It is therefore conceivable that the post-fire recovery of obligate reseeders is facilitated by honeybee pollination *via* seed production. In some fynbos communities plants without the ability to sprout may comprise half the number of species present (Bond, 1997). The frequencies, intensities and seasonalities of fires in the fynbos biome may affect species composition (Bond, 1997) and hence the quality honeybee forage. In the savanna biome fires may help prevent encroachment by trees (Bond, 1997). As trees are likely to be better sources of nectar than the grasses, fire could have a negative impact on honey yield in savanna regions. Fire may also stimulate flowering in some honeybee forage plants, for example flowering by *Graderia scabra* is largely confined to the post-fire period, while

flowering by *Agapanthus africanus* and *Protoparagus compactus* is more common after fires than other periods (Frost, 1984).

Fires also pose a direct threat to honeybees, with nests susceptible to destruction in fire-prone environments. The lack of tree cover and hence rarity of nesting sites at safe heights above ground level and frequent fires in the fynbos biome could possibly have contributed to queen loss and the evolution of thelytokous parthenogenesis in *Apis mellifera capensis*. Fire could also have contributed to the scarcity of trees within the fynbos biome (Stock *et al.*, 1992). Honeybee swarms appear to have a greater preference for potential nest cavities at a height of 3-4 metres than those located at ground level, which has been attributed at least in part to the incidence of fire (Hepburn & Radloff, 1998).

Crop monocultures cover extensive areas in some parts of the country such as the western Cape, where they may represent virtual deserts to honeybees. For example, barley which is automatically self-pollinated, covered 132 000 ha, while oats and wheat, which are wind-pollinated, covered 703 000 ha and 1 382 000 ha respectively in 1997 within South Africa (Crane & Walker, 1984; National Department of Agriculture, 2001).

Lastly, honeybees have probably been affected to a significant extent in all areas of the country by urbanization. In some landscapes urban areas may provide more nesting sites than the natural environment, such as within the largely treeless expanses of the fynbos biome, and/or enhance local foraging conditions in suburban areas. For example, the transformation of areas formerly dominated by grasslands in Johannesburg to a woodland habitat is a case in point. It would be interesting to determine the extent to which the presumably higher carrying capacities of these urban areas have resulted in them acting as reservoirs for the seasonal repopulation of the neighbouring rural areas. In cities established over 300 years ago, such as Cape Town, the cultivation of ornamental plants could also have facilitated selection against

particular morphological traits, with pockets of higher morphological variance associated with the urban areas.

5.3. Honeybee and plant conservation in South Africa

As pollinators of both indigenous and exotic flora in South Africa, honeybees should have an important role to play in the development of conservation management strategies within the country. For example, managed colonies of honeybees could be used to augment the number of feral colonies within an area and so enhance seed set within the wide range of indigenous forage plants visited by honeybees. However, the presence of a large number of exotic forage plant species poses some potentially significant challenges to plant conservation in South Africa. Pollination by honeybees could have facilitated the spread of a number of invasive alien plant species and indigenous species indicative of bush encroachment (Table 5.1). Depending on the flowering phenologies and relative attractiveness of the exotic forage plants this may involve a cost or benefit to the indigenous flora and indirectly the community of seed dispersers.

If the flowering phenologies of the exotic and indigenous flora in a particular area overlap and the exotic flora is more attractive to honeybees, pollination may be reduced in the indigenous honeybee flora. In contrast, the opposite could occur if flowering by attractive forage plants with a high reward status is asynchronous and the honeybee carrying capacity of an area is consequently enhanced. It is tempting to speculate what implications these assumptions may have for indigenous plant communities growing adjacent to *Eucalyptus* plantations. For example, indigenous forage plants flowering in synchrony with the *Eucalyptus* may experience directional or disruptive selection (*sensu* Pianka, 1988) with regard to their

flowering phenology. *Eucalyptus* plantations may also affect the reproductive phenology of honeybees themselves, as has become evident in Zimbabwe where an additional swarming period has been reported associated with the plantations (Hepburn & Radloff, 1998). Exotic plants could also decrease the attractiveness of an area to honeybees, especially if they offer little or no rewards, by obscuring indigenous honeybee forage plants or increasing the distance between them for the flower-constant honeybees (Rebelo, 1987).

Commercial beekeeping activities may pose a threat to indigenous plant-pollinator associations, for example during 1985 c. 52 000 hives were required for deciduous fruit pollination in the southwestern Cape (Rebelo, 1987). This could occur if the availability of nectar in close proximity to apiaries is reduced to unrewarding levels for oligotrophic (*sensu* Proctor *et al.*, 1996) insect pollinators. Rebelo (1987) speculated that honeybees could *via* pollination of oligophiles increase the levels of hybridization between species or decrease seed viability. It is possible that elevated population densities of honeybees may be inversely related to numbers of competing oligotrophs, leading to decreased levels of pollination amongst the latter oligophilic forage plants (Rebelo, 1987). Hived colonies overwintered in indigenous plant communities could also pose a risk to the survival of feral colonies with whom they must compete, with unknown effects on the pollination of their indigenous forage plants in the summer (Rebelo, 1987).

Table 5.1. Declared problem and honeybee forage plants in South Africa according to the Conservation of Agricultural Resources Act, 1983 (Act 43 of 1983) (Notice 2485 of 1999), Republic of South Africa. The plant species are listed alphabetically below in accordance with the biome in which the heaviest infestations can be found (*sensu* Richardson *et al.*, 1997).

Category & Definition
<p>1. "Category 1 plants are weeds and serve no useful economic purpose and possess characteristics that are harmful to humans, animals or the environment." (Notice 2485 of 1999, p.2)</p>
<p><u>Aquatic</u> - <i>Eichhornia crassipes</i>; <u>Forest</u> - <i>Lantana camara</i>; <u>Fynbos</u> - <i>Acacia longifolia</i>, <i>Acacia pycnantha</i>, <i>Acacia saligna</i>, <i>Hakea drupacea</i>, <i>Hakea gibbosa</i>, <i>Hakea sericea</i>, <i>Leptospermum laevigatum</i>, <i>Paraserianthes lophantha</i>; <u>Karoo</u> - <i>Cirsium vulgare</i>, <i>Xanthium strumarium</i>; <u>Savanna</u> - <i>Sesbania punicea</i>; <u>Unknown</u> - <i>Convolvulus arvensis</i>, <i>Echium plantagineum</i>, <i>Pittosporum undulatum</i>, <i>Tecoma stans</i>, <i>Tithonia rotundifolia</i>, <i>Ulex europaeus</i></p>
<p>2. "Category 2 plants are plants that are useful for commercial plant production purposes but are proven plant invaders under uncontrolled conditions outside demarcated areas." (Notice 2485 of 1999, p.2)</p>
<p><u>Forest</u> - <i>Eucalyptus grandis</i>, <i>Passiflora edulis</i>, <i>Psidium guajava</i>; <u>Fynbos</u> - <i>Acacia cyclops</i>, <i>Acacia melanoxylon</i>, <i>Eucalyptus cladocalyx</i>; <u>Grassland</u> - <i>Acacia dealbata</i>, <i>Acacia decurrens</i>, <i>Acacia mearnsii</i>; <u>Savanna</u> - <i>Agave sisalana</i>; <u>Unknown</u> - <i>Atriplex nummularia</i>, <i>Casuarina cunninghamiana</i>, <i>Eucalyptus camaldulensis</i>, <i>Eucalyptus paniculata</i>, <i>Eucalyptus sideroxylon</i>, <i>Gleditsia triacanthos</i>, <i>Hypericum perforatum</i>, <i>Populus deltoides</i>, <i>Prosopis glandulosa</i></p>

3. "Category 3 plants are mainly used for ornamental purposes in demarcated areas but are proven plant invaders under uncontrolled conditions outside demarcated areas."

(Notice 2485 of 1999, p.2)

Forest - *Melia azedarach*, *Morus alba*, *Schinus terebinthifolius*; Fynbos - *Eucalyptus lehmannii*; Grassland - *Acacia baileyana*, *Acacia podalyriifolia*, *Pyracantha angustifolia*; Karoo - *Salix babylonica*; Savanna - *Jacaranda mimosifolia*; Unknown - *Cotoneaster franchetii*, *Cotoneaster pannosus*, *Ligustrum lucidum*, *Metrosideros excelsa*, *Populus x canescens*, *Robinia pseudoacacia*, *Rorippa nasturtium-aquaticum*, *Tipuana tipu*

Indicators of Bush Encroachment. Bush encroachment defined as:

"...stands of woody plants where individuals are closer to each other than twice the mean crown diameter but not further apart from each other than three times the mean crown diameter of each of the kinds of woody plants." (Notice 2485 of 1999, p.2)

Acacia caffra, *Acacia hebeclada*, *Acacia karroo*, *Acacia mellifera*, *Acacia nilotica*, *Acacia robusta*, *Combretum apiculatum*, *Leucosidea sericea*, *Rhamnus prinoides*, *Rhigozum trichotomum*, *Rhus lancea*, *Rhus lucida*, *Tarchonanthus camphoratus*

5.4. Honeybees in the service of man

5.4.1. Commercial crop pollination

Honeybees play an important part in commercial crop production in South Africa. Feral colonies of indigenous honeybees are augmented with managed colonies to pollinate a wide range of crops. A selected list of those crops for which honeybees are known to increase yields (*sensu* Crane & Walker, 1984) appears in Table 5.2 below. Honeybees contribute not only to

national food security, but also to the potential profits of individual private farmers. At least 15 000 to 20 000 hives are required for the production of sunflower seed alone in South Africa (Johannsmeier, 1996). Although, a quantitative assessment of the enhanced volume and value of honeybee pollination for various commercial crops is beyond the scope of this study, Table 5.2 demonstrates the potential importance of honeybee pollination to the national economy. In one study carried out on lucerne seed yields near Oudtshoorn, the Cape honeybee (*Apis mellifera capensis*) was more than twice as successful as a pollinator than the Highveld honeybee (*Apis mellifera scutellata*) and associated with yields more than eight times that obtained in the control experiment (Hepburn & Jacot Guillarmod, 1991).

Besides the direct benefits to crops there may also be significant indirect advantages obtained through pollination, such as the production of lucerne seed used for the cultivation of pastures on which livestock are raised (e.g. dairy farming). There are thus many areas of commercial agriculture which can profit significantly from pollination services.

Table 5.2. The volume and value of commercial crops (Anonymous, 2001) pollinated by honeybees in South Africa. Only those crops for which honeybees are known to enhance yields are listed below (Crane & Walker, 1984).

Crop	Year	Volume (tonnes)	Gross value (X R 1000)	Export Earnings (R Million)
Apricots - <i>Prunus armeniaca</i>	1997/8 ^a	64 217	58 971	18.36 ^c
Avocado - <i>Persea americana</i>	1997/8 ^a	20 073	137 463	90.58 ^c
Cucumber - <i>Cucumis sativus</i>	1999 ^b	2 800	3 178 ^c	-
Lucerne (seed) - <i>Medicago sativa</i>	1997/8 ^a	1 155	13 271	-
Mango - <i>Mangifera indica</i>	1997/8 ^a	31 676	56 090	-

Peaches - <i>Prunus persica</i>	1997/8 ^a	214 040	240 592	30.57 ^c
Pears - <i>Pyrus communis</i>	1997/8 ^a	264 842	424 056	309.94 ^c
Strawberries - <i>Fragaria x ananassa</i>	1997/8 ^a	3 834	17 598	-
Sunflower (seed) - <i>Helianthus annuus</i>	1996/7 ^a	468 000	469 720	-
Watermelon - <i>Citrullus lanatus</i>	1997/8 ^a	37 273	27 955 ^c	-

[Common name nomenclature *sensu* Crane & Walker (1984). X^a = based on sales from 16 markets for the period October - September; X^b = based on sales from 16 markets; X^c = estimated value based on the listed, or otherwise assumed, average R/t (Anonymous, 2001).]

5.4.2. Rural food security

Honeybees pollinate not only commercial crops, but also a number of exotic and indigenous plants which provide valuable sources of food for poor rural communities. A selection of those species utilized for their fruit or seeds are listed in Table 5.3 below. These plants are not of equal importance as food sources, but may augment the diets of rural communities. For example, in the village of Dingleydale B in the South African lowveld, only four species of fruit tree are grown by more than a third of the households sampled by High & Shackleton (2000), namely Mango (82.3%), Peach (43.5%), Marula (40.3%) and Avocado (33.9%). In Dingleydale B (High & Shackleton, 2000) and Port St. Johns (van Eck *et al.*, 1997) in the Transkei, some exotic fruit trees appear to be preferred above indigenous ones. In addition, more than three quarters of the households (n=67 families, 31 villages) investigated by Arnold & Musil (1983) in Gazankulu cultivate watermelons, a crop which has been associated with

honeybee facilitated yield enhancement in the past (Crane & Walker, 1984).

Table 5.3. A selection of fruits and seeds from honeybee forage plants utilized by poor rural communities in South Africa.

Species	Fruit	Seed	Reference
Apricot ^a - <i>Prunus armeniaca</i>	X		High & Shackleton (2000)
Avocado ^a - <i>Persea americana</i>	X		High & Shackleton (2000)
Buffalo-thorn ^b - <i>Zizphus mucronata</i>	X		Liengme (1981)
Calabash ^a - <i>Lagenaria siceraria</i>	X		Arnold & Musil (1983)
Cross-berry ^b - <i>Grewia occidentalis</i>	X		Shackleton <i>et al.</i> (1998)
Dikbas ^b - <i>Lannea discolor</i>	X		Liengme (1981)
Dubbeltjie ^d - <i>Tribulus terrestris</i>	X		Shackleton <i>et al.</i> (1998)
Forest Natal Mahogany ^b - <i>Trichilia dregeana</i>	X		van Eck <i>et al.</i> (1997)
Granadilla ^a - <i>Passiflora edulis</i>	X		High & Shackleton (2000)
Guava ^a - <i>Psidium guajava</i>	X		High & Shackleton (2000)
Kei-apple ^b - <i>Dovyalis caffra</i>	X		van Eck <i>et al.</i> (1997)
Maize ^c - <i>Zea mays</i>		X	Liengme (1981)
Malanguti ^a - <i>Physalis peruviana</i>	X		Liengme (1981)
Mango ^a - <i>Mangifera indica</i>	X		High & Shackleton (2000)
Marula ^b - <i>Sclerocarya birrea</i>	X		High & Shackleton (2000)
Melon ^c - <i>Cucumis melo</i>	X		Liengme (1981)
Mitzeerie ^b - <i>Bridelia micrantha</i>	X		Liengme (1981)
Mobola plum ^b - <i>Parinari curatellifolia</i>	X		Liengme (1981)
Mulberry ^a - <i>Morus alba</i>	X		High & Shackleton (2000)
Natal mahogany ^b - <i>Trichilia emetica</i>	X		Liengme (1981)
Orange ^a - <i>Citrus sinensis</i>	X		High & Shackleton (2000)
Peach ^a - <i>Prunus persica</i>	X		High & Shackleton (2000)
Pear ^a - <i>Pyrus communis</i>	X		High & Shackleton (2000)

Pigweed ^d - <i>Amaranthus hybridus</i>		X	Shackleton <i>et al.</i> (1998)
Pomegranate ^a - <i>Punica granatum</i>	X		High & Shackleton (2000)
Water berry ^b - <i>Syzygium cordatum</i>	X		Liengme (1981), van Eck <i>et al.</i> (1997)
Watermelon ^a - <i>Citrullus lanatus</i>	X		Arnold & Musil (1983)
Wild plum ^b - <i>Harpephyllum caffrum</i>	X		van Eck <i>et al.</i> (1997)

[Common names follow - X^a = reference, X^b = Coates Palgrave (1977), X^c = Crane & Walker (1984), X^d = Pooley (1998).]

5.5. Conclusion

The impact of man on the South African landscape through afforestation, alien plant invasions, bush clearing, fire, livestock farming, crop monoculture and urbanization has been considerable. This has undoubtedly had an effect on the quality of honeybee forage within the country. Likewise, honeybees may also have affected the species composition of plant communities *via* differential pollination of the constituent plants. Very little research has evidently been carried out to quantify the nature of these two facets of the honeybee - forage plant axis in South Africa. Clearly, the potential value of mini-livestock such as honeybees to land management has been under appreciated by agriculturalists and scientists within the country.

5.6. References

- Anonymous. 2001. Abstract of Agricultural Statistics, National Department of Agriculture, South Africa, 112 pp..
- Arnold, T.H. and Musil, K.J. 1983. A preliminary survey of primitive crops cultivated in the northern Transvaal of South Africa. *Bothalia*, 14, 595-601.
- Aucamp, A.J. 1990. Bos in die Bosveld: bate of hindernis vir vleisproduksie. *Agricola*, 8, 11-17. (cited in Smit & Rethman, (1992))
- Bond, W.J. 1997. Fire. Chapter 18. In *Vegetation of Southern Africa*, Cowling, R.M., Richardson, D.M. and Pierce, S.M. (Eds), Cambridge University Press, Cambridge, 421-446.
- Briers, J.H. and Powell, M. 1996. Fuelwood species used in valley bushveld. *Grassland Society of Southern Africa. Special Publication*, December 1996, 46-48.
- Coates Palgrave, K. 1977. *Trees of southern Africa*. First Edition. C. Struik Publishers, Cape Town, 959 pp..
- Crane, E. and Walker, P. 1984. *Pollination directory for world crops*. International Bee Research Association, Gerrards Cross, 183 pp..

Edwards, D. 1984. Fire regimes in the biomes of South Africa. Chapter 2. In Ecological effects of fire in South African ecosystems, Booysen, P. de V. and Tainton, N.M., Ecological Studies 48, Springer-Verlag, Berlin, 19-37.

Frost, P.G.H. 1984. The responses and survival of organisms in fire-prone environments. Chapter 13. In Ecological effects of fire in South African ecosystems, Booysen, P. de V. and Tainton, N.M., Ecological Studies 48, Springer-Verlag, Berlin, 274-309.

Hepburn, H.R. and Jacot Guillarmod, A. 1991. The Cape honeybee and the fynbos biome. South African Journal of Science, 87, 70-73.

Hepburn, H.R. and Radloff, S.E. 1998. Honeybees of Africa. Springer, Berlin, 370 pp..

High, C. and Shackleton, C.M. 2000. The comparative value of wild and domestic plants in home gardens of a South African rural village. Agroforestry Systems, 48, 141-156.

Johannsmeier, M. 1996. Nectar and pollen production of sunflower breeding lines. South African Bee Journal, 68, 140-142.

Kevan, P.G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. Agriculture, Ecosystems and Environment, 74, 373-393.

Lear, E. 1990. Eucalypts in the P.W.V. area. South African Bee Journal, 62, 12-15.

Liengme, C.A. 1981. Plants used by the Tsonga people of Gazankulu. *Bothalia*, 13, 501-518.

Milton, S.J. 1992. Effects of rainfall, competition and grazing on flowering of *Osteospermum sinuatum* (Asteraceae) in arid Karoo rangeland. *Journal of the Grassland Society of Southern Africa*, 9, 158-164.

Milton, S.J. and Dean, W.R.J. 1988. Flower and fruit production of *Rhigozum obovatum* (Bignoniaceae) in road reserves and grazing land. *South African Journal of Science*, 84, 798-799.

Owen-Smith, N. and Danckwerts, J.E. 1997. Herbivory. Chapter 17. In *Vegetation of Southern Africa*, Cowling, R.M., Richardson, D.M. and Pierce, S.M. (Eds), Cambridge University Press, Cambridge, 397-420.

Pianka, E.R. 1988. *Evolutionary Ecology*. Fourth Edition. Harper Collins Publishers, New York, 468 pp..

Pooley, E. 1998. *A field guide to wild flowers: KwaZulu-Natal and the eastern region*. Natal Flora Publications Trust, 630 pp..

Proctor, M., Yeo, P. and Lack, A. 1996. *The natural history of pollination*. Harper Collins Publishers, 479 pp..

- Rebelo, A.G. 1987. Management implications. Chapter 9. In A preliminary synthesis of pollination biology in the Cape flora, Rebelo, A.G. (Ed), South African National Scientific Programmes Report, 141, 193-211.
- Richardson, D.M., MacDonald, I.A.W., Hoffmann, J.H. and Henderson, L. 1997. Alien plant invasions. Chapter 22. In Vegetation of Southern Africa, Cowling, R.M., Richardson, D.M. and Pierce, S.M. (Eds), Cambridge University Press, Cambridge, 535-570.
- Shackleton, S.E., Dzerefos, C.M., Shackleton, C.M. and Mathabela, F.R. 1998. Use and trading of wild edible herbs in the central Lowveld savanna region, South Africa. *Economic Botany*, 52, 251-259.
- Smit, G.N. and Rethman, N.F.G. 1992. Inter-related floristic changes associated with different long-term grazing treatments in Sourish Mixed Bushveld. *Journal of the Grassland Society of Southern Africa*, 9, 76-82.
- Stock, W.D., van der Heyden, F. and Lewis, O.A.M. 1992. Plant structure and function. Chapter 9. In *The Ecology of Fynbos: nutrients, fire and diversity*, Cowling, R.M. (Ed), Oxford University Press, Cape Town, 226-240.
- Struck, M. 1994. Flowers and their insect visitors in the arid winter rainfall region of southern Africa: observations on permanent plots. Insect visitation behaviour. *Journal of Arid Environments*, 28, 51-74.

Van Eck, H., Ham, C. and van Wyk, G. 1997. Survey of indigenous tree uses and preferences in the Eastern Cape Province. *Southern African Forestry Journal*, 180, 61-64.

CHAPTER 6. THE GEOGRAPHICAL AND INTRA-ANNUAL VARIATION OF HONEY RESERVES IN SOUTH AFRICAN HONEYBEE COLONIES.

"The amount of food and oxygen consumed by a small flying insect is enormous; and bees and flies and hawkmoths and humming-birds live on nectar, the richest and most concentrated of foods." (Thompson, 1992 p. 25)

6.1. Introduction

The ability to predict both the timing and magnitude of honey flows would be of enormous benefit to hobbyists and professional beekeepers in South Africa or anywhere else in the world. This chapter has two objectives, the first is to describe the spatial variation of these flows, while the second is to identify the timing of phenological events within colonies of indigenous honeybees. Scale-hive records provide the best *combined* spatial and temporal phenological data coverage for honeybees. Better spatial coverage exists for selected phenotypic traits (Hepburn & Crewe, 1991; Hepburn *et al.*, 1998), but supra-annual data is scarce. The most notable exception to the latter is the work of Allsopp & Hepburn (1997), who reported on, *inter alia*, swarming and supersedure events from 1991 to 1995 within the Cape of Good Hope Nature Reserve.

In order to facilitate the interpretation of the honey flows, both spatially and temporally, the relationship with other intra-colonial phenological traits has been briefly reviewed below. The presence of honey stores and the ability to abscond and/or migrate may be viewed as behavioural adaptations to dearth periods. The adoption of any of these traits is likely to increase the probability of colony survival in tropical climates and hence the passage

of genes to the next generation. Honey stores therefore potentially act as a buffer against adverse weather conditions and/or a lack of floral resources.

6.1.1. The honeybee reproductive cycle

The reproductive cycle in honeybees involves a tripartite interplay between the queen, workers and drones. The quantity of honey and pollen stored by the colony is a partial consequence of these relationships. Female workers are raised from diploid eggs fertilized by spermatozoa stored in the queen's spermatheca, which in turn are obtained on multiple nuptial flights. In contrast, the larger adult male drones are raised from haploid eggs. In a trait largely peculiar to *Apis mellifera capensis*, diploid eggs may also be laid by the workers (Onions, 1912; Mackensen, 1943; Hepburn 1994; Hepburn & Radloff, 1998) and can facilitate interregnum colony survival (Hepburn, 1994).

Ethological differences exist between the reproductive cycles of temperate and tropical races of honeybee. The following caricature of colony phenology is therefore primarily dependent on characteristics of the latter. Pollen plays an important role in the brood cycle of workers of both temperate and tropical races, with brood development dependent on pollen *stores* in the former, but pollen *income* in the latter (Hepburn & Radloff, 1998). Similarly, for *Apis mellifera capensis* and *Apis mellifera scutellata* an increase in worker brood production lags the extra-colonial availability of nectar, a phenomenon known as "follow-flow brood rearing" (Hepburn, 1992). The rate at which the queen lays her diploid eggs therefore fluctuates in sympathy, albeit slightly phase-shifted, with the local flowering regime. When the relative rate at which the queen lays these eggs begins to wane a successor is raised by the colony to replace her, which may involve a period of co-habitation by both queens. This

process is known as supersedure. During supersedure *no* swarming takes place. This is in marked contrast to reproductive swarming. Temperate races of honeybee may also raise a new queen if space within the nest cavity (hive) constrains brood production. The new queen usually leaves to establish another colony with approximately half the workers from the old nest cavity. In productive seasons afterswarms may also be caste off in a similar fashion. An alternative swarming stimulus, namely the rate of pollen income has been proposed by Hepburn & Radloff (1998) for tropical races of honeybee in Africa. Supersedure is therefore driven by intra-colonial factors, whereas reproductive swarming is dependent on extra-colonial stimuli.

Drone production coincides with the swarming season, while an approaching dearth period is usually associated with the eviction of drones from the colony (Crane, 1990). Free & Williams (1975) reported that eviction could be initiated by precluding a colony from foraging or postponed by supplementary feeding or queen removal. Absconding may occur in response to unfavourable extra- or intra-colonial conditions.

6.1.2. Honey storage: a global perspective

The nectar foraging behaviour of a colony is a response to both intra- and extra-colonial conditions. Only the former are considered in the following review. Responses to external stimuli are considered in Chapter seven. Clearly, the honey reserves within a colony must at least in part be dependent on intra-colonial nectar foraging stimuli. These form one of the foci of this section. A consideration of the colony attributes which have been linked to honey production are reviewed in tandem with the aforementioned theme. A number of terms

including honey production, honey reserves, honey storage and honey yield are viewed as synonymous for the purposes of this review.

The storage of honey is a heritable trait of particular importance to the survival of colonies at colder, higher-latitudes (Danka *et al.*, 1987). Temperate races therefore have greater colony thermoregulatory capabilities and propensity to store honey than the races of tropical origin (Danka *et al.*, 1987). The thermal foraging constraints experienced by the former are largely absent from the areas occupied by the latter (Hepburn & Radloff, 1998). In addition, it would appear that in an ultimate sense temperate races have evolved a tendency for colony site fidelity, whereas the tropical races have countered adverse conditions by developing a migratory response to dearth periods (Hepburn & Radloff, 1998).

In a comparative study performed in Venezuela Rinderer *et al.* (1985) found that individuals of temperate origin carried out more foraging trips and collected greater quantities of nectar per flight than their tropical counterparts when nectar was plentiful. Colonies with a temperate affinity were found to have a greater percentage of foragers, recruit more and to store more honey (temperate colonies = 0.41 ± 0.02 honey (kg)/colony/day vs tropical colonies = 0.17 ± 0.01 honey (kg)/colony/day) than tropical colonies during these favourable nectar flow conditions (Rinderer *et al.*, 1985). Two nectar flows were used in their study. The earlier flow was regarded as more and the later flow as less favourable, with the former attributed to *Tabebuia* sp. and the latter to *Gliricidia sepium* trees. Nectar was more freely available during the *Tabebuia* sp flow. During the less favourable *Gliricidia sepium* flow it is notable that the tropical colonies stored more honey than the temperate colonies (tropical colonies = 0.64 ± 0.18 honey (kg)/colony/day vs temperate colonies = 0.48 ± 0.04 honey (kg)/colony/day).

In another comparative study within Venezuela, Danka *et al.* (1987) were able to confirm that temperate colonies had more foragers and were inclined to store more honey than

their tropical counterparts. They found that under low (pollen present, no brood), intermediate (pollen & brood present) and high (no pollen, brood present) levels of incentive to forage, temperate colonies always stored more nectar. More nectar was stored by colonies of both types under low, rather than high incentive conditions. Notwithstanding these differences between the honeybees of different origins it is notable that high honey yields have been obtained from *Apis mellifera scutellata* colonies, ostensibly of tropical affinity, in South Africa. One beekeeper is reputed to have obtained yields of 200kg/colony/annum (Fletcher, 1978).

Intraspecific differences in honey production have also been noted in South Africa between the local races of honeybee. Comparisons between local and imported races will not be reviewed in this chapter. The importation of fertilized queens of temperate stock during the early and mid-20th century ended in 1965 (Fletcher, 1978). However, it is of interest to note that a comparative study in Pretoria revealed that *Apis mellifera scutellata* generally stores greater quantities of honey than *Apis mellifera ligustica* (Hepburn, 1995 & 1998 citing Taylor, 1939). There is some anecdotal evidence that *Apis mellifera adansonii* (*sic*) (or, now *Apis mellifera scutellata*) in certain circumstances (e.g. *Eucalyptus* sp. nectar flows) can produce more honey than *Apis mellifera capensis* in areas to which the latter is supposedly better adapted (Johannsmeier, 1983). This observation has not been supported by field experiments carried out by W-Worswick (1988) near Cape Town. He found *Apis mellifera capensis* stored more honey than *Apis mellifera scutellata*. Colonies of the former experienced a net gain, while those of the latter suffered a net loss in weight.

The difference in honey stores possibly reflects differences in the nectar foraging behaviour of the two races. *Apis mellifera capensis* colonies had more nectar foragers than *Apis mellifera scutellata* colonies, a similar quantity of nectar and pollen foragers, but fewer

foragers returning empty with neither resource (W-Worswick, 1988). In addition, *Apis mellifera capensis* foragers collecting nectar and both nectar and pollen had greater nectar loads than their northern counterparts (W-Worswick, 1988). There were no racial dissimilarities in the concentration of nectar obtained by either the nectar or nectar and pollen foragers (W-Worswick, 1988). It would therefore appear that *Apis mellifera capensis* has a less dispersed distribution of nectar concentration sensitivity thresholds (*sensu* Pankiw & Page, 2000) amongst its foragers than *Apis mellifera scutellata*. Pankiw & Page (2000) found that foragers would collect in order of increasing sensitivity to sucrose concentrations, nothing - nectar and pollen - nectar - pollen - water. Within this context W-Worswick's (1988) "...*unsuccessful foragers*..." (e.g. p.124) would be the least sensitive and require the greatest concentrations of sucrose for stimulation relative to the other categories of foragers. This may also explain why W-Worswick (1988) found "...*no significant difference in the concentration of the nectar collected by*..." (p.126) foragers within the same category, but from different races. As honeybees are flower constant and the herbaceous fynbos biome is known for its species richness, it seems plausible that the foraging characteristics displayed by *Apis mellifera capensis* colonies are an adaptation to widely dispersed sources of nectar.

Finding a satisfactory universal explanation which integrates the relative intra-colonial variations in brood area and honey stores with nectar foraging behaviour is problematic. The honey reserves may be viewed as the difference between the quantity of nectar collected and that consumed by the colony. This energy balance must therefore reflect the ratio of worker brood, house bees and pollen foragers (consumers) to nectar foragers. Nectar foragers in turn may also become consumers if confined to the hive or nest cavity in adverse conditions. As a consequence the greater the number of nectar foragers relative to consumers, the greater the quantity of honey that should be stored by a colony. If an adequate nectar supply was

accessible, one would anticipate that this ratio and hence extent of honey reserves would be greatest in late summer. In accordance with this explanation, the amplitude of the gains and losses during the year should reflect the size of the colony. Larger colonies should experience a greater range of weight changes than relatively smaller colonies. In the above scenario the queen would be expected to play a central role by varying the seasonal intensity of her reproductive output. Evidence in support of some of the facets of the above explanation are provided below. This accords well with the observations by Field (1931) more than 70 years ago who wrote:

“When the settled warm weather commences in September, and honey begins to come in rapidly, the queen bee, after her Winter rest from egg laying starts an intensive egg laying period of six or eight weeks, during which time no surplus honey is stored, as the developing young bees require big quantities of honey on which to grow, and there are only a small number of old bees to bring in the honey. By the middle of October the colonies are up to full bee-power, and then they commence storing surplus honey, from which the bee-keeper reaps his harvest.” (Field, 1931 p.17)

6.1.2.1. Queen traits

The presence, age and weight of queens are all known to effect honey production. Jaycox (1970a) was able to demonstrate in a field experiment at the University of Illinois that queenright colonies experience greater weight gains than broodright colonies during a nectar flow. Locally, Hepburn *et al.* (1984) have demonstrated that the presence of a queen is necessary for comb construction in colonies of *Apis mellifera scutellata*. The presence of a

queen is also known to influence nectar foraging activity (Jaycox, 1970a). It would appear that nectar foraging behaviour is at least partially governed by queen pheromones (Jaycox, 1970a, citing Jaycox, 1970b) and "...*comb volatiles*..." (Hepburn, 1998 p.59).

Aird (1943) more than 50 years ago suggested that the age of queens may have been responsible for variable honey yields in the Cradock area, South Africa. Colonies in Israel store more honey in the presence of younger rather than older queens (Hauser & Lensky, 1994), while Nelson & Gary (1983) determined that the quantity of honey produced by a colony is related to the weight of the mated queens present. To be consistent with the scenario described earlier, one would predict that younger or heavier queens should have a relatively greater reproductive output per unit time and hence larger brood areas than older or lighter queens. Hauser & Lensky (1994) carried out their observations from December 1982 to April 1983 and again from December 1983 to April 1984. During both periods younger queens were associated with significantly greater brood areas (uncapped & capped), although in the initial stages of the latter period no statistically significant differences were detected. Similarly, Nelson & Gary (1983) found a significant correlation ($r = 0.36$, $p < 0.05$) between queen weight (observations = 67 days post-hiving) and the area of capped brood (observations = 65 days post-hiving). It is notable that in both the Hauser & Lensky (1994) and Nelson & Gary (1983) studies that the determination of honey stores largely appears to have post-dated the last observations of the queen and/or brood areas. The only apparent exception being the honey production records taken in mid-April 1984 by Hauser & Lensky (1994). The extent to which this temporal discrepancy may have affected their results is unknown.

In contrast to the results obtained by Hauser & Lensky (1994), Szabo & Lefkovitch (1989) found that the age of the queen had no statistically significant relationship with either the area of brood (eggs + uncapped + capped) or honey produced during their 42-day

experimental period. Their first set of observations commenced in mid-June 1985 and the second set a year later in mid-June 1986. However, by reanalysing their data it was possible to confirm that younger queens have a greater reproductive output per unit time than older queens. For the selected periods (21 days following 18 June 1985 & 17 June 1986) young queens produced on average more worker brood cells than older queens (1985, Young Queens = 15 900 cells vs Old Queens = 10 200 cells; 1986, Young Queens = 6 900 cells vs Old Queens = 5 700 cells).

6.1.2.2. Worker traits

Worker genotype influences the nectar foraging behaviour of workers (Pankiw & Page, 2001). In their experiments two of the colony genotypes selected represented a greater (**SP**) and lesser (**sp**) propensity to store pollen. The average nectar loads of the latter were always heavier and concentrations lower than the former when the respective colonies were exposed to identical foraging conditions, whether the foragers were collecting only nectar or both nectar and pollen. However, the opposite was true for the nectar load weights of foragers who only collected nectar and which were subjected to an unfavourable pollen foraging treatment (Pankiw & Page, 2001). They also found that the average weight and concentration of nectar loads carried by the workers foraging exclusively for nectar were greater than those acquired by the foragers collecting both nectar and pollen. Conversely, lower nectar load concentrations were reported by Pankiw & Page (2001) for the former's **sp** foragers when subjected to their unfavourable pollen foraging treatment. Colonies associated with the favourable pollen foraging treatment had greater quantities of larvae and fewer pollen stores than the colonies incorporated within the unfavourable foraging treatment (Pankiw & Page, 2001).

Nevertheless, their results regarding the concentration of nectar loads need confirmation as they themselves have cautioned that the earlier foraging debut by SP colonies in conjunction with the greater concentration of nectar available to the foragers in the earlier part of their experiment may have confounded their results (Pankiw & Page, 2001). Dreller *et al.* (1999), using colonies of *Apis mellifera ligustica* in their experiments at the University of California (Davis), found no evidence that the sub-population of nectar foragers was influenced by either the ratio of uncapped:capped brood or contact between nursing adults and foragers.

In addition to the classical temporal progression of tasks performed by adult workers, known as age polyethism, there exists a hierarchy within the worker population of a colony (Hillesheim *et al.*, 1989). Workers can be divided into *dominant* and *subordinate* sub-populations (e.g. *Apis mellifera capensis*), revealed by the trophallactic relationship between the two groups, with the former generally fed by the latter (Hillesheim *et al.*, 1989). This state is evident within queenright colonies of *Apis mellifera capensis* (Hillesheim *et al.*, 1989). The ratio (dominant : subordinate) could have important consequences for honey production as colonies with a preponderance of dominant workers are known to store less nectar (sugar syrup) than colonies with a high percentage of subordinate workers (Hillesheim *et al.*, 1989). Other differences reported by Hillesheim *et al.* (1989) may also have a bearing on honey production as subordinate worker-dominated colonies reared more brood than their dominant worker colony counterparts. Whether this reflects the differences in racial composition between the brood (*Apis mellifera carnica*) and the workers (*Apis mellifera capensis*) used in their experiments is unknown. In addition, colonies populated by dominant workers constructed no new comb cells, whereas the colonies composed of subordinate workers did. Clearly this trait displayed by dominant worker colonies could physically limit the potential storage space within a colony and hence honey production.

6.1.2.3. Colony size

It is evident from the data presented by Szabo & Lefkovitch (1989) that the average sizes of the colonies associated with one year old queens were greater in 1986 (\bar{x} = 46 800 workers) than 1985 (\bar{x} = 40 400 workers). The larger colonies in 1986 (\bar{x} = 144.0 kg/colony) accumulated considerably more honey stores than the smaller colonies in 1985 (\bar{x} = 92.0 kg/colony). The extent to which these differences can be attributed to more favourable foraging conditions in 1986 is unknown. Hepburn (1998) pointed out that density effects are apparent within honeybee nesting cavities, with relatively greater densities associated with a reduction in *per capita* honey consumption in winter and relatively greater honey reserves in summer. In both seasons less brood was raised by the more densely inhabited nest cavities. In addition, larger nesting cavities were associated with smaller honey reserves and larger brood areas (Hepburn, 1998).

Fewell & Winston (1996) reporting on earlier work by Wolf & Schmid-Hempel (1990) and Fewell *et al.* (1991), suggested that the intensity of nectar collection is unrelated to colony size in summer, but dependent on it by “...*the end of the season...*” (p.289). They proposed that “...*nectar foraging and colony state in social insects depends on the quantity of energy stores relative to daily energy use*” (Fewell & Winston, 1996 p.289). Foragers in British Columbia from large colonies ($n = c.35\ 000$) visited more flowers per flight and had shorter flower handling times than those from smaller ($n = c. 10\ 000$) ones (Wolf & Schmid-Hempel, 1990). These differences may be related to the quantity of brood present as they were statistically significant early on in the experiment when the larger colonies had twice the amount of brood as the smaller colonies, but not later on when brood levels in the smaller colonies had reached *c. 79%* of those in the other treatment. The quantity of brood in the

smaller colonies increased, while that in the larger colonies decreased over the duration of their experiment. Wolf & Schmid-Hempel (1990) proposed that the relatively extended flower handling times displayed by the foragers from the smaller colonies may reflect a potential increase in exposure to parasitism and predation if they visited more flowers per flight.

Beewolves (*Philanthus diadema*), flies (*Physocephala fascipennis*) and birds are known to prey on foragers at flowers (Anonymous, 1908; Attridge, 1917; Fletcher, 1978; Clauss, 1986).

6.1.2.4. Empty comb area

The association between nectar flows and comb construction has been known for at least 250 years (Hepburn *et al.*, 1984). Rinderer *et al.* (1985, citing Rinderer, 1982) suggested that the area of empty comb in colonies of temperate origin governs both the extent of honey stores and nectar collection. It would appear that temperate colonies increase their honey stores when the comb area is increased during a nectar flow or decreased during a dearth period (Rinderer *et al.*, 1985). In *Apis mellifera scutellata* colonies the house bees may limit comb construction during dearth periods. Hepburn *et al.* (1984) found that the quantity of wax generated was highly correlated ($r = 0.93$, $p < 0.005$) with the quantity of sugar consumed by workers ≤ 21 days old. In a recent review of comb related literature Hepburn (1998) reported that a limited comb area hampered brood production. He also suggested that the construction of new comb was dependent on the duration and intensity of nectar flows when nectar holding space is limited. It would also appear that the availability of pollen may restrict comb construction activities and hence potentially the area available for honey storage. Hepburn *et al.* (1984, citing Goetze & Bessling, 1959 and Freudenstein, 1960) suggested that workers denied pollen produced less wax than those that have recourse to the protein. Recent work by

Dreller *et al.* (1999) has emphasized the importance of the location of the empty comb space. The provision of empty comb alongside, but not at a distance from the brood nest, significantly ($p < 0.05$) increased the sum of foragers collecting nectar (Dreller *et al.*, 1999).

6.1.2.5. Do honey reserves affect the behaviour of nectar foragers?

Fewell & Winston (1996) have suggested that different mechanisms govern the collection of nectar and pollen, although demand for the former may influence foraging for the latter and *vice versa* via the foragers which collect both food types. They found that in their study, carried out in British Columbia, foragers were largely insensitive to the quantity of honey stored within the colony. The extent of honey reserves had little or no effect on colony and individual flight activity, the flower handling times, the nectar loads of foragers, the amount of pollen stored or quantities of brood present. Dreller *et al.* (1999) found that the provision of pollen increased the percentage of nectar foragers in their experimental colonies.

6.2. Methods

6.2.1. Scale-hive records

Geographical variation and intra-annual changes in honey reserves were estimated using scale-hive records obtained from the Plant Protection Research Institute (PPRI), Pretoria, South Africa. The location of known scale-hive records and a brief summary of attribute data appears in Chapter 2. Changes in hive weight are assumed to be a reasonable reflection of changes in the quantity of honey stored. McLellan (1977) demonstrated in his Scottish study

that colony weight and honey reserves are closely related ($r > 0.85$; $p < 0.001$) during summer. Perturbations in this relationship could be ascribed to one or a combination of worker larvae, adult workers and/or pollen stores (McLellan, 1977). The original observers came from a variety of backgrounds, which included farmers, agricultural technicians and professional scientists. The original observations were made in Afrikaans, English and German and varied greatly in quality and hence usefulness. The two main factors governing the quality of the data sets were their temporal continuity and legibility. The latter was largely due to the quality of the photocopying.

Strict criteria were adopted to calculate the monthly changes in colony weight from the values at the end of each month. Months which met one of the following conditions listed below were *excluded* from this study:

- A. No monthly end value.
- B. Monthly end value illegible.
- C. Honey extracted during the month.
- D. Colony fed during the month.
- E. Hive moved to a new location.
- F. Scale-hive replaced.
- G. Scale repairs done.
- H. Other work done to hive.

Data from the following 25 locations (27 records) were used in this study (n = months of data); Berg-en-dal ($n = 6$), Bloemfontein ($n = 3$), Boschfontein ($n = 37$), Canowie Farm ($n = 5$), Compton Ranch ($n = 40$), Duiwelskloof No.1 ($n = 3$), Duiwelskloof No.2 (two records, $n = 17$, $n = 14$), Dunnottar ($n = 28$), Grenshoek ($n = 8$), Grootvadersbosch ($n = 28$), Helshoogte

(n = 61), High Bank (n = 35), Hilton Road (n = 6), Kenwyn (n = 35), Klaasjagersberg (n = 8), Kosi Bay (n = 3), Kraaifontein (n = 6), Nhlazatshe (n = 21), Oudtshoorn (n = 15), Peach Farm (n = 20), Piet Retief (n = 4), Port Durnford (n = 17), Prinsrivier (n = 33), Rust de Winter (n = 18), University of Pretoria Experimental Farm (two records, n = 68, n = 29). These 568 values formed the basis for the geographical analysis of intra-annual variations in honey stores by site and biome.

Two different procedures were employed to carry out comparative analyses of the scale-hive records by site. In the first instance the degree of correlation between those records with 10 or more months of temporally coincident data were determined (*Procedure 1*). The pairwise deletion of data for months with missing values was adopted for the comparison of any two records which met the above conditions. In the second procedure the extent of correlation between the mean monthly values of two records was calculated (*Procedure 2*). Records with two or more consecutive months represented by a single or no value were excluded from the analysis. For the records which remained, where data were absent, estimates of the mean monthly honey stores were obtained by calculating the average of the preceding and following monthly values. Months with only a single value were treated as if none were available.

The level of correlation between the mean monthly values of different biomes were calculated by combining the data from all localities. Biomes with missing monthly data were excluded from the analysis. In addition, the greatest monthly hive weight gain and loss was determined for all 27 records, the selected sites (see *Procedure 2* above), biomes and by rainfall class. Correlations were regarded as significant if the p-level was < 0.05 .

6.2.2. Colony demography

The unpublished data collected by the late John Katanga during 1992 and 1993 in the Andries Vosloo Kudu Reserve, north of Grahamstown, were used to determine the correlation between fourteen colony parameters. These encompassed the number of queen cells present, the total comb size, the percentage of comb in use, the areas covered by uncapped honey, capped honey, both categories of honey, pollen cells, unsealed worker brood, sealed worker brood, both worker brood types, drone comb, drone brood, unsealed drone brood, sealed drone and both drone brood types. Katanga calculated the above by taking photographs of the frames within each hive in the field and subsequently digitizing the areas of interest in the laboratory. Data from a number of hives for each month was collated in the present study in order to calculate the mean monthly values for each parameter. Correlations were regarded as significant if the p-level was < 0.05 . The total values for each parameter per colony and sampling date appear in Appendix 6.A.

6.3. Results

6.3.1. Scale-hive records

6.3.1.1. Site specific intra-annual variation and correlation

Procedure 1

Eight pairs of sites qualified for further analysis following the protocol outlined above (Table

6.1). Only the High Bank - Dunnottar pairing displayed a statistically significant correlation (Spearman $R = 0.60$, $p = 0.0053$, $n = 20$). At two localities, namely Duiwelskloof No.2 and the University of Pretoria Experimental Farm, two records were kept simultaneously. A significant correlation was obtained at the former (Spearman $R = 0.76$, $p = 0.0017$, $n = 14$), but not the latter site (Spearman $R = 0.95$, $p = 0.0513$, $n = 4$). The result obtained for the experimental farm needs to be viewed with caution due to the very small sample size.

Table 6.1. The pairwise correlation between scale-hive records according to *Procedure 1*.

Pair (different localities)	Spearman R	p-value	n
Duiwelskloof No.2.1 vs Peach Farm	0.38	0.2763	10
Helshoogte vs Nhlazatshe	0.33	0.2008	17
Helshoogte vs Rust de Winter	0.18	0.6272	10
Helshoogte vs Compton Ranch	0.14	0.5020	25
High Bank vs Boschfontein	- 0.27	0.3053	16
High Bank vs Dunnottar	0.60	0.0053	20
Port Durnford vs Helshoogte	- 0.31	0.3306	12
Oudtshoorn vs High Bank	0.07	0.8310	11
Pair (same location)			
Duiwelskloof No.2.1 vs Duiwelskloof No.2.2	0.76	0.0017	14
University of Pretoria Experimental Farm No.42 vs University of Pretoria Experimental Fam No.47	0.95	0.0513	4

Procedure 2

Six scale-hive records fulfilled the criteria outlined in *Procedure 2* above (Table 6.2). Mean monthly values needed to be estimated for each locality (1 month = Boschfontein, Dunnottar & Prinsrivier; 2 months = Compton Ranch & High Bank), with the exception of Helshoogte. A mean monthly increase in hive weight takes place in six months at High Bank and Prinsrivier, in five months at Compton Ranch, Dunnottar and Helshoogte, and three months at Boschfontein. The highest and lowest monthly maxima were recorded during September 1945 and January 1948 at Boschfontein (44.84 kg) and Dunnottar (8.15 kg) respectively. The largest and smallest monthly losses in hive weight occurred during October 1942 and September 1944 at Boschfontein (- 15.55 kg) and High Bank (- 4.42 kg) respectively. Boschfontein (60.39 kg) has the greatest annual range in monthly hive weights, while Dunnottar (16.05 kg) has the smallest. The corresponding weights for High Bank (33.32 kg), Helshoogte (25.2 kg), Compton Ranch (20.95 kg) and Prinsrivier (17.69 kg) are of intermediate value. The greatest and smallest range in monthly value occurred in November at High Bank (29.81 kg) and February at Dunnottar (0.06 kg) (Table 6.2). Only Helshoogte had an uninterrupted series of ranges for each month, with a maximum experienced in December (15.33 kg) and a minimum in May (1.32 kg).

The honey flow season never exceeded six months at any of the six localities. The honey flow season is here defined as the number of consecutive months in which gains in mean hive weight were recorded. This excludes isolated months with mean increases in hive weight. The season lasted four months at Compton Ranch (February to May, net gain = 7.32 kg) and Helshoogte (January to March, net gain = 20.58 kg), five months at Dunnottar (November to March, net gain = 19.05 kg) and six months at High Bank (November to April, net gain =

31.40 kg) and Prinsrivier (September to February, net gain = 33.83 kg). No detectable season is present at Boschfontein. The mean annual gain or loss in honey reserves, calculated from the monthly means, represents a loss at Boschfontein (- 1.27 kg) and Dunnottar (- 0.20 kg) and a gain at Compton Ranch (0.33 kg), Helshoogte (1.04 kg), High Bank (1.75 kg) and Prinsrivier (2.03 kg).

Table 6.2. The mean monthly weight (kg) gains and losses for selected scale-hive records (* = estimated mean monthly value - see text for technique).

	Boschfontein	Compton Ranch	Dunnottar	Helshoogte	High Bank	Prinsrivier
	<u>January</u>					
Max.	1.11	- 0.47	8.15	12.31	4.42	-
Min.	- 3.21	- 2.56	4.38	7.26	- 0.11	-
Mean	- 1.61	- 1.53	6.16	9.78	1.97	7.52*
Range	4.32	2.09	3.77	5.05	4.53	-
n	3	3	3	2	3	1
	<u>February</u>					
Max.	1.55	5.44	7.52	7.65	3.97	4.76
Min.	- 3.30	- 1.99	7.46	2.74	- 3.18	1.47
Mean	-1.60	0.36	7.49	5.19	1.47	3.12
Range	4.85	7.43	0.06	4.91	7.15	3.29
n	4	6	2	2	4	2
	<u>March</u>					
Max.	4.27	8.10	3.93	11.48	17.24	- 0.45
Min.	- 3.96	- 4.07	- 0.19	- 3.10	2.15	- 2.27
Mean	- 0.46	1.07	1.87	4.28	11.83	- 1.36

Range	8.23	12.17	4.12	14.58	15.09	1.82
n	3	5	2	5	3	2
	<u>April</u>					
Max.	3.41	-	- 1.49	1.09	-	0.11
Min.	- 2.27	-	- 3.63	- 2.33	-	- 2.27
Mean	0.24	2.32*	- 2.56	- 1.04	5.38*	- 1.16
Range	5.68	-	2.14	3.42	-	2.38
n	4	1	2	4	1	4
	<u>May</u>					
Max.	- 0.64	10.76	- 0.14	- 0.42	1.70	- 0.57
Min.	- 2.96	- 3.61	- 4.99	- 1.74	- 3.86	- 1.81
Mean	- 2.07	3.57	- 2.14	- 1.08	- 1.08	- 1.33
Range	2.32	14.37	4.85	1.32	5.56	1.24
n	4	2	3	2	2	4
	<u>June</u>					
Max.	0.99	1.09	- 4.47	3.13	- 0.91	- 1.02
Min.	- 7.01	- 3.44	- 6.08	- 4.02	- 2.72	- 5.22
Mean	- 2.22	- 0.78	- 5.28	- 1.91	- 1.81	- 2.09
Range	8.00	4.53	1.61	7.15	1.81	4.20
n	4	4	2	7	2	5
	<u>July</u>					
Max.	7.02	14.33	- 3.74	4.08	- 2.04	- 0.68
Min.	- 0.99	- 2.85	- 7.12	- 3.85	- 2.38	- 2.95
Mean	3.70	5.17	- 5.25	- 0.62	- 2.23	- 2.10
Range	8.01	17.18	3.38	7.93	0.34	2.27
n	4	4	3	8	3	4
	<u>August</u>					
Max.	- 2.10	- 1.34	-	14.66	-	- 0.45

Min.	- 6.55	- 2.41	-	- 0.33	-	- 2.72
Mean	- 4.09	- 1.86	- 3.83*	5.41	- 2.29*	- 1.44
Range	4.45	1.07	-	14.99	-	2.27
n	3	3	0	7	1	3
	<u>September</u>					
Max.	-	-	3.89	5.94	0.45	3.40
Min.	-	-	- 7.90	- 7.79	- 4.42	- 1.93
Mean	- 4.62*	- 1.17*	- 2.40	- 2.17	- 2.34	0.74
Range	-	-	11.79	13.73	4.87	5.33
n	1	1	3	4	3	2
	<u>October</u>					
Max.	5.24	0.84	2.58	4.14	0.68	11.68
Min.	- 15.55	- 1.81	- 2.58	- 4.79	- 1.36	3.29
Mean	- 5.15	- 0.48	0.00	- 1.64	- 0.62	7.48
Range	20.79	2.65	5.16	8.93	2.04	8.39
n	2	2	2	7	4	2
	<u>November</u>					
Max.	1.30	0.84	3.71	- 0.99	28.90	4.99
Min.	- 5.44	- 4.16	- 0.19	- 10.54	- 0.91	1.13
Mean	- 1.81	- 1.05	1.53	- 5.01	6.64	3.06
Range	6.74	5.00	3.90	9.55	29.81	3.86
n	3	3	3	6	5	2
	<u>December</u>					
Max.	5.27	3.38	4.61	11.26	18.14	12.47
Min.	3.57	- 6.62	- 2.31	- 4.07	- 1.70	11.34
Mean	4.42	- 1.65	2.00	1.33	4.11	11.91
Range	1.70	10.00	6.92	15.33	19.84	1.13
n	2	6	3	7	4	2

	<u>Year</u>					
Max.	44.84	14.33	8.15	14.66	28.90	12.47
	Sep	Jul	Jan	Aug	Nov	Dec
Min.	-15.55	- 6.62	- 7.90	- 10.54	- 4.42	- 5.22
	Oct	Dec	Sep	Nov	Sep	Jun
Mean	- 1.27	0.33	- 0.20	1.04	1.75	2.03
Range	60.39	20.95	16.05	25.20	33.32	17.69
n	37	40	28	61	35	33

The extent of the correlations between the intra-annual variations in honey reserves for the six localities are listed in Table 6.3 below. A statistically significant ($p < 0.05$) correlation was obtained for two pairs, namely Dunnottar vs High Bank (Spearman $R = 0.59$, $p = 0.0446$, $n = 12$) and Dunnottar vs Prinsrivier (Spearman $R = 0.80$, $p = 0.0019$, $n = 12$).

Table 6.3. The extent of correlation in the intra-annual variation in honey reserves at six selected localities (see Methods - *Procedure 2*)($n = 12$).

Pair	Spearman R	p-value
Boschfontein vs Compton Ranch	0.29	0.3541
Boschfontein vs Dunnottar	0.26	0.4168
Boschfontein vs Helshoogte	0.38	0.2170
Boschfontein vs High Bank	0.52	0.0800
Boschfontein vs Prinsrivier	0.05	0.8799
Compton Ranch vs Dunnottar	- 0.20	0.5273
Compton Ranch vs Helshoogte	- 0.17	0.5868
Compton Ranch vs High Bank	0.12	0.7129
Compton Ranch vs Prinsrivier	- 0.43	0.1591

Dunnottar vs Helshoogte	0.39	0.2081
Dunnottar vs High Bank	0.59	0.0446
Dunnottar vs Prinsrivier	0.80	0.0019
Helshoogte vs High Bank	0.11	0.7292
Helshoogte vs Prinsrivier	0.11	0.7292
High Bank vs Prinsrivier	0.40	0.1993

6.3.1.2. Biome specific intra-annual variation and correlation

The 27 scale-hive records represented the savanna biome [$n(\text{months}) = 280$; $n(\text{localities}) = 11$] best followed by fynbos ($n(\text{months}) = 171$; $n(\text{localities}) = 6$), grassland [$n(\text{months}) = 102$; $n(\text{localities}) = 7$] and succulent karoo [$n(\text{months}) = 15$; $n(\text{localities}) = 1$]. No data was available for the forest, nama karoo or thicket biomes. The greatest monthly gains for the savanna, grassland, succulent karoo and fynbos biomes were 44.84 kg (Boschfontein, September 1945), 28.90 kg (High Bank, November 1943), 19.73 kg (Oudtshoorn, November 1946) and 14.66 kg (Helshoogte, August 1935) respectively (Table 6.4). The greatest monthly losses for the savanna, fynbos, grassland and succulent karoo biomes were -15.55 kg (Boschfontein, October 1942), - 10.54 kg (Helshoogte, November 1937), -7.90 kg (Dunnottar, September 1947) and - 4.99 kg (Oudtshoorn, October 1945) respectively (Table 6.4). The savanna (60.39 kg) and grassland (36.80 kg) biomes have larger annual ranges in monthly hive weights than the fynbos (25.20 kg) or succulent karoo (24.72 kg). Maximum monthly ranges in hive weight within the savanna, grassland and fynbos biomes occur in

September (48.92 kg), November (31.17 kg) and October (19.83 kg) respectively (Table 6.4).

Minimum monthly ranges in hive weight within the savanna, grassland and fynbos biomes occur in August (9.84 kg), April (5.44 kg) and May (1.56 kg) respectively (Table 6.4).

The largest 20 monthly gains were represented by nine months each in the savanna and grassland biomes and one less in the fynbos biome ($n = 8$), while the corresponding number of largest monthly losses occurred in nine, eight and six different months in the savanna, grassland and fynbos biomes. The most populous month in the gains cohort of extreme values was September ($n = 8$) in the savanna, January ($n = 4$) and February ($n = 4$) in grassland and December ($n = 5$) and January ($n = 5$) in the fynbos. The corresponding months for the losses cohort of extreme values were December ($n = 4$) in the savanna, September ($n = 5$) in grassland and November ($n = 7$) in the fynbos.

Only the savanna, grassland and fynbos biomes fulfilled the criteria for the analysis of intra-annual variation in honey reserves outlined in the methods above. The mean monthly values for each of these three biomes are listed in Table 6.4 below. The mean monthly maxima for the biomes occur in September (savanna, 9.51 kg), January (fynbos, 6.22 kg) and March (grassland, 6.24 kg), while the mean monthly minima occur in June (fynbos, - 1.88 kg), July (grassland, - 3.09 kg) and August (savanna, - 1.48 kg). Eight months in the savanna and grassland biomes and seven months in the fynbos biome are associated with mean monthly gains in hive weight. In the savanna two four month long honey flow seasons can be identified interspersed by a dearth period in January (- 0.53 kg). The earlier summer flow season (September to December, net gain = 15.22 kg) is associated with a greater net gain in hive weight than the later summer flow season (February to May, net gain = 5.36 kg). The flow season is longer in the grassland biome (October to March, net gain = 14.04 kg) than the fynbos biome (December to April, net gain = 16.32 kg), but the net gain in hive weight is

greater in the latter. The mean annual gains in weight, calculated from the mean monthly values, are greatest in the savanna (1.46 kg) and least in the grassland (0.86 kg). There is no statistically significant correlation in the intra-annual variations of hive weight between any combination of the three biomes (Table 6.5).

Table 6.4. The mean monthly hive weight (kg) changes in the savanna, grassland and fynbos biomes.

Month	Savanna	Grassland	Fynbos
	<u>January</u>		
Max.	20.46	8.15	12.31
Min.	- 9.01	- 3.95	- 0.65
Mean	- 0.53	1.48	6.22
Range	29.47	12.10	12.96
n	23	11	10
	<u>February</u>		
Max.	11.04	7.52	10.71
Min.	- 5.44	- 5.20	- 1.25
Mean	0.88	2.30	3.09
Range	16.48	12.72	11.96
n	31	8	8
	<u>March</u>		
Max.	28.58	17.24	11.48
Min.	- 4.07	- 1.81	- 3.10
Mean	1.93	6.24	2.62
Range	32.65	19.05	14.58
n	29	6	9
	<u>April</u>		

Max.	35.51	1.81	7.99
Min.	- 2.72	- 3.63	- 2.50
Mean	2.03	- 1.05	0.22
Range	38.23	5.44	10.49
n	26	4	13
	<u>May</u>		
Max.	10.76	24.49	- 0.25
Min.	- 3.61	- 4.99	- 1.81
Mean	0.52	2.15	- 1.02
Range	14.37	29.48	1.56
n	28	7	8
	<u>June</u>		
Max.	7.01	- 0.91	3.13
Min.	- 7.01	- 6.08	- 5.22
Mean	- 1.05	- 3.06	- 1.88
Range	14.02	5.17	8.35
n	28	7	18
	<u>July</u>		
Max.	14.33	0.00	4.72
Min.	- 7.26	- 7.12	- 4.58
Mean	- 0.05	- 3.09	- 1.29
Range	21.59	7.12	9.30
n	28	8	22
	<u>August</u>		
Max.	3.29	8.16	14.66
Min.	- 6.55	- 1.59	- 2.72
Mean	- 1.48	2.68	2.61
Range	9.84	9.75	17.38

n	22	4	16
	<u>September</u>		
Max.	44.84	3.89	7.49
Min.	- 4.08	- 7.90	- 7.79
Mean	9.51	- 1.37	- 0.06
Range	48.92	11.79	15.28
n	16	11	11
	<u>October</u>		
Max.	30.84	3.85	11.68
Min.	- 15.55	- 2.58	- 8.15
Mean	3.91	0.09	0.01
Range	46.39	6.43	19.83
n	12	12	18
	<u>November</u>		
Max.	23.13	28.90	4.99
Min.	- 5.44	- 2.27	- 10.54
Mean	1.79	2.67	- 1.39
Range	28.57	31.17	15.53
n	17	12	19
	<u>December</u>		
Max.	5.33	18.14	12.70
Min.	- 6.62	- 6.55	- 4.07
Mean	0.01	1.26	4.17
Range	11.95	24.69	16.77
n	20	12	19
	<u>Year</u>		
Max.	44.84	28.90	14.66
	September	November	August

Min.	- 15.55	- 7.90	- 10.54
	October	September	November
Mean	1.46	0.86	1.11
Range	60.39	36.80	25.20
n	280	102	171

Table 6.5. The extent of correlations of the intra-annual variations in hive weight of the three biomes; savanna, grassland and fynbos.

Pair	Spearman R	p-value
savanna vs grassland	- 0.05	0.8799
savanna vs fynbos	- 0.05	0.8799
grassland vs fynbos	0.41	0.1826

6.3.1.3. Rainfall

The absolute monthly high (44.84 kg) and low (- 15.55 kg) for hive weight change were associated with the 650 - 750 mm rainfall class (Table 6.6). Both of these values were recorded at Boschfontein, the former during September 1945 and the latter during October 1942. This therefore represents the greatest range in hive weight for any rainfall class (i.e. 60.39 kg). The smallest monthly gain (12.47 kg) and loss (- 5.22 kg) are also associated with one rainfall class, namely the driest (< 300 mm) and one locality, namely Prinsrivier. The monthly gain was recorded during December 1948 and the loss during June 1948. This driest of rainfall classes therefore also represents the one with the narrowest range in monthly hive

weights (17.69 kg).

Table 6.6. The maximum and minimum monthly hive weights (kg) associated with different rainfall classes.

Rainfall (mm)	Locality	Month	Gain / loss	n (months)	n (localities)
<u>Maximum</u>					
> 1050	Duiwelskloof No.1	April 1944	35.51	65	5
900 - 1050	Helshoogte	August 1935	14.66	65	2
750 - 900	Grootvadersbosch	December 1980	12.70	118	7
650 - 750	Boschfontein	September 1945	44.84	205	5
500 - 650	Bloemfontein	May 1947	24.49	27	3
300 - 500	Oudtshoorn	November 1946	19.73	55	2
< 300	Prinsrivier	December 1948	12.47	33	1
<u>Minimum</u>					
> 1050	Grenshoek	January 1943	- 9.01	65	5
900 - 1050	Helshoogte	November 1937	- 10.54	65	2
750 - 900	Kenwyn	October 1942	- 8.15	118	7
650 - 750	Boschfontein	October 1942	- 15.55	205	5
500 - 650	Rust de Winter	February 1938	- 5.44	27	3
300 - 500	Compton Ranch	December 1940	- 6.62	55	2
< 300	Prinsrivier	June 1948	- 5.22	33	1

6.3.1.4. Extreme hive weight variations for all records

The extreme values recorded for each month are presented in Table 6.7. The greatest monthly gain (44.84 kg) and loss (-15.55 kg) in weight for all 27 records both occurred at Boschfontein, with the former taking place during September 1945 and the latter during October 1942. The smallest maximum monthly gain in weight (7.01 kg) occurred during June 1933 at Port Durnford, while the smallest maximum loss in weight (-3.63 kg) took place in April 1948 at Dunnottar. The maximum recorded gains for each month always exceed the maximum recorded losses except in June where they are at parity. June (14.02 kg) has the smallest range in hive weights, while September (52.74 kg) has the largest. The greatest range in monthly hive weights for any locality occurs at Boschfontein (60.39 kg). There is no correlation between the extreme monthly highs and lows (Spearman $R = -0.12$, $p = 0.7129$, $n = 12$).

Table 6.7. The combined monthly extremes (kg) for all 27 scale-hive records.

Month	Max.			Min.			Range
		<u>Year</u>	<u>Locality</u>		<u>Year</u>	<u>Locality</u>	
January (n = 44)	20.46	1938	Rust de Winter	- 9.01	1943	Grenshoek	29.47
February (n = 48)	11.04	1942	Grenshoek	- 5.44	1938	Rust de Winter	16.48
March (n = 46)	28.58	1942	Grenshoek	- 4.07	1940	Compton Ranch	32.65

April (n = 45)	35.51	1944	Duiwelskloof No.1	- 3.63	1948	Dunnottar	39.14
May (n = 44)	24.49	1947	Bloemfontein	- 4.99	1947	Dunnottar	29.48
June (n = 54)	7.01	1933	Port Durnford	- 7.01	1944	Boschfontein	14.02
July (n = 59)	14.33	1936	Compton Ranch	- 7.26	1930	Duiwelskloof No.2.2	21.59
August (n = 43)	14.66	1935	Helshoogte	- 6.55	1946	Boschfontein	21.21
September (n = 39)	44.84	1945	Boschfontein	- 7.90	1947	Dunnottar	52.74
October (n = 44)	30.84	1930	Duiwelskloof No.2.2	- 15.55	1942	Boschfontein	46.39
November (n = 51)	28.90	1943	High Bank	- 10.54	1937	Helshoogte	39.44
December (n = 51)	18.14	1947	High Bank	- 6.62	1940	Compton Ranch	24.76
Extreme	44.84	1945	Boschfontein	- 15.55	1942	Boschfontein	52.74

6.3.2. Colony demography

The results below were calculated from a minimum of 6 (June) and maximum of 16 (October) colonies. June (n = 11) had the least, while December (n = 34) had the most number of

observations available for analysis. Fourteen variables were considered in this study, namely the total comb area, the percentage of available comb area utilised for the storage and raising of brood, the area of uncapped and capped honey, the total area used for honey storage, the area of unsealed and sealed worker brood, the total worker brood area, the total area of drone comb, the area of unsealed and sealed drone brood, the total area of drone brood and the number of queen cells.

6.3.2.1. Total comb area

The total comb area was lowest in October (7997.55 cm²) and highest in May (11798.03 cm²) (Table 6.8). In contrast, the mean percentage of comb utilised was lowest in June (11.15 %) and highest in November (52.43 %) (Table 6.8). There is no statistically significant correlation between these two parameters.

There are statistically significant negative correlations between the total comb area and the comb area occupied by pollen cells (Spearman $R = -0.69$, $p = 0.0139$), sealed worker brood (Spearman $R = -0.70$, $p = 0.0114$), unsealed drone brood (Spearman $R = -0.83$, $p = 0.0007$), sealed drone brood (Spearman $R = -0.86$, $p = 0.0003$) and total drone brood (Spearman $R = -0.89$, $p = 0.0001$). There are no positive correlations with any of the other variables with available data.

The mean percentage of comb area utilised by the honeybees is significantly correlated with the area covered by pollen cells (Spearman $R = 0.67$, $p = 0.0168$), unsealed worker brood (Spearman $R = 0.70$, $p = 0.0114$), sealed worker brood (Spearman $R = 0.93$, $p < 0.0001$), all worker brood (Spearman $R = 0.88$, $p = 0.0002$), unsealed drone brood (Spearman $R = 0.60$, $p = 0.0384$), sealed drone brood (Spearman $R = 0.84$, $p = 0.0007$) and all drone

brood (Spearman $R = 0.79$, $p = 0.0023$). There were no statistically significant negative correlations with any other variables with available data.

Table 6.8. The mean total comb area (cm^2) and percentage (%) of comb utilised in hives within the Andries Vosloo Kudu Reserve during 1992 and/or 1993.

Month	Total comb area (cm^2)	% comb utilised	n(hives)	n(observations)	Years
January	9833.39	37.12	10	20	1993
February	9534.02	52.23	10	19	1992, 1993
March	9585.16	23.27	10	20	1993
April	10190.56	17.61	9	16	1993
May	11798.03	22.24	8	14	1993
June	11735.77	11.15	6	11	1993
July	8743.22	27.97	14	29	1992, 1993
August	8720.62	22.25	13	28	1992, 1993
September	8686.45	34.78	13	24	1992, 1993
October	7997.55	40.83	16	25	1992
November	8845.21	52.43	13	13	1992
December	9381.98	30.13	12	34	1992

6.3.2.2. Honey

The mean monthly levels of honey stores (uncapped + capped) are lowest in September (599.78 cm^2) and greatest in February (2942.37 cm^2) (Table 6.9). The mean monthly values of uncapped and capped honey are lowest in September (uncapped honey = 486.17 cm^2 , capped

honey = 113.61 cm²) and highest in February (uncapped honey = 1621.85 cm², capped honey = 1320.52 cm²). The mean monthly area of uncapped honey comb is greater than that of capped honey for all months, except April (- 281.72 cm²), November (- 380.42 cm²) and December (- 212.75 cm²) when there is a deficit. These differences (uncapped - capped) range from a low in November (- 380.42 cm²) to a high in July (534.07 cm²).

The areas of uncapped (Spearman $R = 0.81$, $p = 0.0014$) and capped honey (Spearman $R = 0.90$, $p = 0.0001$) are each significantly positively correlated with the total area covered by honey filled comb. In addition, the area of capped honey is positively correlated with the area of drone comb (Spearman $R = 0.74$, $p = 0.0058$). No other statistically significant correlations, positive or negative, were obtained for any of the three honey comb related variables mentioned above.

Table 6.9. The mean area (cm²) covered by pollen, uncapped honey, capped honey and all honey comb in the hives within the Andries Vosloo Kudu Reserve in 1992 and/or 1993. The difference in the area (cm²) covered by uncapped and capped honey is also indicated below.

Month	Pollen (cm ²)	Uncapped honey (cm ²)	Capped honey (cm ²)	Uncapped - Capped honey (cm ²)	Total honey (cm ²)
January	107.18	1306.45	1174.52	131.93	2480.97
February	261.22	1621.85	1320.52	301.33	2942.37
March	105.25	958.46	809.75	148.71	1768.21
April	61.75	557.74	839.46	- 281.72	1397.20
May	145.23	975.88	620.59	355.29	1596.47
June	111.92	667.40	245.02	422.38	912.42
July	216.92	1002.81	468.74	534.07	1471.55

August	242.94	541.13	271.92	269.21	813.05
September	235.75	486.17	113.61	372.56	599.78
October	384.42	743.21	223.01	520.20	966.22
November	328.68	723.95	1104.37	- 380.42	1828.32
December	277.47	494.80	707.55	- 212.75	1202.35

6.3.2.3. Pollen

The mean monthly area covered by pollen stores is lowest in April (61.75 cm²) and greatest in October (384.42 cm²) (Table 6.9). The pollen stores are only negatively correlated with the total comb area (Spearman R = - 0.69, p = 0.0139), but positively correlated with the percentage of comb in use (Spearman R = 0.67, p = 0.0168), area of unsealed (Spearman R = 0.79, p = 0.0022) and sealed worker brood (Spearman R = 0.82, p = 0.0011), total area of worker brood (Spearman R = 0.75, p = 0.0051), area of sealed drone brood (Spearman R = 0.82, p = 0.0010) and total area of drone brood (Spearman R = 0.77, p = 0.0031).

6.3.2.4. Worker brood

The mean monthly area of unsealed worker brood is lowest in March (161.84 cm²) and greatest in September (1027.60 cm²) (Table 6.10). This is in advance of the corresponding extremes in the areas covered by sealed worker brood and all worker brood (i.e. unsealed + sealed worker brood). Both these categories have minima in June (sealed worker brood =

68.68 cm², total area of worker brood = 284.04 cm²) and maxima in November (sealed worker brood = 1600.74 cm², total area of worker brood = 2265.25 cm²) (Table 6.10).

There is only one statistically significant negative correlation for any of the above three variables, namely the relationship between the area of sealed worker brood and the total comb area (Spearman $R = -0.70$, $p = 0.0114$). The area of unsealed worker brood (Spearman $R = 0.70$, $p = 0.0114$), sealed worker brood (Spearman $R = 0.93$, $p < 0.0001$) and the total area of worker brood (Spearman $R = 0.88$, $p = 0.0002$) are each related to the total percentage of comb area in use. All three variables, unsealed worker brood (Spearman $R = 0.79$, $p = 0.0022$), sealed worker brood (Spearman $R = 0.82$, $p = 0.0011$) and the total area covered by worker brood (Spearman $R = 0.75$, $p = 0.0051$) are correlated with the area used for pollen storage. The areas covered by unsealed and sealed worker brood are also correlated (Spearman $R = 0.85$, $p = 0.0005$), as are both the above with the total area covered by worker brood (unsealed worker brood: Spearman $R = 0.91$, $p < 0.0001$; sealed worker brood: Spearman $R = 0.95$, $p < 0.0001$). Each of the worker brood categories are related to the areas of unsealed (unsealed worker brood: Spearman $R = 0.60$, $p = 0.0384$; sealed worker brood: Spearman $R = 0.72$, $p = 0.0086$; total area covered by worker brood: Spearman $R = 0.61$, $p = 0.0355$) and sealed drone brood (unsealed worker brood: Spearman $R = 0.75$, $p = 0.0047$; sealed worker brood: Spearman $R = 0.92$, $p < 0.0001$; total area covered by worker brood: Spearman $R = 0.82$, $p = 0.0010$) and the total area covered by the two drone brood types collectively (unsealed worker brood: Spearman $R = 0.70$, $p = 0.0106$; sealed worker brood: Spearman $R = 0.87$, $p = 0.0002$; total area covered by worker brood: Spearman $R = 0.76$, $p = 0.0041$).

Table 6.10. The mean area (cm²) of unsealed, sealed and total worker brood in hives within the Andries Vosloo Kudu Reserve in 1992 and/or 1993.

Month	Unsealed worker brood (cm ²)	Sealed worker brood (cm ²)	Total worker brood (cm ²)
January	293.03	739.88	1032.91
February	766.06	964.58	1730.64
March	161.84	195.29	357.14
April	163.24	171.91	335.14
May	465.96	416.75	882.70
June	215.36	68.68	284.04
July	274.73	452.47	737.58
August	365.31	435.72	801.03
September	1027.60	998.13	2025.73
October	692.10	998.93	1691.03
November	664.51	1600.74	2265.25
December	467.72	866.93	1334.65

6.3.2.5. Drone brood

The total area of drone comb is lowest in July (666.12 cm²) and greatest in January (1133.62 cm²) (Table 6.11). No unsealed drone brood was present in December or from March to June. Similarly no sealed drone brood, and hence drone brood of either type, was present from April to June. The area covered by unsealed drone brood (90.28 cm²) and the total area covered by drone brood (220.02 cm²) are greatest in October, while the area of sealed drone brood (171.68 cm²) reaches a maximum in November.

The total area of drone comb is only significantly correlated with the area of capped honey (Spearman $R = 0.74$, $p = 0.0058$). The total area covered by drone brood is negatively correlated with the total comb area (Spearman $R = -0.89$, $p = 0.0001$), but positively correlated with the mean monthly percentage of comb occupied (Spearman $R = 0.79$, $p = 0.0023$), the area used for pollen storage (Spearman $R = 0.77$, $p = 0.0031$), the area of unsealed (Spearman $R = 0.70$, $p = 0.0106$) and sealed worker brood (Spearman $R = 0.87$, $p = 0.0002$), the total area covered by worker brood (Spearman $R = 0.76$, $p = 0.0041$) and the area of unsealed (Spearman $R = 0.92$, $p < 0.0001$) and sealed drone brood (Spearman $R = 0.98$, $p < 0.0001$).

The areas of unsealed and sealed drone brood are inversely related to the total comb area (unsealed drone brood: Spearman $R = -0.83$, $p = 0.0007$, sealed drone brood: Spearman $R = -0.86$, $p = 0.0003$), but positively correlated with the mean monthly percentage of comb in use (unsealed drone brood: Spearman $R = 0.60$, $p = 0.0384$; sealed drone brood: Spearman $R = 0.84$, $p = 0.0007$). Statistically significant positive correlations were also obtained between the unsealed and sealed drone brood and the following variables; area of pollen stores (only sealed drone brood: Spearman $R = 0.82$, $p = 0.0010$), areas of unsealed (unsealed drone brood: Spearman $R = 0.60$, $p = 0.0384$; sealed drone brood: Spearman $R = 0.75$, $p = 0.0047$) and sealed worker brood (unsealed drone brood: Spearman $R = 0.72$, $p = 0.0086$; sealed drone brood: Spearman $R = 0.92$, $p < 0.0001$), total area covered by worker brood (unsealed drone brood: Spearman $R = 0.61$, $p = 0.0355$; sealed drone brood: Spearman $R = 0.82$, $p = 0.0010$), each other (Spearman $R = 0.83$, $p = 0.0008$) and the total area occupied by drone brood (unsealed drone brood: Spearman $R = 0.92$, $p < 0.0001$; sealed drone brood: Spearman $R = 0.98$, $p < 0.0001$).

Table 6.11. The mean area (cm²) of drone comb, unsealed, sealed and total drone brood in hives within the Andries Vosloo Kudu Reserve in 1992 and/or 1993.

Month	Unsealed drone brood (cm²)	Sealed drone brood (cm²)	Total drone brood (cm²)	Total drone comb (cm²)
January	19.93	8.86	27.46	1133.62
February	16.03	29.73	45.76	982.62
March	0.00	0.22	0.22	972.29
April	0.00	0.00	0.00	1061.25
May	0.00	0.00	0.00	974.09
June	0.00	0.00	0.00	938.34
July	16.16	13.72	27.97	666.12
August	60.96	22.63	79.53	748.62
September	63.00	97.17	157.38	884.92
October	90.28	133.67	220.02	789.86
November	43.38	171.68	208.39	1039.12
December	0.00	12.07	12.07	1119.95

6.3.2.6. Queen cells

The mean number of queen cells is lowest in June (1.00 cell) and greatest in January (6.36 cells) (Table 6.12). There is no statistically significant correlation between the number of queen cells and any other demographic variable reported in this study.

Table 6.12. The mean number of queen cells in hives within the Andries Vosloo Kudu Reserve in 1992 and/or 1993.

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
6.36	4.50	5.29	4.45	2.67	1.00	5.46	5.21	5.13	5.95	4.89	5.22

6.4. Discussion

6.4.1. Geographical variation

6.4.1.1. Geographical correlation of intra-annual variations in honey stores

Location plays a major role in the phenology of honey stores. Only one (High Bank vs Dunnottar) inter-site combination in eight displayed a significant correlation (Table 6.1) after application of *Procedure 1* and only two (Dunnottar vs High Bank, Dunnottar vs Prinsrivier) in 15 after application of *Procedure 2*. In contrast, the results obtained for the intra-site correlations using *Procedure 1* indicate the opposite, with Duiwelskloof No.2 displaying a significant and the University of Pretoria Experimental Farm a marginally insignificant correlation (Table 6.1). These results are supported by the lack of correlation between the mean monthly honey reserves of the savanna, grassland and fynbos biomes (Table 6.5). This appears to indicate that vegetation, at least in part, is an important determinant of the intra-annual variation in honey reserves. A role for climate can also be expected, but has not been

the subject of a thorough examination in this chapter (see Chapter 7).

6.4.1.2. The onset, duration and termination of the honey flow season

The onset, length and termination of the honey flow season varied according to location. Both the onset and termination were earliest at Prinsrivier (onset: September, termination: February) and latest at Compton Ranch (onset: February, termination: May). The duration of the honey flow season varied from four months at Compton Ranch and Helshoogte to six months at High Bank and Prinsrivier. The honey flow season was phase-shifted at Prinsrivier relative to that at Helshoogte, commencing four months earlier with a two month overlap (i.e. January and February). It is difficult to compare this result with those obtained by Hepburn & Jacot Guillarmod (1991), who identified a longitudinal shift in the flowering phenology of plants within the fynbos biome. In their study flowering in the west preceded that in the east, an apparent contradiction with the results above. However, a close inspection of their phenograms for regions B and C revealed that flowering reaches a maximum one month earlier in the latter, albeit only marginally. The difficulty in reconciling these two different results is exacerbated by the difficulty of assigning Helshoogte to region B and Prinsrivier to region C. They appear to lie close to the borders between regions B - C and C - D respectively.

Johnson (1993) has investigated the differences in the regional flowering phenologies of areas west and east of the 21°3' E (*sic*) line of longitude. This in fact appears to be a reference to 21°30'E. Nevertheless, both Helshoogte and Prinsrivier lie west of this dividing line, regardless of which is the correct figure. This line of longitude separated areas which experienced a winter rainfall regime from ones that had a non-seasonal rainfall regime (Johnson, 1993). He found the optimum flowering period in the west slightly preceded that in

the east. The apparent discrepancy between the flowering phenology of the area (Hepburn & Jacot Guillarmod, 1991; Johnson, 1993) and the level of honey stores at the two sites (i.e. Helshoogte & Prinsrivier) therefore merits further investigation. Biomes also differ in the onset, duration and termination of the honey flow season, the implications of which are discussed in further detail in section 6.4.1.5 below.

6.4.1.3. Intra-annual variation in the extremes for all records combined

Extreme monthly maxima and minima for all records combined are unrelated, with the magnitude of the gains in hive weight always greater than or equal to the losses (Table 6.7). June was the only month where the extreme values were equal to one another. The largest monthly gains (> 30 kg) were recorded in early (September - October) and late summer (April) (Table 6.7). Similarly, the greatest monthly losses (> 7.50 kg) were recorded in early (September to November) and mid-summer (January) (Table 6.7). Not surprisingly therefore the largest range in hive weight occurs in September (52.74 kg), while the smallest is associated with June (14.02 kg). The seasonal coincidence between the extremes could be attributed to the effect a large colony size may have on the energy balance within a colony. For example, nectar foragers could become net consumers of energy during adverse foraging conditions.

6.4.1.4. Spatial variation in the magnitude of intra-annual changes in hive weight

The magnitudes of extreme annual monthly maxima exceeds the minima at all localities. This only applies to the records investigated in detail (see *Procedure 2*), namely Boschfontein,

Compton Ranch, Dunnottar, Helshoogte, High Bank and Prinsrivier. One possible interpretation of the lower limit is that it is constrained by the tendency for colonies to abscond under adverse conditions. A loss in hive weight and hence net consumption of honey stores could be the result of poor weather conditions or an increase in the ratio of energy consumers to nectar foragers. It is notable that with the exception of Prinsrivier, where the greatest loss occurred in June, maximum monthly losses always fell in spring and early summer (i.e. September to December). This phenomenon is probably a reflection of the depleted state of honey stores by mid-winter and the build-up of worker brood and pre-foraging age bees (consumers) within the hive. A similar pattern is evident within the savanna, grassland and fynbos biomes where the greatest monthly losses were recorded in spring (September - grassland) and early summer (October - savanna & November - fynbos).

The upper limit, typically experienced in spring and summer (Tables 6.2 & 6.4), could be constrained by the amount of available space within the hive. Interestingly, the maximum monthly value (14.33 kg) and greatest mean monthly value (5.17 kg) occurred in July at Compton Ranch. The cause is difficult to identify, but could possibly be related to flowering *Aloe* spp.. Similarly, Helshoogte (and the fynbos biome) experienced its greatest gain (14.66 kg) in hive weight in late winter (August). It is also the only locality (see *Procedure 2*) with a mean gain for the month (Table 6.2). This could be attributed to the number of *Eucalyptus* spp. (e.g. *E. lehmannii*, *E. leucoxylon*, *E. paniculata*, *E. polyanthemos*) and fynbos species (e.g. *Protea compacta*) typically in flower during the month at Helshoogte (scale-hive record notes).

Boschfontein (60.39 kg) displayed the greatest range in these extreme values and Dunnottar (16.05 kg) the least. As both these locations fall within the same rainfall class (650 mm - 750 mm), but in different biomes, it seems likely that their differences could be ascribed

to the latter and/or an alternative thermal regime. It would appear that potential differences in the honeybee flora are of greater importance as the maximum weight gain at Boschfontein is more than five times greater than the corresponding value for Dunnottar. The range in hive weights was greatest in the savanna biome (60.39 kg) and least in the fynbos (24.72 kg). If, as suggested in section 6.1.2 above, the amplitude of the changes in hive weight are related to the size of the colony, then one would expect colonies within the savanna biome to be largest and those within the fynbos smallest. In New Zealand the quantity of honey produced per colony and per individual increases in sympathy with an increase in the size of the adult worker population (Crane, 1990).

At all locations and within all biomes the amplitude of the maxima for individual months may or may not exceed the minima. The greatest mean annual gain and loss occurred at Prinsrivier and Boschfontein respectively. A loss could reflect the inadequacy of the honey reserves to act as a buffer against dearth periods and highlights the importance of absconding to colony survival. The size of the hive weight gains during the honey flow season are variable, but remain within one order of magnitude. This holds true for both localities and biomes.

6.4.1.5. The implications of spatiotemporal variations in hive weight to commercial honey production

The maximum range and mean annual monthly value, together with the timing, duration and productivity of the honey flow season at a location, or within a biome, can provide potentially useful information to commercial beekeepers. Beekeepers with hives at localities known for large ranges in weight would have to trade off potentially large gains, with potentially large losses. In addition, the magnitude of the changes in hive weight could necessitate an increase

in the intensity of hive manipulation. Localities with a mean net loss in monthly hive weight are possibly not ideally suited to sedentary beekeeping, but may be useful to migratory beekeepers. For example, Dunnottar, with an annual mean monthly loss (- 0.20 kg), has a mean gain during the honey flow season of 19.05 kg. Knowledge of the honey flow seasons at different localities may also be usefully exploited by beekeepers interested in commercial honey production. For example, a beekeeper could exploit the close proximity and differences in the honey flow seasons at Prinsrivier (September to February) and Helshoogte (January to March), potentially extending honey production by a month.

The savanna biome appears to be more favourable for honey production than either the grassland or fynbos biomes in terms of both the overall duration of its two honey flow seasons (2 X 4 months) and the magnitude of their potential cumulative gains (20.58 kg). The grassland biome has a longer honey flow season (6 months vs 5 months), but of lesser magnitude (14.04 kg vs 16.32 kg) than that typically found within the fynbos biome. Further research is required to verify the mid-summer (January) dearth period in the savanna biome and its underlying causes. In addition, the basis for the difference in the gains between the two honey flow seasons in the savanna biome awaits identification. This may be due to weather effects, the structural characteristics of the honeybee forage plants (e.g. trees, shrubs or herbs), the number of species in flower, other factors or a combination of all of the aforementioned.

6.4.2. Colony demography

6.4.2.1. Total comb area

The total comb area is highest in May and lowest in October, the austral autumn and spring respectively. This is contrary to findings reported in the literature (Hepburn, 1986). Comb production should coincide with nectar flows (Hepburn, 1986). Other nectar sinks such as worker and drone brood and honey stores are either unrelated or significantly negatively correlated to the total comb area. It therefore appears unlikely that nectar flows are the cause of the enigmatic characteristics displayed by the total comb area. There is no evidence in this study to support the assertion by Rinderer *et al.* (1985, citing Rinderer, 1982) that areas of empty comb, albeit of races of temperate origin, govern both the extent of honey stores and nectar collection.

6.4.2.2. Honey reserves

The level of honey stores is lowest in spring (September) and highest in mid-summer (February). The areas of uncapped and capped honey are significantly correlated with the total area covered by honey cells of both types, but not with each other. The only other statistically significant correlation occurs between the area of capped honey and the total area of drone comb. These results therefore accord well with those obtained by Fewell & Winston (1996) in British Columbia who found the level of honey stores had no effect on the pollen stored or brood present. It therefore seems likely that extra-colonial conditions have a greater influence on the level of honey reserves than intra-colonial conditions. This is consistent with the results

obtained in the scale-hive study above, where a lack of correlation between localities was attributed to differences in the local botanical and/or possibly climatic conditions (see section 6.4.1.1.). Intra-colonial influences on increased honey reserves are perhaps largely restricted to the effects of an aging work force, where the ratio of nectar consumers to nectar foragers becomes more favourable.

6.4.2.3. Pollen stores

Pollen stores are greatest in spring (October) and least in autumn (April). There is a significant positive correlation between the pollen stores and all categories of worker and drone brood area, except the area of unsealed drone comb. This corroborates and further substantiates Hepburn & Radloff's (1998) assertion that follow-flow brood-rearing is typical of tropical African conditions. This contrasts with data for the Cape Peninsula (Hepburn & Radloff, 1998 p.144), where significant correlations between the level of pollen stores and areas of worker and drone brood were absent. However, both of the latter categories are significantly correlated with the number of plant species in flower (worker brood: Spearman $R = 0.92$, $p < 0.0001$; drone brood: Spearman $R = 0.79$, $p = 0.0022$). This would appear to indicate that there is a greater ratio of pollen consumption to pollen income on the Cape Peninsula relative to that experienced in the Andries Vosloo Kudu Reserve during the initial period of colony build-up. This may be attributed to a greater egg-laying rate of the queen, expressed as worker brood area, a smaller cohort of pollen foragers, more adverse weather conditions for foraging or any combination of the aforementioned during this phenophase. The comb area covered by pollen stores on the Cape Peninsula is greater than that in the Andries Vosloo Kudu Reserve throughout the year.

An examination of data from Shambat and Medani in the Sudanese sahel (Hepburn & Radloff, 1998 p.289), thought to approximate conditions in the Andries Vosloo Kudu Reserve, revealed no significant correlations between the areas of worker and drone brood and the level of pollen stores. However, the extent of correlation between these two brood categories and the flowering regime of the local bee flora remains to be studied.

6.4.2.4. Worker and drone brood

The total area of comb covered by worker and drone brood reaches a maximum in early summer (November) and spring (October), while the corresponding lows occur in winter (June and April to June respectively). The areas of uncapped and capped worker brood and the total area of worker brood fluctuate in synchrony with one another and the corresponding areas of drone brood. This is consistent with the results of a reanalysis of the data presented in Hepburn & Radloff (1998, see p.144) for *Apis mellifera capensis*, where intra-annual variations in worker and drone brood are significantly correlated (Spearman $R = 0.93$, $p < 0.0001$). A similar analysis carried out on data from Medani and Shambat in the Sudanese sahel (Hepburn & Radloff, 1998 p.289), revealed no significant relationships between worker and drone brood.

There is a high degree of correlation between the intra-annual variations in worker (Spearman $R = 0.76$, $p = 0.0040$) and drone brood (Spearman $R = 0.70$, $p = 0.0117$) in the Andries Vosloo Kudu Reserve and the Cape Peninsula. Evidence for trans-equatorial correlations is equivocal as the intra-annual variations in worker brood in the Andries Vosloo Kudu Reserve are significantly correlated with those at Shambat (Spearman $R = 0.79$, $p = 0.0021$), but not at Medani. There are no significant correlations between the variations in

drone brood in the Andries Vosloo Kudu Reserve and those at either Shambat or Medani.

Hepburn & Radloff (1995) have stated that:

"It is particularly striking that the honeybee flora also exhibits a large degree of temporal and spatial overlap on each side of the equator. This results in a time-space causeway for plant and honeybee reproduction and movement. This small flora and its honeybee visitors have both successfully escaped the constraints of biomes and phytochoria." (Hepburn & Radloff, 1995 p.272)

This statement allows for the following predictions:

- A. If the area of worker brood is taken as a surrogate measure of the egg-laying rate of the queen and hence honeybee reproduction, intra-annual variations in the worker brood area should be correlated on either side of the equator.
- B. If the area of drone brood is taken as a measure of honeybee reproduction then intra-annual variations in these areas should be correlated on either side of the equator.
- C. Intra-annual variations in colony phenology within different biomes should be significantly correlated.

In terms of the data presented above, the requirements of predictions A, B and C are partially fulfilled, unfulfilled and fulfilled respectively. The result for prediction C is in contrast to that reported earlier in section 6.4.1.1. (see also Table 6.5) where significant correlations in the honey reserves for the different biomes were not found. The mean area covered by worker and drone brood in colonies on the Cape Peninsula in every month is always greater than that recorded in the Andries Vosloo Kudu Reserve. It would therefore appear that both queen and

worker fecundity is greater in the former area. It is notable that both worker ovariole numbers and spermatheca sizes are greater in Cape Town (ovariole number: 17.4 ± 4.9 , spermatheca size: $21 \pm 4 \mu\text{m}$) than in Port Elizabeth (ovariole number: 12.5 ± 2.8 , spermatheca size: $15 \pm 2 \mu\text{m}$) and East London (ovariole number: 7.1 ± 2.0 , spermatheca size: $14 \pm 3 \mu\text{m}$) (Hepburn & Crewe, 1991). There appears to be conflicting evidence on the importance of queen ovariole numbers to queen fecundity (Hepburn & Radloff, 1998). Nevertheless, there appears to be enough circumstantial evidence linking these morphological traits to queen and worker fecundity to warrant further study.

6.4.2.5. Number of queen cells

The mean number of queen cells present is greatest in January (6.36 cells) and lowest in June (1.00 cell). There are no significant correlations between the mean number of queen cells present and any of the other variables investigated in this study. The high number of queen cells in January could be attributed to enhanced reproductive swarming activity during mid-summer.

In summary, it would appear that flowering and pollen income drive the brood cycle, which precedes an increase in the size of the post-foraging age cohort of workers and hence increase in honey reserves. The extent to which the honey production is influenced by climate is the subject of the next chapter.

6.5. References

Aird, W. 1943. District notes. The South African Bee Journal, 18, 10.

Allsopp, M.H. and Hepburn, H.R. 1997. Swarming, supersedure and the mating system of a natural population of honey bees (*Apis mellifera capensis*). Journal of Apicultural Research, 36, 41-48.

Anonymous. 1908. Birds and bees. Agricultural Journal of the Cape of Good Hope, 32, 281-282.

Attridge, A.J. 1917. Beekeeping in South Africa: A book for beginners. The Specialty Press of South Africa, Ltd., Johannesburg, 95 pp..

Clauss, B. 1986. The status of the banded bee pirate, *Palarus latifrons*, as a honeybee predator in southern Africa. South African Bee Journal, 58, 137-140.

Crane, E. 1990. Bees and beekeeping: science, practice and world resources. Heinemann Newnes, Oxford, 614 pp..

Danka, R.G., Hellmich, R.L. (II), Rinderer, T.E. and Collins, A.M. 1987. Diet-selection ecology of tropically and temperately adapted honey bees. Animal Behaviour, 35, 1858-1863.

Dreller, C., Page, R.E. Jr. 1999. Regulation of pollen foraging in honeybee colonies: effects of young brood, stored pollen, and empty space. *Behavioral Ecology & Sociobiology*, 45, 227-233.

Fewell, J.H. and Winston, M.L. 1996. Regulation of nectar collection in relation to honey storage levels by honey bees, *Apis mellifera*. *Behavioral Ecology*, 7, 286-291.

Fewell, J.H., Ydenberg, R.C. and Winston, M.L. 1991. Individual foraging effort as a function of colony population in the honey bee, *Apis mellifera* L.. *Animal Behavior*, 42, 153-155.

Field, A.N. 1931. Migratory bee-keeping. *The South African Bee Journal*, 6, 17-18.

Fletcher, D.J.C. 1978. The african bee, *Apis mellifera adansonii*, in Africa. *Annual Review of Entomology*, 23, 151-171.

Free, J.B. and Williams, I.H. 1975. Factors determining the rearing and rejection of drones by the honeybee colony. *Animal Behaviour*, 23, 650-675.

Freudenstein, H. 1960. Einfluss der Pollennahrung auf das Bauvermögen, die Wachdrüsen und den Fettkörper der Honigbiene (*Apis mellifera* L.). *Zoologische Jahrbuch*, 69, 95-124.

Goetze, G. and Bessling, B.K. 1959. Die Wirkung verschiedener Fütterung der Honigbiene auf Wachserzeugung und Bautätigkeit. *Zeitschrift für Bienenforschung*, 4, 202-209.

Hauser, H. and Lensky, Y. 1994. The effect of the age of the honey bee (*Apis mellifera* L.) queen on worker population, swarming and honey yields in a subtropical climate. *Apidologie*, 25, 566-578.

Hepburn, H.R. 1986. Honeybees and wax: an experimental natural history. Springer-Verlag, Berlin, 205 pp..

Hepburn, H.R. 1992. "Follow-flow" brood rearing in *capensis* and *scutellata*. *South African Bee Journal*, 64, 104-109.

Hepburn, H.R. 1994. Reproductive cycling and hierarchical competition in Cape honeybees, *Apis mellifera capensis* Esch. *Apidologie*, 25, 38-48.

Hepburn, H.R. 1995. Flight and foraging in *capensis* and *scutellata*. *South African Bee Journal*, 67, 38-42.

Hepburn, H.R. 1998. Reciprocal interactions between honeybees and combs in the integration of some colony functions in *Apis mellifera* L.. *Apidologie*, 29, 47-66.

Hepburn, H.R., Hugo, J.J., Mitchell, D., Nijland, M.J.M. and Scrimgeour, A.G. 1984. On the energetic costs of wax production by the african honeybee, *Apis mellifera adansonii*. *South African Journal of Science*, 80, 363-368.

- Hepburn, H.R. and Crewe, R.M. 1991. Portrait of the Cape honeybee, *Apis mellifera capensis*. *Apidologie*, 22, 567-580.
- Hepburn, H.R. and Jacot Guillarmod, A. 1991. The Cape honeybee and the fynbos biome. *South African Journal of Science*, 87, 70-73.
- Hepburn, H.R. and Radloff, S.E. 1995. First approximation to a phenology of the honeybees (*Apis mellifera*) and flora of Africa. *Oecologia*, 101, 265-273.
- Hepburn, H.R. and Radloff, S.E. 1998. Honeybees of Africa. Springer-Verlag, 370 pp..
- Hepburn, H.R., Radloff, S.E. and Fuchs, S. 1998. Population structure and the interface between *Apis mellifera capensis* and *Apis mellifera scutellata*. *Apidologie*, 29, 333-346.
- Hillesheim, E., Koeniger, N. and Moritz, R.F.A. 1989. Colony performance in honeybees (*Apis mellifera capensis* Esch.) depends on the proportion of subordinate and dominant workers. *Behavioral Ecology and Sociobiology*, 24, 291-296.
- Jaycox, E.R. 1970a. Honey bee foraging behavior: responses to queens, larvae, and extracts of larvae. *Annals of the Entomological Society of America*, 63, 1689-1694.
- Jaycox, E.R. 1970b. Honey bee queen pheromones and worker foraging behavior. *Annals of the Entomological Society of America*, 63, 222-228.

Johannsmeier, M.F. 1983. Experiences with the Cape bee in the Transvaal. *South African Bee Journal*, 55, 130-138.

Johnson, S.D. 1993. Climatic and phylogenetic determinants of flowering seasonality in the Cape flora. *Journal of Ecology*, 81, 567-572.

Mackensen, O. 1943. The occurrence of parthenogenetic females in some strains of honeybees. *Journal of Economic Entomology*, 36, 465-467.

McLellan, A.R. 1977. Honeybee colony weight as an index of honey production and nectar flow: a critical evaluation. *Journal of Applied Ecology*, 14, 401-408.

Nelson, D.L. and Gary, N.E. 1983. Honey productivity of honeybee colonies in relation to body weight, attractiveness and fecundity of the queen. *Journal of Apicultural Research*, 22, 209-213.

Onions, G.W. 1912. South African "fertile-worker bees". *South African Agricultural Journal*, 3, 720-728.

Pankiw, T. and Page, R.E. Jr. 2000. Response thresholds to sucrose predict foraging division of labor in honeybees. *Behavioral Ecology and Sociobiology*, 47, 265-217.

Pankiw, T. and Page, R.E. Jr. 2001. Genotype and colony environment affect honeybee (*Apis mellifera* L.) development and foraging behaviour. *Behavioral Ecology and Sociobiology*, 51, 87-94.

Rinderer, T.E. 1982. Regulated nectar harvesting by the honeybee. *Journal of Apicultural Research*, 21, 88-92.

Rinderer, T.E., Collins, A.M. and Tucker, K.W. 1985. Honey production and underlying nectar harvesting activities of africanized and european honeybees. *Journal of Apicultural Research*, 23, 161-167.

Szabo, T.I. and Lefkovitch, L.P. 1989. Effect of brood production and population size on honey production of honeybee colonies in Alberta, Canada. *Apidologie*, 20, 157-163.

Taylor, F. 1939. A comparison of indigenous and Italian bees in South Africa. *Proceedings of the Entomological Conference, Pretoria, South Africa*, 72-74.

Thompson, D.W. 1992. On growth and form. An abridged edition. Bonner, J.T. (Ed). Cambridge University Press, Cambridge, 346 pp..

Wolf, T.J. and Schmid-Hempel, P. 1990. On the integration of individual foraging strategies with colony ergonomics in social insects: nectar-collection in honey bees. *Behavioral Ecology & Sociobiology*, 27, 103-111.

W-Worswick, P.V. 1988. Comparison of nectar foraging efficiency in the Cape honeybee, *Apis mellifera capensis* Escholtz, and the African honeybee, *Apis mellifera adansonii* Latreille, in the western Cape Province. South African Journal of Zoology, 23, 124-127.

CHAPTER 7. THE INFLUENCE OF CLIMATE ON HONEY RESERVES: A CASE STUDY OF TWO SCALE-HIVE RECORDS FROM THE UNIVERSITY OF PRETORIA EXPERIMENTAL FARM.

"We hope that the great importance of such statistics and records will stimulate the many beekeepers in different districts to do their best and bring any amount of documents covering several successive years, if possible with daily records of scale hives and daily weather conditions, winds and actual dates of rainy days, which may enable us or our successors to arrive at some definite conclusions of the influence of meteorological factors on the honey crop." (Garin, 1931 p.18)

7.1. Introduction

Climatic conditions are known to influence the onset of flowering, flowering duration, the rate of nectar secretion and the nectar concentration of individual species of honeybee forage plants. Climatic conditions are also known to affect the flight of foragers. As all of these aspects are known to affect either the availability of nectar or its collection, they may justifiably be assumed to influence the level of honey reserves within a colony. The manner in which these aspects of the environment are influenced by selected climatic variables are reviewed below. The selected climatic variables are those investigated later in this chapter. A notable omission from the list of variables discussed is wind velocity, which is known to severely restrict flight by honeybees when > 4 m/s (Eisikowitch, 1978). For further comment on the effects of wind on both plants and honeybees or the lack thereof see Garin (1931), Butler (1945), Jorgensen & Markham (1946), Mitchener (1955), Szabo (1980), Kevan &

Baker (1983, 1984), Tribe (1983), Gerlach (1985), Crane (1990), Hepburn & Jacot Guillardmod (1991), Engelbrecht (1996) and Hepburn & Radloff (1998).

7.1.1. Air pressure (hPa)

Very little research appears to have been carried out on the impact of air pressure on either flowering or honey production. Esler (1999) has speculated that changes in air pressure associated with passing cold fronts may be related to flowering in certain geophytes.

Jorgensen & Markham (1946) used scale-hives in Michigan, U.S.A., to study the effect of air pressure on changes in hive weight. They didn't subject their data to rigorous statistical techniques, simply calculating the means of selected categories based on ranges of air pressure and changes in hive weight. This hampers the interpretation of their data, as does their conversion of observed air pressures to sea-level equivalents. Nevertheless, they suggested air pressures between 29.90 and 30.09 inches were optimal for gains in hive weight. If they were referring to inches of mercury these air pressures would equate to 1010.08 and 1016.50 hPa respectively.

7.1.2. Cloud cover

Cloud cover influences the intensity of light and solar radiation registered at the surface of the earth (Oertel, 1971; Rosenberg *et al.*, 1983). To avoid potentially confusing comments made by previous researchers on the effects of solar radiation and light intensity on plants and honeybees, only light intensity has been considered in this review. As honeybees are able to navigate successfully on overcast days and able to forage at night it seems likely that any

effects of cloud cover on foraging behaviour are due to the effects of the changing light regime on their forage plants (Fletcher, 1978; Dyer & Gould, 1981). Honeybees are able to forage at light intensities as low as one lux (Rinderer *et al.*, 1985). Szabo (1980) found a significant ($p < 0.05$) positive correlation between light intensity and both flight activity and a change in hive weight on at least one day on which observations were made during honey flows.

Moffett & Parker (1953) found in a study covering many summers (May to August) that the 10 years with the strongest nectar flows had fewer cloud-free days than the 10 years with the weakest flows. They speculated that the lower transpiration rates associated with cloudy conditions were more conducive to nectar secretion than those on clear days. In contrast, Jorgensen & Markham (1946) provide evidence which indicates that the best days for honey production were associated with twice the number of clear days and half the number of cloudy days than for the worst days of honey production (see section 7.1.5 below). There were an equal number of partly cloudy days associated with each of these categorical extremes. They also suggested that elevated temperatures may mitigate the effects of cloud cover on honey production. If "...*dappled shade*..." (Acutt, 1988 p.61) can be equated with cloud cover then a similar situation appears to prevail in KwaZulu-Natal, South Africa. Acutt (1988) suggested that hives below *Eucalyptus* sp. trees produced less honey than colonies in the sun. Clearly, cloud cover can have an impact on the honey reserves within a colony, although the exact nature of this impact appears to be uncertain.

7.1.3. Duration of daily sunshine

Daylength and photoperiod are regarded as synonyms for the duration of daily sunshine in this section. The effect of photoperiod on flowering is well known and has already been discussed

in Chapter four. Krishnamurti (1939) and Gerlach (1985) both noted a degree of coincidence in the changes in hive weight and the duration of sunshine. A statistical reanalysis of the inter-annual (1928-1938) variations in hive weight and duration of sunshine presented in Krishnamurti (1939) only detected a statistically significant correlation between the two variables in July (Spearman $R = 0.85$, $p = 0.0008$, $n = 11$) and none in May and June. The relationship between the duration of daily sunshine and honey production appears to have been little studied and requires further investigation.

7.1.4. Evaporation

Evaporation has the potential to affect hive weight both directly and indirectly. Evaporation is believed to influence both the concentration and quantity of nectar available from plants (Cruden *et al.*, 1983) and to facilitate the transformation of nectar to honey within a hive (Gerlach, 1985). Gerlach (1985) ascribed a fall in hive weight at night to evaporation.

7.1.5. Rainfall

Rainfall can influence the flowering phenology and nectar rewards of honeybee forage plants, the flight of foragers and the weight of scale-hives. As the relationship between rainfall and flowering has already been discussed in Chapter four it will not be reviewed any further in this section. In order to conceptualize the effects of rainfall on honey flows a distinction needs to be made between preceding and coincident rainfall events. The former tend to have a cumulative positive effect on honey reserves, while the latter can have an immediate negative effect on nectar and foragers. Statistically significant positive correlations between rainfall for

periods of varying duration and intervals preceding honey flows and honey production have been reported by a number of researchers *inter alia* Moffett & Parker (1953), Crane (1975) and Hepburn & Radloff (1996). Nectar flow (*sensu* Moffett & Parker, 1953) has been equated with honey flow for the purposes of this discussion. Two sets of data, reported by Munro (1929) and Jorgensen & Markham (1946) respectively, illustrate the negative effect rainfall can have on changes in hive weight. The data from North Dakota presented by Munro (1929) showed that more than three times the amount of honey was produced during July and August 1927 than the corresponding period a year later. The latter period was associated with rainfall in excess of four times that recorded in 1927. There were only marginal differences in the duration of sunshine (i.e. 40.9 hrs) and temperature range (i.e. 1.2 °F) between the two periods, so the negative effect of rainfall would appear to be real. This is corroborated by data from Michigan presented in Jorgensen & Markham (1946). A far greater percentage (+ 37.92 %) of days with rainfall occurred amongst the worst (61.25 %)(n = 240) rather than the best (23.33 %)(n = 240) yielding days within each "...season..." (p.11).

The data for both categories appears to have been based on 24 equal sample sizes (n = 10) selected separately from each year between 1921 and 1944. Nevertheless, the findings of these two studies need to be interpreted cautiously as Moffett & Parker (1953) obtained equivocal results in Kansas. The mean monthly rainfall values of the 10 best and worst years for honey production were greater in June and August, but lower in July for the most favourable years. Only the differences in the two categories for June were found to be statistically significant (Moffett & Parker, 1953). A result, which at least for June, contradicts what had been found earlier by Munro (1929) and Jorgensen & Markham (1946).

The availability and concentration of nectar are both affected by rainfall. Moisture stress can retard nectar secretion (Vogel, 1983), while rainfall can dilute nectar or flush it from

flowers (Cruden *et al.*, 1983; Szabo & Mueller, 1996). Rainfall can also have a direct effect on honeybees and hive boxes. Honeybees may be prevented from flying by rain, while wet hive boxes may complicate the interpretation of scale-hive records (Hambleton, 1925). As flight has been reported at low rainfall intensities (Fletcher, 1978) it would appear that it only becomes a limiting factor above an unknown threshold and if coincident with potential foraging activity (Jorgensen & Markham, 1946).

7.1.6. Relative humidity (%)

Relative humidity is reputed to affect flowering, nectar traits, honeybees and honey production. For example, Smith-Ramírez & Armesto (1994), working in Chile, found a statistically significant negative correlation between the monthly flowering intensity of the plant community and relative humidity. In general, researchers appear to associate an increase in relative humidity with an increase in volume (Cruden *et al.*, 1983), but a decrease in concentration of the available nectar (Park, 1929; Scullen, 1940; Oertel, 1946; Cruden *et al.*, 1983). This has been ascribed to atmospheric water absorption by the nectar (Cruden *et al.*, 1983). Oertel (1946) found that all statistically significant correlations between relative humidity and nectar concentration were negative, although both negative and a single positive correlation had been detected for the various periods studied. Hambleton (1925, citing Hommell, 1919) reported that nectar secretion itself may be positively related to relative humidity. An assertion repeated 60 years later for lime in Germany (Gerlach, 1985). Gerlach (1985) suggested that elevated levels of relative humidity enhanced nectar secretion.

Relative humidity is known to affect the water relations of honeybees in certain circumstances, which may ultimately influence their foraging behaviour and hence the level of

honey reserves within a colony. For example, Atmowidjojo *et al.* (1997) illustrated graphically how water loss is inversely related to relative humidity at 35°C. Szabo (1980) found a statistically significant negative correlation between relative humidity and flight activity on at least two of three study days in each of the northern hemisphere summers of 1976, 1977 and 1978. Szabo (1980) also monitored the effect of relative humidity on changes in hive weight on the same six days in 1977 and 1978 and obtained a similar result. A statistically significant negative correlation on at least two days in each year, except on this occasion the two insignificant correlations were positive and not negative as before. Similarly, Gerlach (1985) attributed decreases in hive weight to increases in relative humidity. In contrast, a reanalysis in this study of Hambleton's (1925) data for the autumn of 1922 found no correlation between the mean values for diurnal relative humidity and hive weight changes in the corresponding period.

Data presented by Jorgensen & Markham (1946)(see section 7.1.5. above) showed that more of the best days for honey yield fell in the 50- 59 % relative humidity class than any other, while the corresponding peak for the worst honey yielding days lay in the 70-79 % relative humidity class. However, a simplistic interpretation of these two maxima would be unwise as the second highest number of days for both the best and worst days for honey yield fall within the 60-69 % relative humidity class. Furthermore, the third highest values fall within the reciprocal peak's classes. As an additional complication, Jorgensen & Markham (1946) have pointed out that their values for relative humidity may have been over-estimated due to the time of day (19h30) when the relative humidity measurements were made.

7.1.7. Southern Oscillation Index (SOI)

The SOI is a measure of the difference in air pressure at sea level between Darwin, Australia and Tahiti. El Niño events are characterized by large negative values for the SOI, while La Niña episodes have large positive indices (Sillett *et al.*, 2000). Ashton *et al.* (1988) reported a clear relationship between El Niño events and the flowering phenology of Dipterocarpaceae in parts of Malaysia. As a consequence, one could anticipate that flowering in honeybee forage plants and hence honey production may also be affected by these climatic conditions.

However, Cramb (1997), commenting on the situation in Western Australia, appears to have been unable to detect any meaningful connection between the SOI and honey production. El Niño events in the South African interior are usually associated with drier than average conditions (Joubert, 1998). Nevertheless, even during the most extreme events the effects on summer rainfall remain moderate (Joubert, 1998) and therefore are unlikely to have had a significant impact on rainfall and hence the honey reserves of the scale-hive colonies at the University of Pretoria Experimental Farm.

7.1.8. Temperature (°C)

Temperature can influence flowering phenology, nectar traits, the behaviour of honeybees and honey production. The effects of temperature on flowering phenology will not be discussed here as they have already been reviewed in Chapter four. Nectar secretion and concentration are positively related to increases in temperature (Oertel, 1946; Percival, 1965; Vogel, 1983). As a consequence, an increase in temperature is also likely to affect the attractiveness of forage plants to honeybees. Nevertheless, exceptions can occur, for example Oertel (1946)

found a negative, but marginally insignificant correlation, between temperature and the concentration of goldenrod (*Solidago altissima*) nectar in one year near Baton Rouge, Louisiana. However, as most of the research reviewed above has been carried out in the temperate regions of the world it is unclear to what extent it is applicable to South African conditions. For example, in some African plant species nectar secretion reportedly occurs preferentially in the cooler periods of the diurnal cycle (Fletcher, 1978). Plants are reputed to have both minimum and maximum temperature thresholds for nectar secretion (e.g. minimum, 8°C - *Prunus avium*; maximum, c. 25°C - white clover, *Trifolium repens*)(Percival, 1965).

Honeybees are directly affected by temperature as both individuals and as a colony. As a colony honeybees respond to low temperatures by clustering and to high temperatures by fanning and dispensing small quantities of water into comb cells (Southwick, 1988; Heinrich, 1993). For individuals 4.5 °C (Heinrich, 1996) and 46 °C (Heinrich, 1996) (possibly 48 °C, Kevan & Baker, 1983) are the minimum and maximum reported air temperatures respectively for flight and hence foraging. An anecdotal account from Natal appears to indicate that the minimum threshold for foraging lay between 10 °C and 11 °C (Fletcher, 1978). The minimum thresholds for flight appear to vary with the time of year, being lower in spring (12 °C to 14 °C) than summer (16 °C to 18 °C) (Kevan & Baker, 1983). Individuals utilize their thoracic muscles to warm-up and regurgitated droplets to cool down (Southwick, 1988; Heinrich, 1996).

Honey production is usually positively correlated with increases in temperature (e.g. Szabo, 1980). Szabo (1980) found statistically significant positive correlations between temperature and both flight activity and changes in hive weight. In contrast, Moffett & Parker (1953) reported a negative, albeit statistically insignificant correlation between June temperatures and hive weight changes for the month at Manhattan, Kansas. Nevertheless,

these changes in hive weight were still significantly ($p < 0.01$) and positively correlated with the mean temperature recorded earlier in April. From the tabular data presented by Jorgensen & Markham (1946) for the best and worst days for honey production at a site in Michigan (see section 7.1.5 above), it is evident that the daily temperature maxima may be more important for gains in hive weight than either the daily temperature minima or the daily temperature range. Both of the latter are best represented in the same temperature class for both categorical extremes of honey production. The maximum temperatures on the best days for honey production fall most frequently into a temperature class warmer than the corresponding class for the worst days of honey production.

The effect of temperature on South African honey yields is difficult to discern from the literature. Garin (1931) reporting on honey yields at Morokwen in the early part of the twentieth century was of the opinion that "*the average temperature of every month does not seem to have much influence on the honey crop*" (p.18). Nevertheless, honey yields from *Faurea saligna* at least are enhanced by cool and wet conditions while the plants are in bud and flower (Johannsmeier, 1975). Conversely, he also stated that for *Eucalyptus grandis*, "*occasional cold spells may bring the flow to an abrupt halt*" (p. 184). It is unclear from the text whether Johansmeier (1975) was referring to nectar or honey flows, although the effects on honey production are likely to be similar.

7.2. Methods

The two scale-hive records from the University of Pretoria Experimental Farm (see Chapter six) were reused in this study. This location has the longest time-span (1968-1991) of any scale-hive record from within South Africa, which potentially makes it the most suitable for

time series analysis. Both the hive and climatic data were subjected to a number of statistical procedures which are listed and briefly described below. The climatic data was obtained electronically from the Weather Bureau or transcribed from their publications. Data was only transcribed if the required data was thought to be unavailable electronically from the Weather Bureau. The transcribed data only covered the period from January 1985 to September 1989. For three variables, namely the mean monthly rainfall, the average daily sunshine hours and the mean monthly air pressure, surrogate data from the weather station, Pretoria (Forum) (0513314AX, 25°44'S 28°11'E, 1330m), was used to augment the climatic data from the University of Pretoria's Experimental Farm (0513465 1, 25°45'S 28°16'E, 1372m). This facilitated an investigation of the effects of rainfall over a longer time period than would otherwise have been the case if only the data from the experimental farm had been used. Daily sunshine and air pressure data were unavailable from the experimental farm. Standardized values of the Southern Oscillation Index (SOI) were obtained from a NOAA website (*viz.* www.cpc.ncep.noaa.gov/data/indices/).

7.2.1. Descriptive statistics

The number of observations, mean, standard deviation, maximum and minimum value were determined for each of the variables. The same data set used to calculate these values also provided the basis for all the subsequent statistical analyses described below.

7.2.2. Spearman Rank Order Correlations

This non-parametric technique was used to assess the strength of the correlation between any

two variables. No lag effects were investigated. Only the statistically significant ($p < 0.05$) correlations have been reported in this study.

7.2.3. Time series analyses

7.2.3.1. Autocorrelation & cross-correlation

The level of auto- and cross-correlation was determined for each variable for lag periods from -24 to 24 months. Only the five largest positive and negative correlations greater than 0.5 have been reported below. Only the cross-correlations between the changes in hive weight and climatic variables have been investigated and none of those between the climatic variables themselves.

7.2.3.2. Spectral analyses

Two types of spectral analysis were carried out, the first involved a single series fourier analysis of individual variables, while the second entailed a cross-spectrum analysis of the relationship between the two scale-hive records and the climatic variables. The means were subtracted and the series detrended for each calculation. Missing data was interpolated from adjacent observations. To satisfy the requirements of the fourier analysis the last observation of uneven series was excluded from the calculations. For the single series fourier analysis only the monthly periods with the five largest periodogram values were reported in the results. For the cross-spectrum analysis only the periods longer than 12 months, with variable densities greater than 1.0 and squared coherency values greater than 0.5 have been included in the

results below. Only the five largest squared coherency values have been reported when more than this number fulfilled the criteria above.

7.3. Results

7.3.1. Scale-hive records (kg)

The descriptive statistics for the changes in hive weight at the University of Pretoria Experimental Farm are presented in Table 7.1. On average colony H47 consistently had greater gains in hive weight than colony H42 for every calendar month, with the exception of December when the opposite was true. Similarly, in February when both colonies had a mean monthly loss this was less for H47 than H42. The comparison of the means was hampered by the lack of data for one colony during October (H47) and November (H42). The very small sample sizes from which many of these monthly means were calculated suggests the results should be regarded as provisional estimates. Mean increases in the honey reserves appear to be greatest in spring and early summer and smallest in late summer, autumn and winter. Indeed, mean losses were experienced in colony H42 from January to April and again from June to August. Mean losses in hive weight were restricted to only two months for H47, namely December and February.

There was only one statistically significant Spearman Rank Order Correlation between either of the two scale-hive records and any of the climatic variables, namely between H42 and the rainfall record from the experimental farm (Spearman $R = -0.44$, $p = 0.0480$, $n = 21$). In addition, no cross-correlation > 0.5 or stronger than -0.5 was found between either scale-hive record and any of the climatic variables at any of the lags investigated. Autocorrelations were

detected at one (H42, autocorrelation = 0.85, S.E. = 0.06; H47, autocorrelation = 0.87, S.E. = 0.07), two (H42, autocorrelation = 0.62, S.E. = 0.06; H47, autocorrelation = 0.74, S.E. = 0.07), three (H47, autocorrelation = 0.62, S.E. = 0.07), four (H47, autocorrelation = 0.56, S.E. = 0.06) and five (H47, autocorrelation = 0.51, S.E. = 0.06) month periods.

The results of the single series fourier analyses on the monthly changes in hive weight for each scale-hive record appear in Table 7.2. Neither scale-hive record had a period with the five largest periodogram values in common. In both instances these values represent multiples of one another or very close approximations to multiples (e.g. H42, 252.00 = 126.00 X 2, 28.00 X 9, 16.80 X 15, 14.82 X 17; H47, 230.00 = 115.00 X 2, 76.67 X 3, 57.50 X 4, 38.33 X 6).

The results of the cross-spectrum analyses between the hive data and the climatic variables are displayed in Table 7.3. Not shown are the periods with the strongest relationships between the changes in hive weight for the two scale-hive records, namely 15.14 (cross-amplitude = 15.66, squared coherency = 0.79), 16.31 (cross-amplitude = 17.14, squared coherency = 0.69), 26.50 (cross-amplitude = 32.27, squared coherency = 0.65) and 23.56 (cross-amplitude = 28.67, squared coherency = 0.64) months. None of these periods are represented in the five strongest relationships detected during the single series fourier analyses (Table 7.2). The two scale-hive records have no periods in common amongst the five strongest relationships for any variable. In contrast, a few periods occur recurrently in the five strongest relationships between the two scale-hive records and the different climatic variables (i.e. H42, 12.00, 28.00, 63.00, 252.00; H47, 12.11, 15.33, 17.69, 19.17, 32.86, 38.33, 57.50, 115.00, 230.00) (see Table 7.3). Note that these periods are sometimes multiples of one another, such as the two sequences 19.17 - 38.33 and 57.50 - 115.00 - 230.00 associated with the scale-hive record H47.

Table 7.1. Descriptive statistics for the changes in hive weight (kg) calculated from the two scale-hive records (H42 & H47) from the University of Pretoria Experimental Farm (n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).

[illegible]

Table 7.2. The results of the single series fourier analyses carried out on the monthly changes in hive weight associated with the two scale-hive records (* = uneven series, see methods for details).

Record	Period	Periodogram	Record	Period	Periodogram
<u>Hive 42</u>	252.00	638.42	<u>Hive 47*</u>	57.50	746.06
(n = 252)	126.00	134.29	(n = 230)	76.67	427.69
	16.80	113.67		230.00	328.97
	14.82	105.43		38.33	301.30
	28.00	98.93		115.00	293.50

Table 7.3. The results of the cross-spectrum analyses on the monthly changes in hive weight associated with the two scale-hive records (¹ = repetitive periods within each scale-hive record are underlined, PF = Pretoria (Forum), SOI = Southern Oscillation Index (standardized), UP = University of Pretoria Experimental Farm, * = uneven series, see methods for details).

Variable	H42 n	Period ¹	Cross - amplitude	Squared coherency	H47 n	Period	Cross - amplitude	Squared coherency
Rainfall UP	56*	-	-	-	40	13.33	142.06	0.57
		-	-	-		40.00	199.29	0.56
Rainfall PF	252	<u>12.00</u>	280.09	0.67	230*	<u>230.00</u>	991.21	0.92
		<u>63.00</u>	216.07	0.63		<u>38.33</u>	603.53	0.78
		<u>28.00</u>	349.65	0.52		<u>32.86</u>	505.09	0.74
		-	-	-		<u>115.00</u>	1132.91	0.72
		-	-	-		25.56	457.57	0.69
Evaporation UP	56*	-	-	-	40	-	-	-
Max. T°C UP	252	<u>12.00</u>	179.32	0.66	230*	<u>57.50</u>	53.72	0.75
		-	-	-		<u>15.33</u>	18.54	0.70

		-	-	-		<u>230.00</u>	39.96	0.69
		-	-	-		<u>12.11</u>	126.72	0.59
		-	-	-		14.38	14.95	0.57
Min. T°C UP	252	<u>252.00</u>	47.51	0.84	230*	16.43	16.69	0.79
		84.00	22.91	0.72		<u>15.33</u>	20.44	0.75
		<u>12.00</u>	272.30	0.69		<u>57.50</u>	34.87	0.64
		126.00	35.94	0.67		<u>12.11</u>	190.73	0.60
		14.00	8.52	0.67		<u>17.69</u>	10.42	0.52
Air pressure 14h00 PF	252	<u>252.00</u>	127.99	0.79	230*	<u>230.00</u>	58.95	0.86
		21.00	12.18	0.74		<u>19.17</u>	12.75	0.79
		<u>63.00</u>	17.72	0.74		20.91	8.88	0.79
		<u>12.00</u>	141.38	0.69		<u>115.00</u>	77.18	0.76
		50.40	15.23	0.67		<u>57.50</u>	57.83	0.74
Relative Humidity UP	164	-	-	-	124	41.33	275.05	0.69
		-	-	-		62.00	358.39	0.68
		-	-	-		15.50	157.74	0.64
		-	-	-		17.71	136.00	0.60
		-	-	-		124.00	258.84	0.60
Daily sunshine hours PF	252	<u>12.00</u>	349.11	0.72	230*	<u>230.00</u>	176.36	0.71
		16.80	113.02	0.70		<u>38.33</u>	159.88	0.65
		<u>28.00</u>	80.55	0.65		<u>19.17</u>	68.39	0.58
		12.60	265.97	0.63		<u>32.86</u>	99.42	0.56
		18.00	82.82	0.51		<u>17.69</u>	54.57	0.55
Cloud cover 14h00 UP	56*	56.00	9.40	0.53	40	-	-	-
SOI	252	<u>252.00</u>	58.85	0.76	230*	<u>57.50</u>	98.85	0.75
		42.00	26.23	0.51		<u>230.00</u>	32.84	0.69

		-	-	-		76.67	71.74	0.55

7.3.2. Air pressure (hPa) at 14h00

The mean monthly air pressure at 14h00 recorded at Pretoria (Forum) ranges from a low of 868.95 hPa in January to a high of 875.53 hPa in July (Table 7.4). There are statistically significant relationships with the mean monthly values for cloud cover, daily sunshine hours, evaporation, rainfall, relative humidity, maximum and minimum daily temperature. All of these relationships are negative apart from that with daily sunshine for which there is a weak positive correlation (Table 7.5).

Table 7.4. The descriptive statistics for the mean monthly air pressure (hPa) at 14h00 for Pretoria (Forum)(n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).

[illegible]

Table 7.5. The statistically significant Spearman Rank Order Correlations between the mean monthly air pressure (hPa) at 14h00 for Pretoria (Forum) and the other climatic variables investigated (except Pretoria (Forum))(PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).

	n	Spearman R	p
vs Cloud cover 14h00 UP	50	-0.67	< 0.0001
vs Daily sunshine PF	288	0.29	< 0.0001
vs Evaporation UP	50	-0.76	< 0.0001
vs Rainfall UP	40	-0.63	< 0.0001
vs Relative humidity UP	131	-0.50	< 0.0001
vs Max. T°C UP	286	-0.75	< 0.0001
vs Min. T°C UP	283	-0.80	< 0.0001

7.3.3. Cloud cover (octas) at 14h00

The mean monthly cloud cover at 14h00 recorded at the University of Pretoria Experimental Farm is least in July (0.40 octas) and greatest in December (4.33 octas) (Table 7.6). There are statistically significant correlations with the mean monthly air pressure at 14h00, daily sunshine hours, evaporation, rainfall, relative humidity, maximum and minimum daily temperatures. All of these relationships are positive apart from those for air pressure at 14h00 and the daily sunshine hours which are negative (Table 7.7).

Table 7.6. The descriptive statistics for the mean monthly cloud cover (octas) at 14h00 for the University of Pretoria Experimental Farm (n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
n	3	4	5	5	5	5	5	4	4	4	3	3
\bar{x}	4.00	4.25	3.40	2.60	1.40	0.80	0.40	1.00	1.75	4.25	4.00	4.33
STD	0.00	0.50	1.14	1.95	0.89	0.45	0.55	1.41	1.71	0.50	1.00	0.58
Max.	4.00	5.00	5.00	4.00	3.00	1.00	1.00	3.00	4.00	5.00	5.00	5.00
Min.	4.00	4.00	2.00	0.00	1.00	0.00	0.00	0.00	0.00	4.00	3.00	4.00

Table 7.7. The statistically significant Spearman Rank Order Correlations between the mean monthly cloud cover (octas) at 14h00 for the University of Pretoria Experimental Farm and the other climatic variables investigated (except Pretoria (Forum))(PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).

	n	Spearman R	p
vs Air Pressure 14h00 PF	50	-0.67	< 0.0001
vs Daily sunshine PF	50	-0.64	< 0.0001
vs Evaporation UP	48	0.53	0.0001
vs Rainfall UP	37	0.66	< 0.0001
vs Relative humidity UP	47	0.49	0.0005
vs Max. T°C UP	48	0.65	< 0.0001
vs Min. T°C UP	48	0.77	< 0.0001

Table 7.9. The statistically significant Spearman Rank Order Correlations between the mean monthly daily sunshine hours for Pretoria (Forum) and the other climatic variables investigated (except Pretoria (Forum))(PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).

	n	Spearman R	p
vs Air Pressure 14h00 PF	288	0.29	< 0.0001
vs Cloud cover 14h00 UP	50	-0.64	< 0.0001
vs Rainfall UP	40	-0.46	0.0025
vs Relative humidity UP	131	-0.51	< 0.0001
vs Min. T°C UP	283	-0.38	< 0.0001

7.3.5. Evaporation (mm/day)

The mean monthly daily evaporation is lowest in June (3.24 mm/day) and greatest in October (7.90 mm/day) (Table 7.10). There are statistically significant correlations with air pressure at 14h00, cloud cover at 14h00, rainfall, maximum and minimum daily temperature (Table 7.11). All of these relationships are positive except for that with the mean monthly air pressure at 14h00 for which there is a negative correlation (Table 7.11).

Table 7.10. The descriptive statistics for the mean monthly evaporation (mm/day) for the University of Pretoria Experimental Farm (n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
n	2	4	5	5	5	5	5	5	4	3	4	3
\bar{x}	7.55	6.63	5.26	4.54	3.72	3.24	3.62	4.82	5.85	7.90	6.15	6.50
STD	1.91	0.75	0.65	1.09	0.70	0.47	0.35	0.54	0.89	2.14	0.99	1.05
Max.	8.90	7.60	6.10	5.90	4.50	3.70	4.00	5.50	6.70	9.60	7.20	7.60
Min.	6.20	5.90	4.70	3.50	2.60	2.50	3.30	4.30	4.60	5.50	5.00	5.50

Table 7.11. The statistically significant Spearman Rank Order Correlations between the mean monthly daily evaporation for the University of Pretoria Experimental Farm and the other climatic variables investigated (except Pretoria (Forum))(PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).

	n	Spearman R	p
vs Air Pressure 14h00 PF	50	-0.76	< 0.0001
vs Cloud cover 14h00 UP	48	0.53	0.0001
vs Rainfall UP	39	0.53	0.0006
vs Max.T°C UP	48	0.84	< 0.0001
vs Min. T°C UP	48	0.79	< 0.0001

7.3.6. Rainfall (mm/month)

The mean monthly rainfall at Pretoria (Forum) and the University of Pretoria Experimental

Table 7.13. The statistically significant Spearman Rank Order Correlations between the mean monthly rainfall for the University of Pretoria Experimental Farm and the other climatic variables investigated (PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).

	n	Spearman R	p
vs Air Pressure 14h00 PF	40	-0.63	< 0.0001
vs Cloud cover 14h00 UP	37	0.66	< 0.0001
vs Daily sunshine PF	40	-0.46	0.0025
vs Evaporation UP	39	0.53	0.0006
vs Rainfall PF	40	0.95	< 0.0001
vs Relative humidity UP	37	0.52	0.0009
vs Max. T°C UP	38	0.55	0.0003
vs Min. T°C UP	38	0.66	< 0.0001

7.3.7. Relative humidity (%)

The mean monthly relative humidity is lowest in September (35.55 %) and highest in January (55.33 %)(Table 7.14). There are statistically significant correlations with the air pressure at 14h00, cloud cover at 14h00, daily sunshine hours, rainfall, maximum and minimum daily temperature (Table 7.15). All of these relationships are positive apart from two which are negative, namely the air pressure at 14h00 and the daily sunshine hours (Table 7.15).

Table 7.14. The descriptive statistics for the mean monthly relative humidity (%) for the University of Pretoria Experimental Farm (n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
n	12	12	10	11	12	10	9	11	11	10	11	12
\bar{x}	55.33	54.08	53.20	49.18	42.42	41.80	36.33	35.82	35.55	41.70	47.82	53.08
STD	8.56	6.75	9.10	9.68	7.43	7.33	6.22	10.08	8.86	6.60	8.52	10.77
Max.	72.00	66.00	63.00	62.00	57.00	50.00	48.00	63.00	56.00	51.00	63.00	71.00
Min.	47.00	45.00	39.00	34.00	31.00	26.00	30.00	27.00	24.00	31.00	40.00	34.00

Table 7.15. The statistically significant Spearman Rank Order Correlations between the mean monthly relative humidity for the University of Pretoria Experimental Farm and the other climatic variables investigated (except Pretoria (Forum))(PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).

	n	Spearman R	p
vs Air Pressure 14h00 PF	131	-0.50	< 0.0001
vs Cloud cover 14h00 UP	47	0.49	0.0005
vs Daily sunshine PF	131	-0.51	< 0.0001
vs Rainfall PF	37	0.52	0.0009
vs Max. T°C UP	131	0.37	< 0.0001
vs Min. T°C UP	129	0.55	< 0.0001

7.3.8. Southern Oscillation Index (SOI)

The mean monthly SOI (standardized) ranges from a low in February (-0.33) to a high in May (0.06)(Table 7.16). There are no statistically significant correlations between the SOI (standardized) and any of the other variables investigated.

Table 7.16. The descriptive statistics for the mean monthly SOI (standardized) (n = number of observations, \bar{x} = mean, STD = standard deviation, Max. = maximum value, Min. = minimum value).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
n	24	24	24	24	24	24	24	24	24	24	24	24
\bar{x}	-0.09	-0.33	-0.30	-0.12	0.06	-0.11	-0.06	-0.20	-0.01	-0.13	-0.09	-0.25
STD	1.36	1.73	1.30	0.87	0.94	0.83	1.07	1.04	1.26	1.04	1.23	1.29
Max.	2.70	2.00	2.20	1.70	1.30	1.10	2.10	1.90	2.40	1.70	2.90	2.30
Min.	-4.20	-4.60	-3.40	-1.90	-2.10	-1.70	-1.90	-2.50	-2.00	-2.20	-3.20	-2.80

7.3.9. Temperature (°C)

The mean monthly daily maxima and minima are lowest in June (maximum temperature, 18.93 °C; minimum temperature, 3.48 °C) and highest in January (maximum temperature, 27.95 °C; minimum temperature, 16.00 °C)(Table 7.17). The mean monthly daily maxima and minima are significantly and positively correlated with the cloud cover at 14h00, evaporation, rainfall, relative humidity and each other, but significantly and negatively correlated with the air

Table 7.18. The statistically significant Spearman Rank Order Correlations between the mean monthly daily maxima and minima for the University of Pretoria Experimental Farm and the other climatic variables investigated (except Pretoria (Forum))(PF = Pretoria (Forum), UP = University of Pretoria Experimental Farm).

	n	Spearman R	p
<u>Max. T°C</u>			
vs Air Pressure 14h00 PF	286	-0.75	< 0.0001
vs Cloud cover 14h00 UP	48	0.65	< 0.0001
vs Evaporation UP	48	0.84	< 0.0001
vs Rainfall PF	38	0.55	0.0003
vs Relative humidity UP	131	0.37	< 0.0001
vs Min. T°C UP	283	0.91	< 0.0001
<u>Min. T°C</u>			
vs Air Pressure 14h00 PF	283	-0.80	< 0.0001
vs Cloud cover 14h00 UP	48	0.77	< 0.0001
vs Daily sunshine PF	283	-0.38	< 0.0001
vs Evaporation UP	48	0.79	< 0.0001
vs Rainfall PF	38	0.66	< 0.0001
vs Relative humidity UP	129	0.55	< 0.0001
vs Max.T°C UP	283	0.91	< 0.0001

7.4. Discussion

As could have been expected a number of the climatic variables are related to one another.

Cloud cover (14h00) is inversely related to the duration of sunshine (Spearman R = - 0.64, $p <$

0.0001) and to the air pressure (14h00) (Spearman $R = -0.67$, $p < 0.0001$). The relationship between the latter and cloud cover could be attributed to either the arrival of cold fronts or the development of cumulus clouds associated with surface heating and consequent thermal activity. Typically, the cold fronts could be expected to occur more commonly in winter and the latter in summer. The strong negative correlation between the air pressure (14h00) and both the maximum (Spearman $R = -0.75$, $p < 0.0001$) and minimum (Spearman $R = -0.80$, $p < 0.0001$) temperature would appear to indicate that the surface heating effects associated with the development of cumulus clouds predominate. Conversely, clear skies could be attributed to descending air and consequently elevated air pressures (14h00). It is therefore unsurprising that rainfall is positively correlated with maximum (Spearman $R = 0.55$, $p = 0.0003$) and minimum (Spearman $R = 0.66$, $p < 0.0001$) temperature and cloud cover (14h00) (Spearman $R = 0.66$, $p < 0.0001$), but negatively correlated with air pressure (14h00) (Spearman $R = -0.63$, $p < 0.0001$). These results are consistent with the summer dominated rainfall regime recorded at the University of Pretoria Experimental Farm (Table 7.12). The positive correlation between the evaporation values and the maximum (Spearman $R = 0.84$, $p < 0.0001$) and minimum (Spearman $R = 0.79$, $p < 0.0001$) temperature, cloud cover (14h00) (Spearman $R = 0.53$, $p = 0.0001$) and rainfall (Spearman $R = 0.53$, $p = 0.0006$) and negative correlation with air pressure (14h00) (Spearman $R = -0.76$, $p < 0.0001$) are consistent with the surface heating hypothesis mentioned above. Relative humidity is positively correlated with the maximum (Spearman $R = 0.37$, $p < 0.0001$) and minimum (Spearman $R = 0.55$, $p < 0.0001$) temperature, cloud cover (14h00) (Spearman $R = 0.49$, $p = 0.0005$) and rainfall (Spearman $R = 0.52$, $p = 0.0009$), but negatively correlated with air pressure (14h00) (Spearman $R = -0.50$, $p < 0.0001$). This may be attributed to the incursion of warm moist tropical air into the Pretoria area during the summer months.

Only one statistically significant correlation was detected between changes in the weight of the scale-hives and the climatic variables. The changes in weight for one scale-hive record, namely H42, were negatively correlated with the rainfall values recorded at the University of Pretoria Experimental Farm (Spearman $R = -0.44$, $p = 0.0480$). This negative effect of rainfall on hive weight corroborates the results obtained by Munro (1929) and Jorgensen & Markham (1946). The absence of any cross-correlations between the changes in hive weight for the two scale-hive records and any of the climatic variables investigated, up to and including a lag period of 24 months, indicates a lack of simple correlations between the variables concerned. This may be due to one or a combination of two features which characterise the University of Pretoria Experimental Farm, namely the thermal regime and its suburban location. Maximum temperatures are probably seldom limiting with the lowest mean maximum temperature for the entire record and for an individual year occurring in June, namely 18.93 °C and 16.30 °C respectively (Table 7.17).

One or both of two traits are present amongst the strongest autocorrelations of each variable, namely a lag period of one month and seasonal effects. The duration of sunshine was the only variable without any autocorrelations which fulfilled the criteria for this study. All of the remaining variables, except the rainfall record from Pretoria (Forum), exhibited this one month lag period. These autocorrelations were always positive and reminiscent of a random-walk model (STATISTICA 6.0). Seasonal effects are apparent for air pressure (14h00), cloud cover (14h00), evaporation, rainfall (only Pretoria (Forum)) and the maximum and minimum temperature values. Seasonal effects are interpreted here as autocorrelations with a lag period of six months or a multiple thereof, with positive values indicating same (*i.e.* summer:summer) and negative values contrasting (*i.e.* summer:winter) seasons. The rainfall (only Pretoria (Forum)) and maximum and minimum temperature values have both the positive and negative

relationships present, whereas air pressure (14h00) and evaporation have only the former and cloud cover (14h00) only the latter evident. For some of the variables there are other relationships which closely approximate these “seasonal” intervals. For example, lag periods of 5 (*i.e.* H47), 7 (*i.e.* cloud cover (14h00)), 11 (*i.e.* air pressure (14h00), evaporation) and 13 (*i.e.* air pressure (14h00), cloud cover (14h00), maximum temperature) months are represented in the lists of the five strongest autocorrelations for some of the variables investigated in this study.

The relative importance of the periods identified in both the single series fourier and cross-spectral analyses for honey production needs further investigation. Nevertheless, if the most frequently occurring of these periods are taken as a measure of their significance an initial assessment can be made of some temporal patterns and their underlying causes. In the single series fourier analyses a 12 month seasonal period is very evident, having the largest periodogram values for air pressure (14h00), duration of sunshine, rainfall (only Pretoria (Forum)), relative humidity and the maximum and minimum temperature. A spectral analysis of the rainfall data for a part of the summer rainfall zone in southern Africa detected statistically significant periods of 2.3 ($p < 0.01$), c.3.5 and 18 years ($p < 0.01$) (Tyson, 1986). Statistically significant periods of between 6 to 7 and 4 to 5 years also appear to have been identified at some localities. It is notable that periods of 2.33 and 4.67 years were detected in this study for the rainfall record from the University of Pretoria Experimental Farm. These two periods represent the second and fourth largest periodogram values respectively. Similarly, periods of 2.33 (only H42), 4.79 (only H47) and 6.39 (only H47) years occur amongst the five largest periodogram values for each scale-hive record.

The cross-spectral analyses between the two scale-hive records and the various climatic variables gave mixed results. Only two periods are repeated more than twice in each

scale-hive record. One of these periods for each scale-hive record is equal to the listed variables individual sample sizes. For example, for record H42 the relevant period is 252 months, which equates to the sample sizes for air pressure (14h00), SOI and the minimum temperature. The corresponding period for record H47 is 230 months, the sample size for air pressure (14h00), duration of sunshine, rainfall (only Pretoria (Forum)), SOI and maximum temperature. These results are therefore interpreted as artefacts of the statistical procedure and assumed not to represent supra-annual fluctuations in the variables concerned. The most frequently recurring period in each instance is 12 months and 57.50 months for the scale-hive records H42 and H47 respectively. The former appears to represent the annual seasonal cycle, while the latter is almost identical to the most prominent period for the SOI (*viz.* 57.60 months). As the SOI is one of the four variables with a strong association with the changes in hive weight for this period, it may indicate a link between the two phenomena. The paucity of correlations between the changes in hive weight and the climatic variables investigated in this study could be a consequence of the monthly time interval selected for the analyses. A similar set of analyses as those carried out here needs to be applied to daily data.

7.5. References

- Acutt, P. 1988. Observations on beekeeping in the Richmond area. *South African Bee Journal*, 60, 61-62.
- Ashton, P.S., Givnish, T.J. and Appanah, S. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *The American Naturalist*, 132, 44-66.

Atmowidjojo, A.H., Wheeler, D.E., Erickson, E.H. and Cohen, A.C. 1997. Temperature tolerance and water balance in feral and domestic honey bees, *Apis mellifera* L.. Comparative Biochemistry and Physiology, 118A, 1399-1403.

Butler, C.G. 1945. The influence of various physical and biological factors of the environment on honeybee activity. An examination of the relationship between activity and nectar concentration and abundance. Journal of Experimental Biology, 21, 5-12.

Cramb, J. 1997. Climatic influences on honey production. The Australasian Beekeeper, 98, 406-412.

Crane, E. (Ed).1975. Honey: a comprehensive survey. Heinemann, London.

Crane, E. 1990. Bees and beekeeping: science, practice and world resources. Heinemann Newnes, Oxford, 614 pp..

Cruden, R.W., Hermann, S.M. and Peterson, S. 1983. Patterns of nectar production and plant-pollinator coevolution. Chapter 3. In Bentley, B. and Elias, T. (Eds). The biology of nectaries. Columbia University Press, New York, 80-125.

Dyer, F.C. and Gould, J.L. 1981. Honey bee orientation: a backup system for cloudy days. Science, 214, 1041-1042.

- Eisikowitch, D. 1978. Insect visiting of two subspecies of *Nigella arvensis* under adverse seaside conditions. In Richards, A.J. (Ed), The pollination of flowers by insects, Linnean Society Symposium Series, No. 6, Academic Press, p.125-132.
- Engelbrecht, T. 1996. Sommige faktore wat 'n invloed het op bye-aktiwiteit, bestuiwing en saad-opbrengs van saadsonneblom. South African Bee Journal, 68, 149-153.
- Esler, K.J. 1999. Plant reproductive ecology. Chapter 8. In Dean, W.R.J. and Milton, S.J. (Eds), The Karoo: ecological patterns and processes. Cambridge University Press, p.123-144.
- Fletcher, D.J.C. 1978. The african bee, *Apis mellifera adansonii*, in Africa. Annual Review of Entomology, 23, 151-171.
- Garin, H. 1931. Morokwen (Bechuanaland) Records. The South African Bee Journal, unknown volume, 15-18.
- Gerlach, J. 1985. The dependence of honey-bee behaviour on weather - shown by the results of weighing bee-hives in the period of 1969 to 1978 in the region of the Beekeepers' Association of Hannover. International Journal of Biometeorology, 29, 67-85.
- Hambleton, J.I. 1925. The effect of weather upon the change in weight of a colony of bees during the honey flow. United States Department of Agriculture, Department Bulletin No. 1339, 52 pp..

- Heinrich, B. 1993. The hot-blooded insects: strategies and mechanisms of thermoregulation. Springer-Verlag, Berlin, 601 pp..
- Heinrich, B. 1996. How the honey bee regulates its body temperature. *Bee World*, 77, 130-137.
- Hepburn, H.R. and Jacot Guillarmod, A. 1991. The Cape honeybee and the fynbos biome. *South African Journal of Science*, 87, 70-73.
- Hepburn, H.R. and Radloff, S.E. 1996. Beeswax exports and rainfall in the savanna woodlands of east central Africa. *Apidologie*, 27, 473-478.
- Hepburn, H.R. and Radloff, S.E. 1998. Honeybees of Africa. Springer-Verlag, 370 pp..
- Hommell, R. 1919. Apiculture. Paris, 501 pp..
- Johannsmeier, M.F. 1975. Commercial beekeeping in the Transvaal in relation to honeyplants. *Proceedings I Congress Entomological Society of Southern Africa*, 181-184.
- Jorgensen, C. and Markham, F. 1946. Weather factors influencing honey production. Michigan State College, Agricultural Experiment Station, Section of Horticulture, East Lansing, Special Bulletin 340, 22 pp..

- Joubert, A. 1998. El Niño, La Niña and summer rainfall variability over South Africa. *South African Journal of Science*, 94, 2.
- Kevan, P.G. and Baker, H.G. 1983. Insects as flower visitors and pollinators. *Annual Review of Entomology*, 28, 407-453.
- Kevan, P.G. and Baker, H.G. 1984. Insects on flowers. Chapter 20. In Huffaker, C.B. and Rabb, R.L. (Eds), *Ecological Entomology*, John Wiley and Sons, New York, p. 607-631.
- Krishnamurti, B. 1939. A brief analysis of eleven years (1928-38) records of scale-hives, at the Rothamsted bee laboratory. *The Bee World*, 20, 121-123.
- Mitchener, A.V. 1955. Manitoba nectar flows 1924-1954, with particular reference to 1947-1954. *Journal of Economic Entomology*, 48, 514-518.
- Moffett, J.O. and Parker, R.L. 1953. Relation of weather factors to nectarflow in honey production. Technical Bulletin 74, Kansas Agricultural Experiment Station, Manhattan, Kansas, 27 pp..
- Munro, J.A. 1929. A study of the factors influencing the yield of honey during the main nectar flow. *Journal of Economic Entomology*, 22, 518-521.
- Oertel, E. 1946. Effect of temperature and relative humidity on sugar concentration of nectar. *Journal of Economic Entomology*, 39, 513-515.

Oertel, E. 1971. Solar radiation and honey production. *Gleanings in Bee Culture*, 99, 397-398.

Park, O.W. 1929. The influence of humidity upon sugar concentration in the nectar of various plants. *Journal of Economic Entomology*, 22, 534-544.

Percival, M. 1965. *Floral biology*. Pergamon Press, Oxford.

Rinderer, T.E., Collins, A.M. and Tucker, K.W. 1985. Honey production and underlying nectar harvesting activities of africanized and european honeybees. *Journal of Apicultural Research*, 23, 161-167.

Rosenberg, N.J., Blad, B.L. and Verma, S.B. 1983. *Microclimate: the biological environment*. Second Edition. John Wiley and Sons, New York, 495 pp..

Scullen, H.A. 1940. Relative humidity and nectar concentration in fireweed. *Journal of Economic Entomology*, 33, 870-871.

Sillett, T.S., Holmes, R.T. and Sherry, T.W. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science*, 288, 2040-2042.

Smith-Ramírez, C. and Armesto, J.J. 1994. Flowering and fruiting patterns in the temperate rainforest of Chiloé, Chile - ecologies and climatic constraints. *Journal of Ecology*, 82, 353-365.

- Southwick, E.E. 1988. Thermoregulation in honey-bee colonies. Chapter 28. In Needham, G.R., Page, R.E. Jr, Delfinado-Baker, M. and Bowman, C.E. (Eds), Africanized honey bees and bee mites, 223-236.
- Szabo, T.I. 1980. Effect of weather factors on honeybee flight activity and colony weight gain. *Journal of Apicultural Research*, 19, 164-171.
- Szabo, T.I. and Mueller, A.E. 1996. Factors affecting the weight changes of honey bee colonies. *American Bee Journal*, 136, 417-419.
- Tribe, G.D. 1983. What is the Cape bee? *South African Bee Journal*, 55, 77-87.
- Tyson, P.D. 1986. Climatic change and variability in southern Africa. Oxford University Press, Cape Town, 220 pp..
- Vogel, S. 1983. Ecophysiology of zoophilic pollination. In Pirson, A. and Zimmermann, M.H. (Eds), *Encyclopedia of Plant Physiology, New Series, Volume 12C*, 559-624.

CHAPTER 8. CONCLUSIONS

8.1. Introduction

The morphological and behavioural traits of biological organisms are clearly a consequence of natural selection. The variation in elements of their physical and biological environments drives this process in conjunction with other processes operating at the genetic level. This variation in the physical and biological environments is both spatially and temporally heterogenous.

Within this context, the results obtained in this study, while applicable at one scale may not be applicable at others. Individuals may interact and be influenced by individuals of both different and their own species. Inter- and intra-specific interactions would include their trophic position in the former and inter- and intra-sexual interactions in the latter. In addition, environmental attributes important in one stage of an insect's life-cycle may be less so in another. For economically important organisms such as the honeybee many if not all of the above facets need to be taken into account if they are to be managed successfully.

The foci of this study have been the interaction between the honeybees and their forage plants and the impact of selected climatic variables on honey production. The two are closely related in the sense that climate potentially affects the flowering regime and floral rewards on offer and the flight of foraging honeybees. The key results of this study and some of those from the literature are listed in Appendix 8.A.

8.2. Phylogeny of honeybee forage plants in South Africa

At least 944 plant species are visited by honeybees in South Africa for their nectar and/or

pollen, with more than half providing both rewards (Appendix 3.A). The entire known honeybee flora encompasses 532 genera and 137 families. The number of species within this flora can be divided almost equally between those of indigenous and exotic origin. The Asteraceae have the largest number of genera and the Fabaceae the greatest number of species within the known honeybee flora. The Orchidaceae and *Conophytum* are the largest family and genus respectively without any honeybee visitation records. Almost all (>80%) families of indigenous honeybee forage plant have a cosmopolitan or pantropic distribution. In addition, at least 40% of the angiosperm families within southern Africa have at least one species with a South African honeybee visitation record.

These observations are consistent with the hypothesis first postulated by Hepburn & Radloff (1998), namely that honeybees have facilitated the widespread dispersal of their forage plants in Africa. Honeybees must also therefore have had a significant impact on frugivores and seed predators. Of the 21 best represented honeybee plant genera, more than half are centred on the fynbos biome, which may reflect the species diversity of the biome and/or the relative amount of research effort in the past.

The nectar sugar compositions of most honeybee forage plants are either hexose- or sucrose-dominant. Comparative tests have shown that sucrose is preferred by honeybees to other sugars (Wykes, 1952; Waller & Buchman, 1981). As sucrose-dominated nectars have not been found in this study to occur as frequently as expected in relation to the above studies, it is assumed here that other factors play a more important role in determining the attractiveness of nectars to honeybees in South Africa. Free (1993) suggested that concentration and volume were the most important factors governing the value of nectar to honeybees, which may explain the above result.

8.3. Flowering phenology of South African honeybee forage plants

The flowering phenology of the honeybee forage plants is the primary determinant of the availability of nectar and pollen. Various climatic and biological factors may modify the availability and/or attractiveness of the floral rewards on offer. Flowering in the null honeybee flora reached a climax in spring (October) with a subsidiary peak in late summer (March). The phenological minimum occurred in early winter (May). The flowering phenologies of the different reward categories of the indigenous forage plants are all significantly and positively correlated at the 0.05 level. Similarly, species offering both rewards are significantly and positively correlated with the flowering phenology of the null flora. The same results were obtained for correlations between the different reward categories of the exotic forage plants in South Africa. The type of reward on offer therefore does not appear to have played a significant role in the evolution of flowering times in the honeybee flora.

The species comprising the null flora flowered for an average duration of seven months. The distribution of flowering durations for the null flora differed significantly from normality at the 0.05 level, was positively skewed and platykurtic. This indicates that most species probably flower for shorter periods, with the large number of species flowering throughout the year boosting the average calculated duration of the flowering period. All three reward categories for both the indigenous and exotic honeybee forage plants have a flowering duration of between five and seven months. Indigenous plant species utilised for both their nectar and pollen flower for the longest and exotic species utilised only for their pollen flower for the shortest duration. Indigenous and exotic forage plants that only offer nectar as a reward flower on average for longer durations than their counterparts which offer only pollen as a

reward. (Table 4.1). None of the categories have normally distributed flowering durations at the 0.05 level of significance, are positively skewed and platykurtic.

Rathcke & Lacey (1985) have suggested that the duration of flowering is inclined to be shorter in species capable of self-pollination. Alternatively, they suggested that a spatial or temporal dearth of resources necessary for seed development may lead to prolonged flowering. If nectar concentration and volume are of greater significance than nectar composition, as alluded to in section 8.2 above, forage plants offering only pollen as a reward may have very little and/or low concentrations of nectar available. If this is true it may indicate that in some forage plants the selfing pathway has been adopted *in lieu* of the energetically more costly production of nectar. As the distributions of the flowering durations for indigenous forage plants for all reward categories are positively skewed, it would appear to indicate that there has been directional selection towards shorter flowering regimes. However, as exotic forage plants show the same trend this argument becomes less convincing. These apparently contradictory results could be attributed to phylogenetic constraint if the different reward categories are composed of species with similar taxonomic affinities. Alternatively, the results may indicate similar selection pressures have been experienced by the forage plants within each reward category in the past in different geographical areas of origin. The platykurtic (dispersed) nature of the flowering durations within each reward category may be indicative of competition for pollination within each reward category or an attempt to avoid inter-specific pollination. Divergent inter-specific flowering regimes within a plant community have been ascribed to both pollinator-limitation and inter-specific pollination (Rathcke & Lacey, 1985).

Of the three families which met the selection criteria for further analysis in this study, namely the Asteraceae, Ericaceae and Fabaceae, the first and last were significantly ($p < 0.05$) and positively correlated, while the Ericaceae were insignificantly ($p > 0.05$) and negatively correlated with both the Asteraceae and the Fabaceae. The indigenous and exotic Asteraceae are insignificantly ($p < 0.05$) positively correlated, while the corresponding categories of the Fabaceae are significantly ($p < 0.05$) and positively correlated. The flowering phenologies of both the Asteraceae and Fabaceae are significantly ($p < 0.05$) and positively correlated with the flowering phenology of the null flora. These results would appear to indicate that the indigenous Asteraceae and Fabaceae may be competing for pollinators or respond to similar flowering stimuli. Similarly, the indigenous and exotic Fabaceae appear to be in competition for pollinators. As the indigenous and exotic Asteraceae are not significantly correlated it would appear that they do not respond to the same flowering stimuli or are phylogenetically constrained in their flowering times. Alternatively it may indicate that the exotic Asteraceae in South Africa have evolved different flowering regimes in widely dispersed areas of origin.

The indigenous species of Asteraceae and Fabaceae have longer average flowering durations than the corresponding exotic species. The average flowering duration for species within the indigenous Asteraceae and Ericaceae is longer, but that for the indigenous Fabaceae shorter than that of the null flora. The extended nature of the indigenous flowering durations within the Asteraceae and Fabaceae in relation to their exotic counterparts may reflect an adaptation amongst the local forage plants to harsher environmental conditions in their respective areas of origin. For example, a spatial or temporal dearth of resources necessary for seed development (*sensu* Rathcke & Lacey, 1985).

The Shapiro-Wilk's (W) test for normality indicated that the flowering durations of the

indigenous Ericaceae and Fabaceae are normally distributed, while the indigenous Asteraceae are not. The distributions for the indigenous Asteraceae and Ericaceae are negatively skewed and platykurtic, whereas the distribution of flowering durations for the indigenous Fabaceae is positively skewed and leptokurtic. As the distribution of the flowering durations for the Fabaceae is both normal and leptokurtic, they appear to have been the subject of stabilising selection for this trait. In contrast, the opposite appears to be true for the indigenous Asteraceae, where directional selection appears to be favouring extended flowering durations. The dispersed nature of their flowering durations indicates a wide variety of flowering durations are pursued by the constituent species. The extended length of the flowering durations amongst the indigenous Asteraceae may reflect a tendency of these species to be pioneers which quickly colonise disturbed or marginal environments. By extending their flowering times they may increase their chances of seed development and hence propagation in these environments relative to other species. The flowering durations within the indigenous Ericaceae do not appear to have been the exposed to significant selection.

Of the 30 species pairs which fulfilled the criteria for selection, 23 occurred in sympatry, 5 in allopatry and 2 in possible parapatry. Excluding the species pairs which had complete overlap of flowering times or with one species which flowered year round, nine of the 30 species pairs which were significantly ($p < 0.05$) correlated. Two of these nine species pairs were negatively correlated, while the rest were positively correlated. Both of the species pairs in parapatry and two of the five species pairs in allopatry are significantly ($p < 0.05$) and positively correlated. This excludes the two allopatric species pairs in which one of the species flowers all year round. Of the remaining five significantly ($p < 0.05$) correlated species pairs in sympatry three are positively correlated, while two are negatively correlated. This excludes species pairs with

identical flowering times or pairs where one species flowers all year round. In more than two-thirds of the species pairs one species flowers for at least a 25% shorter duration than the other.

Interspecific differences in the time of flower production and fruit availability in the sympatric and myrmecochorous *Agathosma stenopetala* and *A. apiculata* have been attributed to past competition for agents of pollination and dispersal (Pierce, 1984). The two negatively correlated species pairs that occur in sympatry in this study (*Crassula arborescens* - *C. ovata* and *Euclea racemosa* - *E. tomentosa*) could reflect a similar cause. All the remaining significantly positively correlated species pairs could represent examples of facilitation by the species, a response to similar flowering stimuli and/or evolution of a different mechanism to avoid competition for pollinators. Examples of possible mechanisms include making similar rewards available at different times of the day or extension of the duration of flowering. As mentioned above the latter is evident in two-thirds of the species pairs, where one species flowers for a 25% shorter duration than its counterpart.

There is no statistically significant ($p < 0.05$) correlation between the flowering phenology of the *Eucalyptus* species studied and the indigenous honeybee (all rewards) or null flora's flowering phenologies. Only half of the selected *Eucalyptus* species had significantly ($p < 0.05$) and positively correlated flowering phenologies between Australia and South Africa. In all species except *E. platypus*, flowering was longer in South Africa than Western Australia. The *Eucalyptus* flower on average for 8 months per annum in South Africa. The distribution of flowering durations is significantly ($p < 0.01$) positively skewed and platykurtic. This implies that flowering within the *Eucalyptus* species visited by honeybees tends to occur for shorter rather than longer durations and that there are a wide variety of flowering durations

displayed by these species. The longer flowering durations in South Africa may represent a release from the competitive constraints for resources which they may experience in Australia.

Evidence for the phylogenetic constraint of flowering phenologies amongst indigenous honeybee forage plants is equivocal. Two possible explanations were suggested in Chapter 4, namely that honeybees select species with similar flowering times or that it represents an effect of selection by them for another floral trait such as nectar and pollen quality. There is evidence for both competition and facilitation within different indigenous species pairs. The presence of such a high percentage of exotic plant species in the South African honeybee flora is both beneficial and costly. *Eucalyptus* species in particular have been recognised for their economic importance to South Africa's commercial beekeepers. Nevertheless, the flowering phenologies of the exotic species have considerable potential to disrupt the pollination of indigenous forage plants. For example, the flowering phenologies of *Eucalyptus* and the indigenous Fabaceae are significantly ($p < 0.05$) and positively correlated. Ironically, honeybee pollination may have exacerbated the threat posed to the indigenous flora by the exotic species as they are known to visit at least some of the species of alien invaders (see Appendix 3.A).

The following generalisations therefore appear to be applicable to honeybee forage plants within South Africa:

- A. Flowering phenologies are bimodal with a peak in early summer and a subsidiary peak in late summer.
- B. The durations of flowering regimes are positively skewed and platykurtic.

8.4. Geographical variation in intra-annual changes in hive weight

Scale-hive records from 25 localities were used to determine the extent of geographical

variation in intra-annual changes in hive weight. These changes in hive weight were taken to represent fluctuations in the level of honey reserves within the colonies.

In *Procedure 1* the monthly variations in honey stores were found to be significantly and positively correlated between only one of a possible eight combinations, namely High Bank and Dunnottar. In contrast, at Duiwelskloof No.2 and the University of Pretoria Experimental Farm where two scale-hive records were kept simultaneously, the records were positively correlated at each locality. The correlation was significant at the former and marginally insignificant at the latter. This may have been an artefact of the small sample size ($n = 4$) as the correlation was very strong (Spearman $R = 0.95$). These results would appear to indicate that honey yields are site specific and represent responses of the honeybee forage plants and foragers to local environmental conditions.

In *Procedure 2* statistically significant ($p < 0.05$) correlations between the intra-annual variations in honey reserves were only recorded between two of a possible 15 combinations, namely between Dunnottar and High Bank and Dunnottar and Prinsrivier. This supports the results obtained using *Procedure 1*, namely that honey yields reflect local and not regional conditions.

No statistically significant ($p < 0.05$) correlations in the intra-annual variations in hive weight were detected between the biomes investigated. This result appears to corroborate those reported above. Climate via its effect on both flowering, nectar quality and quantity and foraging may therefore be the most important factor which determines the extent of honey stored by a colony of honeybees.

The general lack of inter-site and presence of intra-site correlation would appear to indicate marked geographical differences in the intra-annual variation of honey reserves in South Africa. Further research is required to determine whether these geographical differences

are due to botanical and/or climatic influences. As the extreme annual monthly maxima invariably exceed the minima at all the localities investigated, it would appear that the lower limit is constrained by the tendency of colonies to abscond in adverse conditions. The greatest monthly losses in hive weight usually occurred in spring or early summer, except at Prinsrivier where it occurred in June. This could be attributed to depletion of the honey stores by mid-winter and the build-up of worker brood and pre-foraging age bees (consumers) within a colony. Similarly, the greatest monthly losses in hive weight occurred in spring or early summer in the savanna, grassland and fynbos biomes. The ranges in hive weights were largest in the savanna and smallest in the fynbos biomes, which could indicate that colonies in the former tend to be larger than those in the latter. In New Zealand the quantity of honey produced per colony and per individual increases in sympathy with an increase in the size of the adult worker population (Crane, 1990). The summed duration of the two honey flow seasons and their potential cumulative gains are greater than the corresponding values for either of the single honey flow seasons in the grassland or fynbos biomes. The lack of geographical correlation in the intra-annual variation in honey stores and the near absence of any statistically significant ($p < 0.05$) honey related intra-annual intra-colonial correlations may indicate that the former is more important than the latter for the determination of the level of honey reserves within a colony.

8.5. Colony demography

As nectar and pollen serve the nutritional needs of honeybees one could anticipate correlations between these rewards and various colony traits, such as the area of worker and drone brood. At the Andries Vosloo Kudu Reserve the mean monthly levels of honey (uncapped + capped),

uncapped honey and capped honey stores were lowest in September and greatest in February (Table 6.9). In contrast the mean monthly area covered by pollen stores is lowest in April and greatest in October.

The areas of uncapped and capped honey are each significantly positively correlated with the total area covered by honey filled comb. Only one other colony trait was correlated with the area covered by uncapped and capped honey or the area covered by all honey filled comb. The area of capped honey was significantly ($p < 0.05$) and positively correlated with the area covered by drone comb. The pollen stores are only negatively correlated with the total comb area, but positively correlated with the percentage of comb in use, area of unsealed and sealed worker brood, total area of worker brood, area of sealed drone brood and total area of drone brood.

It therefore seems likely that extra-colonial conditions have a greater influence on the level of honey reserves than intra-colonial conditions. These results are similar to those obtained by Fewell & Winston (1996) in British Columbia who found that the level of honey stores had no effect on the pollen stores or brood present. In contrast the results for pollen stores are consistent with Hepburn & Radloff's (1998) assertion that follow-flow brood-rearing is typical of tropical African conditions. This contrasts with data for the Cape Peninsula (Hepburn & Radloff, 1998 p.144), where significant correlations between the level of pollen stores and areas of worker and drone brood were absent. However, both of the latter categories were significantly correlated with the number of plant species in flower.

8.6. The influence of climate on honey reserves: a case study of two scale-hive records from the University of Pretoria Experimental Farm

Only one statistically significant correlation was found between either scale hive record from the University of Pretoria Experimental Farm and any of the selected climatic variables. The changes in hive weight associated with one record (H42) were significantly ($p < 0.05$) negatively correlated with the rainfall recorded at the experimental farm. This negative effect of rainfall on hive weight corroborates the results obtained by Munro (1929) and Jorgensen & Markham (1946).

Autocorrelations were detected at one (H42 & H47), two (H42 & H47), three (H47), four (H47) and five (H47) month periods. No positive or negative cross-correlations > 0.5 were detected for any lag period between either scale-hive record and the selected climatic variables investigated.

The results of the single series fourier analysis of the monthly changes in hive weight for each scale-hive record showed that neither scale-hive record had a period with the five largest periodogram values in common. In both instances these values represent multiples of one another or very close approximations to multiples. In the cross-spectrum analysis none of the periods representing the five strongest relationships between either of the two scale-hive records and the selected climatic variables were the same. However, a number of periods occur recurrently in the five strongest relationships between the two scale-hive records and the different climatic variables (i.e. H42, 12.00, 28.00, 63.00, 252.00; H47, 12.11, 15.33, 17.69, 19.17, 32.86, 38.33, 57.50, 115.00, 230.00) (Table 7.3). Like the results obtained for the single series fourier analyses, these periods sometimes represent multiples of one another, such as the two sequences 19.17 - 38.33 and 57.50 - 115.00 - 230.00 associated with the scale-hive

record H47.

The lack of correlations between the scale-hive records and the selected climatic variables may be due to the mild temperature regime or suburban location of the experimental farm. A one month lag period and/or possible seasonal effects were detected for each variable, with the exception of the duration of sunshine, in the autocorrelation analyses. A possible 12 month seasonal period was also identified in the single series fourier analyses for a number of variables. Similarly, 12 months was also the most frequently recurring period in the cross-spectral results for the one scale-hive record (H42). The corresponding period for the other scale-hive record (H47) is 57.60 months, which also represents the most significant period for the SOI. This may indicate a possible link between the two phenomena *via* the effect the oscillation has on rainfall. El Niño events in South African interior are usually associated with drier than average conditions (Joubert, 1998). Ashton *et al.* (1988) reported a clear relationship between El Niño events and the flowering phenology of Dipterocarpaceae in parts of Malaysia. Cramb (1997), commenting on the situation in Western Australia, appears to have been unable to detect any meaningful connection between the SOI and honey production. The present study may be the first which has identified a possible link between these two phenomena.

The paucity of correlations between the changes in hive weight and the climatic variables investigated in this study could be a consequence of the monthly time interval selected for the analyses. A similar set of analyses as those carried out here needs to be applied to daily data.

8.7. Conclusion

Any activities which have an impact on the landscape have the potential to affect honeybees and/or their forage plants. For example, afforestation can substantially alter the foraging environment for honeybees and possibly the likelihood of pollination of species in the surrounding indigenous plant communities. Honeybee crop or plant pollination may also enhance yields for commercial farmers and facilitate rural food security. While this study has attempted to document, synthesise and identify the associations between honeybees, their forage plants and the climate much work remains to be done. This study provides the most extensive list of honeybee forage plants in South Africa and has considered the largest number of scale-hive records in any study done in the country. The study also represents the first attempt at either a phylogenetic analysis or characterisation of the nectar compositions of the honeybee forage plants in South Africa. In addition, this study has considered a greater number of climatic variables than most other studies of a similar nature. Future research needs to carry out systematic studies on the nature of the relationship between honeybees and their forage plants, particularly in view of the possible implications exotic plants may have for the pollination of local flora. The relative preferences for different plant species in terms of their nectar and pollen rewards on offer and the effects of climate on the flowering phenologies of the forage plants also needs to be ascertained.

8.8. References

Acutt, P. 1988. Observations of beekeeping in the Richmond area. *South African Bee Journal*, 60, 61-62.

Aird, W. 1943. District notes. *The South African Bee Journal*, 18, 10.

Anderson, R.H., Buys, B. and Johannsmeier, M.F. 1983. *Beekeeping in South Africa*. Bulletin 394, Department of Agricultural Technical Services, Pretoria, 207 pp..

Anonymous. 2001. *Abstract of Agricultural Statistics*, National Department of Agriculture, South Africa, 112 pp..

Arnold, T.H. and Musil, K.J. 1983. A preliminary survey of primitive crops cultivated in the northern Transvaal of South Africa. *Bothalia*, 14, 595-601.

Ashton, P.S. Givnish, T.J. and Appanah, S. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *The American Naturalist*, 132, 44-66.

Bond, W.J. 1997. Fire. Chapter 18. In *Vegetation of Southern Africa*, Cowling, R.M., Richardson, D.M. and Pierce, S.M. (Eds), Cambridge University Press, Cambridge, 421-446.

Cramb, J. 1997. Climatic influences on honey production. *The Australasian Beekeeper*, 98, 406-412.

Crane, E. (Ed). 1975. *Honey: a comprehensive survey*. Heinemann, London.

- Crane, E. 1990. Bees and beekeeping: science, practice and world resources. Heinemann Newnes, Oxford, 614 pp..
- Crane, E. and Walker, P. 1984. Pollination directory for world crops. International Bee Research Association, Gerrards Cross, 183 pp..
- Cruden, R.W., Hermann, S.M. and Peterson, S. 1983. Patterns of nectar production and plant-pollinator coevolution. Chapter 3. In Bentley, B. and Elias, T. (Eds). The biology of nectaries. Columbia University Press, New York, 80-125.
- Danka, R.G., Hellmich, R.L. (II), Rinderer, T.E. and Collins, A.M. 1987. Diet-selection ecology of tropically and temperately adapted honey bees. *Animal Behaviour*, 35, 1858-1863.
- Esler, K.J. 1999. Plant reproductive ecology. Chapter 8. In Dean, W.R.J. and Milton, S.J. (Eds), The Karoo: ecological patterns and processes. Cambridge University Press, p.123-144.
- Fewell, J.H. and Winston, M.L. 1996. Regulation of nectar collection in relation to honey storage levels by honey bees, *Apis mellifera*. *Behavioral Ecology*, 7, 286-191.
- Fletcher, D.J.C. 1978. The african bee, *Apis mellifera adansonii*, in Africa. *Annual Review of Entomology*, 23, 151-171.
- Free, J.B. 1993. Insect pollination of crops. 2nd Edition. Academic Press, London, 684 pp..

- Frost, P.G.H. 1984. The responses and survival of organisms in fire-prone environments. Chapter 13. In Ecological effects of fire in South African ecosystems, Booysen, P. de V. and Tainton, N.M., Ecological Studies 48, Springer-Verlag, Berlin, 274-309.
- Garin, H. 1931. Morokwen (Bechuanaland) Records. The South African Bee Journal, April, 15-18.
- Gerlach, J. 1985. The dependence of honey-bee behaviour on weather - shown by the results of weighing bee-hives in the period of 1969 to 1978 in the region of the Beekeepers' Association of Hannover. International Journal of Biometeorology, 29, 67-85.
- Hambleton, J.I. 1925. The effect of weather upon the change in weight of a colony of bees during the honey flow. United States Department of Agriculture, Department Bulletin No. 1339, 52 pp..
- Hepburn, H.R. 1992. "Follow-flow" brood rearing in *capensis* and *scutellata*. South African Bee Journal, 64, 104-109.
- Hepburn, H.R. 1998. Reciprocal interactions between honeybees and combs in the integration of some colony functions in *Apis mellifera* L.. Apidologie, 29, 47-66.
- Hepburn, H.R., Hugo, J.J., Mitchell, D., Nijland, M.J.M. and Scrimgeour, A.G. 1984. On the energetic costs of wax production by the african honeybee, *Apis mellifera adansonii*. South African Journal of Science, 80, 363-368.

- Hepburn, H.R. and Jacot Guillarmod, A. 1991. The Cape honeybee and the fynbos biome. *South African Journal of Science*, 87, 70-73.
- Hepburn, H.R. and Radloff, S.E. 1998. *Honeybees of Africa*. Springer-Verlag, Berlin, 370 pp..
- Hilton-Taylor, C. 1996a. Red Data List of southern African plants. *Strelitzia*, 4, 117 pp..
- Hilton-Taylor, C. 1996b. Red Data List of southern African plants. 1. Corrections and additions. *Bothalia*, 26, 177-182.
- Jaycox, E.R. 1970a. Honey bee foraging behavior: responses to queens, larvae, and extracts of larvae. *Annals of the Entomological Society of America*, 63, 1689-1694.
- Jaycox, E.R. 1970b. Honey bee queen pheromones and worker foraging behavior. *Annals of the Entomological Society of America*, 63, 222-228.
- Johannsmeier, M.F. 1988. Beekeeping potential of native flora of South Africa. *South African Bee Journal*, 60, 98-108.
- Johannsmsier, M.F. 1995. Beeplants of the south-western Cape: nectar and pollen sources of honeybees. Department of Agriculture, Pretoria, 59 pp..
- Johannsmeier, M. and Allsopp, M. 1995. Beeplants for South African suburban gardens. *South African Bee Journal*, 67, 70-75.

- Jorgensen, C. and Markham, F. 1946. Weather factors influencing honey production. Michigan State College, Agricultural Experiment Station, Section of Horticulture, East Lansing, Special Bulletin 340, 22 pp..
- Joubert, A. 1998. El Niño, La Niña and summer rainfall variability over South Africa. South African Journal of Science, 94, 2.
- Kevan, P.G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. Agriculture, Ecosystems and Environment, 74, 373-393.
- Kevan, P.G. and Baker, H.G. 1983. Insects as flower visitors and pollinators. Annual Review of Entomology, 28, 407-453.
- Kochmer, J.P. and Handel, S.N. 1986. Constraints and competition in the evolution of flowering phenology. Ecological Monographs, 56, 303-325.
- Krishnamurti, B. 1939. A brief analysis of eleven years (1928-1938) records of scale-hives, at the Rothamsted bee laboratory. The Bee World, 20, 121-123.
- May, A.F. 1961. Beekeeping in southern Africa. Haum, Cape Town, 210 pp..
- McLellan, A.R. 1977. Honeybee colony weight as an index of honey production and nectar flow: a critical evaluation. Journal of Applied Ecology, 14, 401-408.

Milton, S.J. 1992. Effects of rainfall, competition and grazing on flowering of *Osteospermum sinuatum* (Asteraceae) in the arid Karoo rangeland. Journal of the Grassland Society of Southern Africa, 9, 158-164.

Mitchener, A.V. 1955. Manitoba nectar flows 1924-1954, with particular reference to 1947-1954. Journal of Economic Entomology, 48, 514-518.

Moffett, J.O. and Parker, R.L. 1953. Relation of weather factors to nectarflow in honey production. Technical Bulletin 74, Kansas Agricultural Experiment Station, Manhattan, Kansas, 27 pp..

Munro, J.A. 1929. A study of the factors influencing the yield of honey during the main nectar flow. Journal of Economic Entomology, 22, 518-521.

Oertel, E. 1946. Effect of temperature and relative humidity on sugar concentration of nectar. Journal of Economic Entomology, 39, 513-515.

Owen-Smith, N. & Danckwerts, J.E. 1997. Herbivory. Chapter 17. In Vegetation of Southern Africa, Cowling, R.M., Richardson, D.M. and Pierce, S.M. (Eds), Cambridge University Press, Cambridge, 397-420.

Park, O.W. 1929. The influence of humidity upon sugar concentration in the nectar of various plants. Journal of Economic Entomology, 22, 534-544.

Percival, M. 1965. *Floral biology*. Pergamon Press, Oxford.

Phillips, J.F.V. 1926. General biology of the flowers, fruits, and young regeneration of the more important species of the Knysna forests. *South African Journal of Science*, 23, 366-417.

Pierce, S.M. 1984. A synthesis of plant physiology in the Fynbos Biome. *South African National Scientific Programmes Report*, 88, 57 pp..

Rathcke, B. and Lacey, E.P. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics*, 16, 179-214.

Rebelo, A.G. 1987. Management implications. Chapter 9. In *A preliminary synthesis of pollination biology in the Cape flora*, Rebelo, A.G. (Ed), *South African National Scientific Programmes Report*, 141, 193-211.

Schnettler, E.A. 1946. Honey production record. *The South African Bee Journal*, 21, 10.

Scullen, H.A. 1940. Relative humidity and nectar concentration in fireweed. *Journal of Economic Entomology*, 33, 870-871.

Sillett, T.S., Holmes, R.T. and Sherry, T.W. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science*, 288, 2040-2042.

Smit, G.N. and Rethman, N.F.G. 1992. Inter-related floristic changes associated with different long-term grazing treatments in Sourish Mixed Bushveld. *Journal of the Grassland Society of Southern Africa*, 9, 76-82.

Smith, F.G. 1960. *Beekeeping in the tropics*. Longmans, London, 265 pp..

Smith-Ramírez, C. and Armesto, J.J. 1994. Flowering and fruiting patterns in the temperate rainforest of Chiloé, Chile - ecologies and climatic constraints. *Journal of Ecology*, 82, 353-365.

Steyn, H.M., van Rooyen, N., van Rooyen, M.W. and Theron, G.K. 1996. The phenology of Namaqualand ephemeral species. The effect of water stress. *Journal of Arid Environments*, 33, 49-62.

Stock, W.D., van der Heyden, F. And Lewis, O.A.M. 1992. Plant structure and function. Chapter 9. In *The Ecology of Fynbos: nutrients, fire and diversity*, Cowling, R.M. (Ed), Oxford University Press, Cape Town, 226-240.

Szabo, T.I. 1980. Effect of weather factors on honeybee flight activity and colony weight gain. *Journal of Apicultural Research*, 19, 164-171.

Szabo, T.I. 1982. Phenotypic correlations between colony traits in the honey bee. *American Bee Journal*, 122, 711-716.

- Szabo, T.I. 1996. Scale colony records as indicators for nectar-producing plants in southern Ontario. *American Bee Journal*, 136, 733-736.
- Szabo, T.I. and Mueller, A.E. 1996. Factors affecting the weight changes of honey bee colonies. *American Bee Journal*, 136, 417-419.
- Thompson, J.D. 1980. Skewed flowering distributions and pollinator attraction. *Ecology*, 61, 572-579.
- Vogel, S. 1983. Ecophysiology of zoophilic pollination. In Pirson, A. and Zimmermann, M.H. (Eds), *Encyclopedia of Plant Physiology, New Series, Volume 12C*, 559-624.
- Waller, G.D. and Buchman, W.W. 1981. Use of honey-sac load and dance characteristics of worker honeybees to determine their sugar preferences. *Journal of Apicultural Research*, 20, 23-27.
- Wykes, G.R. 1952. The preferences of honeybees for solutions of various sugars which occur in nectar. *Journal of Experimental Biology*, 29, 511-519.

Appendix

Appendix 2.A. Notes on known scale-hive records from southern Africa. The notes are listed in the same order in which they occur in Figure 2.1.

Name: Balgowrie Location: 32°11'S 25°40'E Duration: 1937-1943
1: 50 000 Toposheet: 3225BA Cradock Altitude: -
Beekeeper: W. Aird
Notes: Exact location unknown.

Name: Beluluane Location: 25°55'S 32°24'E Duration: 1939-1941
1: 50 000 Toposheet: - (Mozambique) Altitude: <i>c.</i> 50 m
Beekeeper: Mr F. Crisp
Notes: A railway station or siding <i>c.</i> 16 km from Maputo harbour.

Name: Berg-en-dal Location: 23°45'S 30°03'E Duration: 1983-1992
1: 50 000 Toposheets: 2330CA Duiwelskloof, 2330CC Tzaneen Altitude: <i>c.</i> 950 m
Beekeeper: Mr George Altona
Notes: Records taken by “Robby” an employee of Mr Altona’s. (M.F. Johannismeier, pers.comm.1996/09/13).

Name: Bloemfontein Location: 29°08'S 26°13'E Duration: 1946-1947
1: 50 000 Toposheets: 2926AA Bloemfontein, 2926AB Maselspoort Altitude: -
Beekeeper: W. Walker
Notes: -

Name: Boschfontein Location: 25°47'S 27°16'E Duration: 1942-1946
1: 50 000 Toposheet: 2527CD Rex Altitude: c. 1200 m
Beekeeper: Mr C.M. Robinson
Notes: -

Name: Canowie Farm Location: 30°06'S 30°02'E Duration: 1983-1986
1: 50 000 Toposheet: 3030AA Ixopo Altitude: c. 1300 m
Beekeeper: Lianne McGregor
Notes: -

Name: Cape Point Nature Reserve Location: 34°16'S 18°26'E Duration: 1948-1960
1: 50 000 Toposheet: 3418AB & AD Kaapse Skiereiland Altitude: c. 50 m
Beekeeper: Miss J. Minicki
Notes: -

Name: Compton Ranch Location: 27°15'S 24°29'E Duration: 1931-1941
1: 50 000 Toposheets: 2724AB Geluk, 2724AD Steekdorings, 2724BA Naples, 2724BC Pudimoe Altitude: c. 1350 m
Beekeeper: Mr Frank Short
Notes: -

Name: Duiwelskloof No.1 Location: 23°42'S 30°08'E Duration: 1943-1944
1: 50 000 Toposheet: 2330CA Duiwelskloof Altitude: c. 900 m
Beekeeper: Mr J.D. van der Merwe
Notes: Approximately 11 km south of Mooihoek.

Name: Duiwelskloof No.2 Location: 23°43'S 30°08'E Duration: 1929-1931
1: 50 000 Toposheet: 2330CA Duiwelskloof Altitude: -
Beekeeper: Mr A.W. Murray
Notes: Approximately 14 km south of Mooihoek.

Name: Dunottar Location: 26°21'S 28°26'E Duration: 1945-1948
1: 50 000 Toposheet: 2628AD Springs Altitude: c. 1600 m
Beekeeper: Mr S. Ring
Notes: -

Name: Gordon's Bay Location: 34°10'S 18°51'E Duration: 1976-1983
1: 50 000 Toposheet: 3418BB Somerset West Altitude: -
Beekeeper: Mr Clive Haynes-Swart
Notes: -

Name: Grenshoek Location: 23°47'S 30°04'E Duration: 1941-1943
1: 50 000 Toposheets: 2330CA Duiwelskloof, 2330CC Tzaneen Altitude: c. 850 m
Beekeeper: Mr "Jackie" van der Merwe
Notes: This appears to be the same beekeeper who kept the scale-hive record for Duiwelskloof No.1, as the Grenshoek record ends in October 1943 while the former commences in November 1943. This now appears to be the Sepakoe Tea Estate.

Name: Grootvadersbosch Location: 34°00'S 20°50'E Duration: 1977-1983
1: 50 000 Toposheets: 3320DD Warmwaterberg, 3420BB Heidelberg (Kaap) Altitude: -
Beekeeper: Major-General Graham D. Moodie
Notes: -

Name: Helshoogte Location: 33°55'S 18°56'E Duration: 1931-1938
1: 50 000 Toposheet: 3318DD Stellenbosch Altitude: -
Beekeeper: Mr F.H Cooper
Notes: -

Name: High Bank Location: 30°21'S 29°15'E Duration: 1943-1948
1: 50 000 Toposheets: 3029AC Cedarville, 3029AD Franklin Altitude: c. 1500 m
Beekeeper: Mr W. Calder Potts
Notes: -

Name: Hilton Road Location: 29°33'S 30°18'E Duration: 1953-1960
1: 50 000 Toposheet: 2930CB Pietermaritzburg Altitude: c. 1150 m
Beekeeper: J.L. Peel
Notes: -

Name: Kalkfontein Location: 27°38'S 27°02'E Duration: 1986-1990
1: 50 000 Toposheet: 2727CA Kroonstad Altitude: c. 1350 m
Beekeeper: Dr P.F.A. van Lingen
Notes: -

Name: Keimoes Location: 28°42'S 21°01'E Duration: 1939-1945
1: 50 000 Toposheets: 2820DB Keimoes, 2821CA Kanoneiland Altitude: c. 750 m
Beekeeper: G.H. Compion
Notes: -

Name: Kenwyn Location: 33°57'S 22°27'E Duration: 1939-1944
1: 50 000 Toposheet: 3322CD George Altitude: -
Beekeeper: Mrs R.G. Brydone
Notes: Location assumed to be the present suburb of Heatherlands, George.

Name: Kosi Bay Location: 26°57'S 32°50'E Duration: 1984-1985
1: 50 000 Toposheet: 2632DD Kosibaa Altitude: -
Beekeeper: Dr Robert & Diane Kyle
Notes: -

Name: Kraaifontein Location: 33°51'S 18°43'E Duration: 1940-1942
1: 50 000 Toposheets: 3318DC Belville, 3318DD Stellenbosch Altitude: c. 100 m
Beekeeper: Mr C.A.M. (Montie) Andrews
Notes: Montie Andrews appears to have kept scale-hive records at Peach Farm (1929-1932), Port Durnford (1933-1939) and Kraaifontein (1940-1942). This apiary formerly belonged to A.J. Attridge.

Name: Mooihoek Location: 23°37'S 30°10'E Duration: 1932-1938
1: 50 000 Toposheet: 2330CA Duiwelskloof Altitude: c. 750 m
Beekeeper: Mr J. Elphinstone
Notes: -

Name: Morokwen(g) Location: 26°08'S 23°46'E Duration: 1924-1930
1: 50 000 Toposheets: 2623BA Kgareyatlhose, 2623BB Morokweng Altitude: c. 1150 m
Beekeeper: Mr W.H. Edmunds
Notes: Unclear whether the data in Garin (1931) refers to a scale-hive record or not. Garin, H. (1931). Morokwen (Bechuanaland) records. The South African Bee Journal, 6, 1, 15-18.

Name: Nhlazatshe Location: 28°10'S 31°14'E Duration: 1931-1934
1: 50 000 Toposheets: 2831AA Nhlazatshe, 2831AB Mahlabatini Altitude: -
Beekeeper: Mr T.E. Quequin
Notes: -

Name: Noorspoort Location: 33°18'S 24°22'E Duration: 1979-1986
1: 50 000 Toposheet: 3324AD Steytlerville Altitude: c. 1450 m
Beekeeper: Dr George H. Craven
Notes: -

Name: Oudtshoorn Location: 33°37'S 22°13'E Duration: 1944-1948
1: 50 000 Toposheet: 3322CA Oudtshoorn Altitude: -
Beekeeper: Mr J.H. Louw
Notes: See notes for Prinsrivier.

Name: Peach Farm Location: 28°39'S 31°29'E Duration: 1929-1932
1: 50 000 Toposheets: 2831CB Melmoth, 2831DA Nkwalini Altitude: c. 650 m
Beekeeper: Mr C.A.M. (Montie) Andrews
Notes: See Kraaifontein and Port Durnford scale-hive notes.

Name: Piet Retief Location: 27°00'S 30°48'E Duration: 1983-1985
1: 50 000 Toposheets: 2630DD Kemp, 2730BB Piet Retief Altitude: -
Beekeeper: Mr Arthur Paquet
Notes: -

Name: Poortjiesfontein Location: 29°38'S 26°01'E Duration: 1973-1986
1: 50 000 Toposheets: 2925DB Edenburg, 2926CA Reddersburg Altitude: c. 1350 m
Beekeeper: A. Herrmann
Notes: Wurasoord = 29°37'S 26°00'E.

Name: Port Durnford Location: 28°55'S 31°50'E Duration: 1933-1939
1: 50 000 Toposheet: 2831DD Felixton Altitude: -
Beekeeper: Mr C.A.M (Montie) Andrews
Notes: Follows on from his Peach Farm scale-hive record. "Inyosi apiaries" marked on the map west of the intersection between the main road and side-road to Mon Desir. See Kraaifontein scale-hive notes.

Name: Prinsrivier Location: 33°30'S 20°51'E Duration: 1948-1953
1: 50 000 Toposheets: 3320BD Floriskraal, 3320DB Plathuis Altitude: c. 450 m
Beekeeper: J.H. Louw
Notes: Appears to be the same beekeeper who kept the Oudtshoorn scale-hive records.

Name: Rust-de-Winter Research Station Location: 25°11'S 28°37'E Duration: 1937-1940
1: 50 000 Toposheet: 2528BA Rust de Winter Altitude: c. 1000 m
Beekeeper: -
Notes: -

Name: Swartkopskloof Location: 29°36'S 30°18'E Duration: 1940-1947
1: 50 000 Toposheet: 2930CB Pietermaritzburg Altitude: -
Beekeeper: Mr C.S. Hayter
Notes: Location of Swartkopskloof needs to be checked.

Name: Taylor's siding/halt Location: 29°41'S 30°11'E Duration: 1927-1935
1: 50 000 Toposheet: 2930CA Merrivale Altitude: c. 1100 m
Beekeeper: Mr C.S. Hayter
Notes: -

Name: The Springs Location: 33°37'S 25°27'E Duration: 1976-1990
1: 50 000 Toposheet: 3325CB Uitenhage (Noord) Altitude: c. 150 m
Beekeeper: -
Notes: -

Name: Towoomba Research Station Location: 24°54'S 28°20'E Duration: 1984-1995
1: 50 000 Toposheet: 2428CD Warmbad Altitude: c. 1100 m
Beekeeper: -
Notes: -

Name: University of Pretoria Experimental Farm Location: 25°45'S 28°16'E Duration: 1968-1991
1: 50 000 Toposheets: 2528CA Pretoria, 2528CB Silverton, 2528CC Lyttelton, 2528CD Rietvleidam Altitude: c. 1400 m
Beekeeper: Mr M.F. Johansmeier and co-workers.
Notes: -

Name: White River Location: 25°20'S 31°01'E Duration: 1983-1986
1: 50 000 Toposheets: 2530BD Nelspruit, 2531AC Witrivier Altitude: c. 950 m
Beekeeper: Mr T.G. (Tony) Bester
Notes: -

APPENDIX 3.A. SELECTED FLOWERING PHENOLOGIES OF KNOWN HONEYBEE FLORA IN SOUTHERN AFRICA

[N&P = 1, Recorded as a nectar or pollen source]

[*=exotic plant in southern Africa, (**) = unknown whether reference is to exotic and/or indigenous species; X^{1, 2 or 3} = Classification category in Conservation of Agricultural Resources Act 1983,

Proposed Amendment, Notice 2485 of 1999, National Department of Agriculture]

[B=Indicator of bush encroachment (Source: see above)]

All indigenous and exotic species names and species author names according to Arnold & de Wet (1993), except where otherwise indicated.

[AD = Arnold & de Wet (1993), APNI = Australian Plant Names Index, FE = Flora Europaea, IPNI(IK) = Index Kewensis listing in the International Plant Names Index,

and MBG = Missouri Botanical Gardens W3TROPICOS website]

[Flowering times are based on sources A - E. The flowering times of the species below without flowering times therein have been left blank.]

FAMILY	BOTANICAL NAME		VALUE		SOURCE	FLOWERING PHENOLOGY											
	GENUS	SPECIES	N	P		1	2	3	4	5	6	7	8	9	10	11	12
Caprifoliaceae ^{MBG}	<i>Abelia</i>	<i>grandiflora</i> L.	1	1	20												
Caprifoliaceae ^{MBG}	<i>Abelia</i>	x <i>grandiflora</i> (Rovelli ex André) Rehder*	1	1	19, B	1	1	1	1						1	1	1
Makr:aceae ^{MBG}	<i>Abutilon</i>	<i>hybridum</i> hort.	1	1	20												
Fabaceae ^{MBG}	<i>Acacia</i>	<i>acinacea</i> Lindl.*		1	19, B							1	1	1	1		
					3, 19, 20, 29, 41,												
Fabaceae ^{AD}	<i>Acacia</i>	<i>baileyana</i> F. Müll.* ³	1	1	B, C, E							1	1	1	1		
Fabaceae ^{AD}	<i>Acacia</i>	<i>burkei</i> Benth.	1		1, E										1	1	1
Fabaceae ^{AD}	<i>Acacia</i>	<i>caffra</i> (Thunb.) Willd. ^B	1	1	1, 18, 29, 36, C, E	1	1						1	1	1	1	1
Fabaceae ^{AD}	<i>Acacia</i>	<i>cultriformis</i> A. Cunn.*		1	3, 19, 29, 41, B, C							1	1	1	1		
Fabaceae ^{AD}	<i>Acacia</i>	<i>cyclops</i> A. Cunn. ex G. Don* ²		1	19, B, E	1	1	1	1	1				1	1	1	1
Fabaceae ^{AD}	<i>Acacia</i>	<i>dealbata</i> Link* ²		1	29, C, E	1	1	1	1	1	1	1	1	1	1	1	1
Fabaceae ^{AD}	<i>Acacia</i>	<i>decurrens</i> Willd.* ²		1	29, 41, C, E							1	1	1	1		
Fabaceae ^{MBG}	<i>Acacia</i>	<i>drummondii</i> Benth.*		1	19, B								1	1			
Fabaceae ^{AD}	<i>Acacia</i>	<i>erioloba</i> E. Mey.	1	1	36, E									1	1		
Fabaceae ^{AD}	<i>Acacia</i>	<i>hebeclada</i> DC. ^B	1		1, E									1	1	1	
					1, 2, 3, 18, 29, 34,												
Fabaceae ^{AD}	<i>Acacia</i>	<i>karroo</i> Hayne ^B	1	1	35, 36, 41, A, C, E	1	1	1							1	1	1
Fabaceae ^{AD}	<i>Acacia</i>	<i>longifolia</i> (Andr.) Willd.* ¹	1	1	19, 49, B							1	1	1	1		
					3, 19, 29, 41, B, C,												
Fabaceae ^{AD}	<i>Acacia</i>	<i>mearnsii</i> De Wild.* ²	1	1	E								1	1	1	1	1
Fabaceae ^{AD}	<i>Acacia</i>	<i>melanoxylon</i> R. Br.* ²	1	1	19, 29, 41, B, C							1	1	1	1		
Fabaceae ^{AD}	<i>Acacia</i>	<i>mellifera</i> (Vahl) Benth. ^B	1	1	1, 9, 18, 36, 51, A,								1	1	1	1	
Fabaceae ^{AD}	<i>Acacia</i>	<i>nilotica</i> (L.) Willd. ex Del. ^B			23, E											1	1
Fabaceae ^{AD}	<i>Acacia</i>	<i>podalyriifolia</i> A. Cunn. ex G. Don* ³		1	19, 20, 41, B, E					1	1	1					
Fabaceae ^{AD}	<i>Acacia</i>	<i>pycnantha</i> Benth.* ¹	1	1	19, 49, B								1	1	1		
Fabaceae ^{AD}	<i>Acacia</i>	<i>robusta</i> Burch. ^B			29, C, E								1	1	1	1	1
Fabaceae ^{AD}	<i>Acacia</i>	<i>saligna</i> (Labill.) Wendl.* ¹	1	1	19, B							1	1	1	1		
Fabaceae ^{AD}	<i>Acacia</i>	<i>sieberiana</i> DC.	1	1	34, E	1	1	1							1	1	1
Fabaceae ^{AD}	<i>Acacia</i>	<i>terminalis</i> (Salisb.) MacB. ³	1		19, 41, B											1	1
Fabaceae ^{MBG}	<i>Acacia</i>	<i>visite</i> Griseb.*	1	1	19, 20, B										1	1	1
Acanthaceae ^{FE}	<i>Acanthus</i>	<i>mollis</i> L.*		1	19, B												1
Aceraceae ^{MBG}	<i>Acer</i>	<i>buergerianum</i> Miq.*	1	1	19, B								1	1	1		
Aceraceae ^{FE}	<i>Acer</i>	<i>negundo</i> L.*	1	1	19, B								1	1			
Asteraceae ^{AD}	<i>Achillea</i>	<i>millefolium</i> L. sens. lat.*	1	1	19, D, E	1	1	1	1	1						1	1
Asteraceae ^{AD} (Compositae) ^{FE}	<i>Achillea</i>	<i>tomentosa</i> L.*	1	1	19												
Rutaceae ^{AD}	<i>Acmadenia</i>	<i>heterophylla</i> P.E. Glover	1	1	19												
Actinidiaceae ^{MBG}	<i>Actinidia</i>	<i>deliciosa</i> (Sw.) C.F. Liang & A.R. Ferguson*		1	19, B										1	1	
Rutaceae ^{AD}	<i>Adenandra</i>	<i>fragrans</i> (Sims) Roem. & Schultes	1		19												
Rutaceae ^{AD}	<i>Adenandra</i>	<i>uniflora</i> (L.) Willd.	1		19, B					1	1	1	1	1	1	1	
					19, B					1	1	1	1	1	1	1	1

[illegible]

Asteraceae ^{AD}	<i>Arctotis</i>	<i>auriculata</i> Jacq.	1	1	19																
Asteraceae ^{AD}	<i>Arctotis</i>	<i>fastuosa</i> Jacq.	1	1	19, B									1	1						
Asteraceae ^{AD}	<i>Arctotis</i>	<i>stoechadifolia</i> Berg.	1	1	19, B										1	1	1	1	1		
Papaveraceae ^{AD}	<i>Argemone</i>	<i>mexicana</i> L.*		1	2, D, E			1	1	1	1	1	1	1	1	1	1	1	1	1	
Iridaceae	<i>Aristea</i>	spp.		1	19																
Plumbaginaceae ^{FE}	<i>Armeria</i>	<i>maritima</i> (Mill.) Willd.*	1	1	19																
Asteraceae ^{AD}	<i>Artemisia</i>	<i>afra</i> Jacq. ex Willd.		1	19, B, E				1	1	1	1	1	1						1	
Asteraceae ^{MBG}	<i>Artemisia</i>	<i>dracunculus</i> L.*		1	19																
Asclepiadaceae ^{AD}	<i>Asclepias</i>	<i>buchenaviana</i> Schinz			10																
Asclepiadaceae ^{AD}	<i>Asclepias</i>	<i>cancellata</i> Burm. f.	1		19, B					1	1	1	1	1	1	1	1	1	1	1	
Asclepiadaceae ^{AD}	<i>Asclepias</i>	<i>fruticosa</i> L.	1	1	3, 19, E			1	1	1	1					1	1	1	1	1	
Asclepiadaceae ^{AD}	<i>Asclepias</i>	<i>physocarpa</i> (E. Mey.) Schltr.	1		19, B, E			1	1	1	1	1	1	1	1	1	1	1	1	1	
Fabaceae ^{AD}	<i>Aspalathus</i>	<i>angustifolia</i> (Lam.) Dahlg.			19																
Fabaceae ^{AD}	<i>Aspalathus</i>	<i>araneosa</i> L.			19																
Fabaceae ^{AD}	<i>Aspalathus</i>	<i>astroites</i> L.			19																
Fabaceae ^{AD}	<i>Aspalathus</i>	<i>chortophila</i> Eckl. & Zeyh.			10, D			1	1	1	1	1	1	1	1	1	1	1	1	1	1
Fabaceae ^{AD}	<i>Aspalathus</i>	<i>cordata</i> (L.) Dahlg.			19																
Fabaceae ^{AD}	<i>Aspalathus</i>	<i>cymbiformis</i> DC.			19																
Fabaceae ^{AD}	<i>Aspalathus</i>	<i>juniiperina</i> Thunb.			19																
Fabaceae ^{AD}	<i>Aspalathus</i>	<i>laricifolia</i> Berg.			19																
Fabaceae ^{AD}	<i>Aspalathus</i>	<i>linearis</i> (Burm. f.) Dahlg.	1		10, 19, B			1	1	1						1	1	1	1	1	1
Fabaceae ^{AD}	<i>Aspalathus</i>	<i>quinquefolia</i> L.	1		19																
Fabaceae ^{AD}	<i>Aspalathus</i>	<i>spinescens</i> Thunb.			10																
Fabaceae ^{AD}	<i>Aspalathus</i>	<i>spinosa</i> L.			19, D			1	1	1	1	1				1	1	1	1	1	1
Fabaceae ^{AD}	<i>Aspalathus</i>	<i>subtingens</i> Eckl. & Zeyh.			10, 19																
Asteraceae ^{AD}	<i>Athanasia</i>	<i>trifurcata</i> (L.) L.	1	1	10, 19, B			1	1	1	1									1	1
Chenopodiaceae ^{AD}	<i>Atriplex</i>	<i>nummularia</i> Lindl.* ²		1	19, E										1						
Proteaceae	<i>Banksia</i>	spp.*	1	1	19																
Acanthaceae ^{AD}	<i>Barleria</i>	<i>obtusula</i> Nees	1	1	19, B, D, E				1	1	1	1	1	1	1	1	1				
Fabaceae ^{MBG}	<i>Bauhinia</i>	<i>blakeana</i> Dunn*	1	1	19, 20, B			1	1	1	1	1	1	1	1	1	1	1	1	1	1
Fabaceae ^{AD}	<i>Bauhinia</i>	<i>galpinii</i> N.E. Br.	1	1	29, C, E			1	1	1	1	1	1	1	1	1	1	1	1	1	1
Fabaceae ^{AD}	<i>Bauhinia</i>	<i>variegata</i> L.*	1	1	19, 20, B						1	1	1	1	1	1	1	1	1	1	1
Asteraceae ^{AD} (Compositae) ^{FE}	<i>Bellis</i>	<i>perennis</i> L.*	1	1	19, B									1	1	1	1	1			
Asteraceae ^{AD}	<i>Berkheya</i>	<i>carlinifolia</i> (DC.) Rössl.			10																
Asteraceae ^{AD}	<i>Berkheya</i>	<i>fruticosa</i> (L.) Ehrh.			10, 47																
Asteraceae ^{AD}	<i>Berkheya</i>	<i>heterophylla</i> (Thunb.) O. Hoffm.			10																
Bruniaceae ^{AD}	<i>Berzelia</i>	<i>ecklonii</i> Pillans		1	19, B															1	1
					1, 4, 19, 20, 34, A,																
Asteraceae ^{AD}	<i>Bidens</i>	<i>formosa</i> (Bonato) Sch. Bip.*	1	1	B, D			1	1	1	1	1								1	1
Asteraceae ^{AD}	<i>Bidens</i>	<i>pilosa</i> L.*	1	1	19, E			1	1	1	1					1	1	1	1	1	1
Ericaceae ^{AD}	<i>Blaeria</i>	<i>ericoides</i> L.	1	1	19, B			1	1	1	1	1	1	1							
Acanthaceae ^{AD}	<i>Blepharis</i>	<i>extenuata</i> S. Moore			47																
Asteraceae ^{AD}	<i>Blumea</i>	<i>mollis</i> (D. Don) Merr.			40, D, E			1	1	1	1				1	1	1	1	1	1	1
Fabaceae ^{AD}	<i>Bolusanthus</i>	<i>speciosus</i> (H. Bol.) Harms	1	1	3, 29, 41, C, E											1	1	1	1	1	1
Boraginaceae ^{FE}	<i>Borago</i>	<i>officinalis</i> L.*	1	1	19, 20																
Capparaceae ^{AD}	<i>Boscia</i>	<i>albitrunca</i> (Burch.) Gilg & Ben.	1		41, E													1	1	1	1
Proteaceae ^{AD}	<i>Brabejum</i>	<i>stellatifolium</i> L.	1	1	1, 19, A, B			1												1	1
Sterculiaceae ^{MBG}	<i>Brachychiton</i>	<i>acerifolius</i> (Cunn.) Macarthur*	1	1	19, B			1										1	1	1	1
Sterculiaceae ^{MBG}	<i>Brachychiton</i>	<i>discolor</i> F. Muell.*	1	1	19, B														1	1	1
Sterculiaceae ^{MBG}	<i>Brachychiton</i>	<i>populneus</i> (Schott & Endl.) R. Br.*	1	1	19, 20, B			1	1									1	1	1	1
Asteraceae ^{AD}	<i>Brachylaena</i>	<i>discolor</i> DC.	1	1	29, 51, C													1	1	1	
Asteraceae ^{AD}	<i>Brachylaena</i>	<i>neriifolia</i> (L.) R. Br.	1	1	19, B			1	1	1	1										1
Brassicaceae ^{AD} (Cruciferae) ^{FE}	<i>Brassica</i>	<i>napus</i> L.*	1	1	19																
Euphorbiaceae ^{AD}	<i>Bridelia</i>	<i>micrantha</i> (Hochst.) Baill.			23, E														1	1	1

[illegible]

[illegible]

Cunoniaceae ^{AD}	<i>Cunonia</i>	<i>capensis</i> L.	1	1	18, 19, B		1	1	1	1	1								
Lythraceae ^{MBG}	<i>Cuphea</i>	<i>ignea</i> A. DC.*	1		19														
Cornaceae ^{AD}	<i>Curtisia</i>	<i>dentata</i> (Burm. f.) C.A. Sm.	1	1	19, 41, B, E	1	1	1				1	1	1	1	1			
Cornaceae ^{MBG}	<i>Curtisia</i>	<i>faginea</i> W.Ait.	1	1	29, C	1							1	1	1	1			
Fabaceae ^{AD}	<i>Cyclopia</i>	<i>maculata</i> (Andr.) Kies			19, B								1	1					
Rosaceae ^{AD}	<i>Cydonia</i>	<i>oblonga</i> Mill.*	1	1	19, B								1	1					
Asteraceae ^{AD} (Compositae) ^{FE}	<i>Cynara</i>	<i>scolymus</i> L.*	1	1	19														
Poaceae	<i>Cynodon</i>	sp.			1	1													
Boraginaceae ^{AD}	<i>Cynoglossum</i>	<i>amabile</i> Stapf & Drummond*	1	1	19														
Solanaceae ^{AD}	<i>Cyphomandra</i>	<i>betacea</i> (Cav.) Sendtn.*			1	19, B						1	1	1					
Vitaceae ^{AD}	<i>Cyphostemma</i>	<i>hypoleucum</i> (Harv.) Descoings ex Wild & Drum.			40, D		1	1	1	1	1				1	1	1		
Fabaceae ^{AD} (Leguminosae) ^{FE}	<i>Cytisus</i>	<i>decumbens</i> (Durande) Spach*			1	19, 20													
Fabaceae ^{MBG}	<i>Cytisus</i>	<i>proliferus</i> L. f.*			1	29, C							1	1	1	1	1		
Fabaceae ^{AD}	<i>Cytisus</i>	<i>scoparius</i> L.*	1	1	19														
Hamamelidaceae ^{AD} (Asteraceae) ^{MBG}	<i>Dahlia</i>	<i>imperialis</i> Roez l ex Orgies*	1	1	19, 20, B				1	1									
Hamamelidaceae ^{AD} (Asteraceae) ^{MBG}	<i>Dahlia</i>	<i>pinnata</i> Cav.*	1	1	19														
Thymelaeaceae ^{AD}	<i>Dais</i>	<i>cotinifolia</i> L.	1	1	19, B, E	1								1	1	1			
Ranunculaceae	<i>Delphinium</i>	spp.*			1	19													
Hydrangeaceae ^{FE} (Saxifragaceae) ^{MBG}	<i>Deutzia</i>	<i>gracilis</i> Siebold & Zucc.*	1	1	19, B								1	1					
Hydrangeaceae ^{FE}	<i>Deutzia</i>	<i>scabra</i> Thunb.*	1	1	19, B											1	1		
Apiaceae ^{AD}	<i>Deverra</i>	<i>denudata</i> (Viv.) Pfisterer & Podl.			10														
Caryophyllaceae ^{FE}	<i>Dianthus</i>	<i>barbatus</i> L.*	1		19														
Scrophulariaceae ^{AD}	<i>Diascia</i>	<i>vigilis</i> Hilliard & Burt			1	44													
Acanthaceae	<i>Dicliptera</i>	sp.	1		1														
Asteraceae ^{AD}	<i>Didelta</i>	<i>carnosa</i> (L. f.) Ait.	1	1	19, B							1	1	1	1	1	1		
Asteraceae ^{AD}	<i>Didelta</i>	<i>spinosa</i> (L. f.) Ait.			1	19, 47, B				1	1	1	1						
Scrophulariaceae ^{FE}	<i>Digitalis</i>	<i>purpurea</i> L.*	1		19, B							1	1	1	1				
Asteraceae ^{AD}	<i>Dimorphotheca</i>	<i>pluvialis</i> (L.) Moench	1	1	19, B							1	1	1					
Asteraceae ^{AD}	<i>Dimorphotheca</i>	<i>sinuata</i> DC.	1	1	19, B							1	1	1					
Rutaceae	<i>Diosma</i>	spp.	1	1	19														
Ebenaceae ^{AD}	<i>Diospyros</i>	<i>dichrophylla</i> (Gand.) De Winter	1		1, E				1										
Ebenaceae ^{AD}	<i>Diospyros</i>	<i>glabra</i> (L.) De Winter	1	1	19, B									1	1	1			
Ebenaceae ^{MBG}	<i>Diospyros</i>	<i>kaki</i> L. f.*	1	1	19														
Ebenaceae ^{AD}	<i>Diospyros</i>	<i>lycioides</i> Desf.	1		1, 18, 34, 43, E	1	1	1	1	1	1	1	1	1	1	1	1	1	
Ebenaceae ^{AD}	<i>Diospyros</i>	<i>whyteana</i> (Hiern) F. White	1	1	19, B, E					1	1	1	1	1	1	1	1	1	
Sapindaceae ^{AD}	<i>Dodonaea</i>	<i>angustifolia</i> L. f.			1	18, 19, B, E	1	1	1	1	1	1	1	1	1	1	1	1	
Sterculiaceae ^{AD}	<i>Dombeya</i>	<i>burgessiae</i> Gerr. ex Harv.	1	1	18, 19, 20, B, E	1	1	1	1	1	1	1	1	1	1	1	1	1	
Sterculiaceae ^{AD}	<i>Dombeya</i>	<i>cymosa</i> Harv.			7, E					1	1	1	1						
					1, 3, 7, 18, 29, 41,														
Sterculiaceae ^{AD}	<i>Dombeya</i>	<i>rotundifolia</i> (Hochst.) Planch.	1	1	51, A, C, E							1	1	1	1	1			
Mesembryanthemaceae ^{AD}	<i>Dorotheanthus</i>	<i>bellidiformis</i> (Burm. f.) N.E. Br.	1	1	19, B					1	1	1	1	1					
Flacourtiaceae ^{AD}	<i>Dovyalis</i>	<i>caffra</i> (Hook. f. & Harv.) Hook. f.	1	1	3, 19, 29, B, C, E	1						1	1	1	1	1			
Hyacinthaceae	<i>Drimia</i>	sp.			1	11													
Mesembryanthemaceae ^{AD}	<i>Drosanthemum</i>	<i>floribundum</i> (Haw.) Schwant.	1	1	19, 20, B									1	1	1	1		
Mesembryanthemaceae ^{AD}	<i>Drosanthemum</i>	<i>hispidum</i> (L.) Schwant.	1	1	19, B	1								1	1	1	1		
Proteaceae	<i>Dryandra</i>	spp.*	1	1	19														
Verbenaceae ^{AD}	<i>Duranta</i>	<i>erecta</i> L.*	1	1	19, 20, 29, B, C, E	1	1	1	1	1	1	1	1	1	1	1	1	1	
Mesembryanthemaceae	<i>Eberlanzia</i>	sp.			17														
Boraginaceae ^{MBG}	<i>Echium</i>	<i>fastuosum</i> Aiton*	1	1	19, 37, B									1	1	1			
Boraginaceae ^{AD}	<i>Echium</i>	<i>plantagineum</i> L.* ¹	1	1	1, 19, A, B, D, E	1	1	1	1					1	1	1	1	1	
Boraginaceae ^{AD}	<i>Ehretia</i>	<i>rigida</i> (Thunb.) Druce	1	1	18, 35, E	1	1	1						1	1	1	1	1	
Pontederiaceae ^{AD}	<i>Eichhornia</i>	<i>crassipes</i> (Mart.) Solms-Laub.* ¹			1	19, B, D	1	1	1	1	1						1	1	
Meliaceae ^{AD}	<i>Ekebergia</i>	<i>capensis</i> Sparrm.			1	39, E								1	1	1	1		
Elaeagnaceae ^{MBG}	<i>Elaeagnus</i>	<i>pungens</i> Thunb.*	1		19, B					1	1	1							

[illegible]

[illegible]

Myrtaceae ^{APNI}	<i>Eucalyptus</i>	<i>salubris</i> F. Muell.*	1	1	19, 20, 29, B, C	1	1	1						1	1	1
Myrtaceae ^{APNI}	<i>Eucalyptus</i>	<i>scabra</i> Dum.Cours.*	1	1	29, C	1	1	1	1	1					1	1
Myrtaceae ^{APNI}	<i>Eucalyptus</i>	<i>siderophloia</i> Benth.*	1	1	29, C	1	1	1	1	1	1					1
					1, 3, 4, 9, 16, 19, 20, 27, 29, 34, 35, 36, 41, A, B, C											
Myrtaceae ^{APNI}	<i>Eucalyptus</i>	<i>sideroxylon</i> A.Cunn. ex Woolls (or Woolls)* ²	1	1		1	1	1	1	1	1	1	1	1	1	1
Myrtaceae ^{APNI}	<i>Eucalyptus</i>	<i>sieberi</i> L.A.S.Johnson*	1		29, C	1								1	1	1
Myrtaceae ^{APNI}	<i>Eucalyptus</i>	<i>smithii</i> R.T.Baker*	1	1	29, C	1	1	1	1	1				1	1	1
					1, 2, 16, 19, 29, A, B, C											
Myrtaceae ^{APNI}	<i>Eucalyptus</i>	<i>tereticornis</i> Sm.*	1	1		1	1	1			1	1	1	1	1	1
Myrtaceae ^{APNI}	<i>Eucalyptus</i>	<i>tetraptera</i> Turcz.*	1	1	20											
Myrtaceae ^{APNI}	<i>Eucalyptus</i>	<i>torquata</i> Luehm.*	1	1	19, 20, B	1	1						1	1	1	1
Myrtaceae ^{APNI}	<i>Eucalyptus</i>	<i>triantha</i> Link*	1	1	29, C	1								1	1	1
					1, 3, 27, 29, 41, A, C											
Myrtaceae ^{APNI}	<i>Eucalyptus</i>	<i>viminalis</i> Labill.*	1	1		1	1	1						1	1	1
Ebenaceae ^{AD}	<i>Euclea</i>	<i>racemosa</i> Murray	1	1	1, 19, B	1	1	1	1	1	1					1
Ebenaceae ^{AD}	<i>Euclea</i>	<i>tomentosa</i> E. Mey. ex A. DC.	1	1	1, 19, B						1	1	1	1		
Ebenaceae ^{AD}	<i>Euclea</i>	<i>undulata</i> Thunb.	1		1, E	1	1	1	1	1	1					1
Myrtaceae ^{MBG}	<i>Eugenia</i>	<i>jambos</i> L.*	1		19											
Myrtaceae ^{APNI}	<i>Eugenia</i>	<i>myrtifolia</i> Sims*	1	1	19, 20, B	1	1	1	1	1	1	1	1	1	1	1
Euphorbiaceae ^{AD}	<i>Euphorbia</i>	<i>coerulescens</i> Haw.	1	1	1											
Euphorbiaceae ^{AD}	<i>Euphorbia</i>	<i>decussata</i> E. Mey. ex Boiss.		1	10, 47											
Euphorbiaceae ^{AD}	<i>Euphorbia</i>	<i>esculenta</i> Marloth	1		43											
Euphorbiaceae ^{AD}	<i>Euphorbia</i>	<i>filiflora</i> Marloth		1	47											
Euphorbiaceae ^{AD}	<i>Euphorbia</i>	<i>ingens</i> E. Mey. ex Boiss.	1		43, E				1	1	1	1				
Euphorbiaceae ^{AD}	<i>Euphorbia</i>	<i>ledienii</i> Berger	1	1	1, 43, A						1	1	1	1	1	
Euphorbiaceae ^{AD}	<i>Euphorbia</i>	<i>marginata</i> Pursh	1	1	19, 20, B	1	1								1	1
Euphorbiaceae ^{AD}	<i>Euphorbia</i>	<i>mauritanica</i> L.	1	1	19, 47, B							1	1	1		
Euphorbiaceae ^{AD}	<i>Euphorbia</i>	<i>splendens</i> Boj.	1	1	19, B	1	1	1	1	1	1	1	1	1	1	1
Euphorbiaceae ^{AD}	<i>Euphorbia</i>	<i>tetragona</i> Haw.	1	1	1, A				1	1	1	1				
Euphorbiaceae ^{AD}	<i>Euphorbia</i>	<i>triangularis</i> Desf.	1	1	1, E						1					
Asteraceae ^{AD}	<i>Euryops</i>	<i>chrysanthemoides</i> (DC.) B. Nord.	1	1	19, B, D	1	1	1	1	1	1	1	1	1	1	1
Asteraceae ^{AD}	<i>Euryops</i>	<i>pectinatus</i> (L.) Cass.	1	1	19											
Asteraceae ^{AD}	<i>Euryops</i>	<i>virginicus</i> (L. f.) DC.	1	1	19, 20, B						1	1	1	1		
Polygonaceae ^{AD}	<i>Fagopyrum</i>	<i>esculentum</i> Moench*	1	1	1, 9, 16, A, E	1	1	1	1	1						1
Polygonaceae ^{FE}	<i>Fallopia</i>	<i>aubertii</i> (L. Henry) Holub	1	1	20											
Polygonaceae ^{AD}	<i>Fallopia</i>	<i>convolvulus</i> (L.) Holub	1	1	19, E	1	1	1	1	1				1	1	1
					1, 3, 7, 9, 16, 18, A, E											
Proteaceae ^{AD}	<i>Faurea</i>	<i>saligna</i> Harv.	1	1		1	1	1					1	1	1	1
Myrtaceae ^{MBG}	<i>Feijoa</i>	<i>sellowiana</i> (O. Berg) O. Berg*		1	19, B	1								1	1	1
Asteraceae ^{AD}	<i>Felicia</i>	<i>amelloides</i> (L.) Voss	1	1	19, 20, B	1	1	1	1	1	1	1	1	1	1	1
Asteraceae ^{AD}	<i>Felicia</i>	<i>bergerana</i> (Spreng.) O. Hoffm.	1	1	19, B							1	1	1		
Asteraceae ^{AD}	<i>Felicia</i>	<i>filifolia</i> (Vent.) Burt Davy	1	1	19, D, E	1	1	1	1	1	1	1	1	1	1	1
Asteraceae ^{AD}	<i>Felicia</i>	<i>fruticosa</i> (L.) Nicholson	1	1	19, B, E	1			1	1	1	1	1	1	1	
Cyperaceae	<i>Ficinia</i>	spp.		1	19											
Apiaceae ^{AD}	<i>Foeniculum</i>	<i>vulgare</i> Mill.*	1	1	19, 20, B, E	1	1	1	1	1	1				1	1
Rosaceae ^{MBG}	<i>Fragaria</i>	<i>ananassa</i> Duch.	1	1	20											
Rosaceae ^{FE}	<i>Fragaria</i>	x <i>ananassa</i> Duchesne*	1	1	19, B				1	1	1	1	1	1	1	
Oleaceae	<i>Fraxinus</i>	spp.*		1	19, 20, 35											
Scrophulariaceae ^{AD}	<i>Freylinia</i>	<i>lanceolata</i> (L. f.) G. Don	1	1	19, B	1	1	1	1	1	1	1	1	1	1	1
Asteraceae ^{AD}	<i>Gaillardia</i>	<i>aristata</i> Pursh*	1	1	19											
Asteraceae ^{AD}	<i>Gazania</i>	<i>krebsiana</i> Less.	1	1	19, B, D, E	1	1	1	1	1	1	1	1	1	1	1
Asteraceae ^{AD}	<i>Gazania</i>	<i>rigens</i> (L.) Gaertn.	1	1	10, 19, B, D	1	1	1	1	1	1	1	1	1	1	1
Iridaceae ^{AD}	<i>Geissorhiza</i>	<i>aspera</i> Goldbl.	1		19, B							1	1			

[illegible]

[illegible]

[illegible]

[illegible]

Geraniaceae ^{AD}	Pelargonium	capitatum (L.) L'Hérit.	1	1	19, 20, B, D	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Geraniaceae ^{AD}	Pelargonium	coronopifolium Jacq.			48														
Geraniaceae ^{AD}	Pelargonium	crithmifolium J.E. Sm.	1	1	19, B					1	1	1	1	1	1				
Geraniaceae ^{AD}	Pelargonium	cucullatum (L.) L'Hérit.	1	1	19, 48, B	1	1							1	1	1	1	1	1
Geraniaceae ^{AD}	Pelargonium	dolomiticum Knuth			48, 53, E	1	1	1	1	1				1	1	1	1	1	1
Geraniaceae ^{AD}	Pelargonium	fruticosum (Cav.) Willd.			48														
Geraniaceae ^{AD}	Pelargonium	fulgidum (L.) L'Hérit.	1		19, B						1	1	1	1	1	1	1		
Geraniaceae ^{AD}	Pelargonium	glutinosum (Jacq.) L'Hérit.			48, E										1	1	1		
Geraniaceae ^{AD}	Pelargonium	grossularioides (L.) L'Hérit.			48														
Geraniaceae ^{AD}	Pelargonium	papilionaceum (L.) L'Hérit.			48														
Geraniaceae ^{AD}	Pelargonium	scabrum (Burm. f.) L'Hérit.	1		19, 48, B	1				1	1	1	1	1	1	1	1	1	1
Geraniaceae ^{AD}	Pelargonium	tricolor Curt.		1	30, 48														
Fabaceae ^{AD}	Peltophorum	africanum Sond.	1	1	7, 29, 41, 51, C, E	1									1	1	1	1	1
Asteraceae	Pentzia	sp.			17														
Acanthaceae ^{AD}	Peristrophe	cernua Nees			40, D	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lauraceae ^{MBG}	Persea	americana Mill.*	1	1	1, 19, 20, A, B					1	1	1	1	1	1	1			
Polygonaceae ^{AD}	Persicaria	attenuata (R. Br.) Sojak	1	1	19, B, D, E	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Polygonaceae ^{AD}	Persicaria	capitata (Buch.-Ham. ex D. Don) H. Gross*	1	1	19, 20														
Acanthaceae	Petalidium	spp.	1	1	1														
Verbenaceae ^{MBG}	Petrea	volubilis L.*	1	1	19, 20, B	1	1	1	1						1	1	1	1	1
Apiaceae ^{AD}	Petroselinum	crispum (Mill.) A.W. Hill*	1	1	19														
Hydrophyllaceae ^{MBG}	Phacelia	campanularia A. Gray*	1	1	19, 20, B										1	1	1	1	1
Hydrophyllaceae ^{FE}	Phacelia	tanacetifolia Benth.*	1	1	19, 20														
Fabaceae ^{AD} (Leguminosae) ^{FE}	Phaseolus	coccineus L.	1	1	1, 4, 9, 16, 36, A	1	1	1	1										
Araceae ^{MBG}	Philodendron	selloum K. Koch*			19														
Polemoniaceae ^{MBG}	Phlox	drummondii Hook.*	1		19														
Arecaceae ^{AD} (Palmae) ^{FE}	Phoenix	canariensis hort. ex Chabaud*		1	19, B	1	1	1									1	1	1
Liliaceae ^{FE}	Phormium	tenax J.R.Forst. & G.Forst.*	1	1	19, 20, B	1										1	1	1	1
Rosaceae	Photinia	spp.*	1	1	19														
Verbenaceae ^{AD}	Phyla	nodiflora (L.) Greene	1	1	20, D, E	1	1	1					1	1	1	1	1	1	1
Rhamnaceae ^{AD}	Phyllica	ericoides L.	1	1	19, 22														
Solanaceae ^{AD}	Physalis	peruviana L.*	1	1	19, 20, B, E	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Solanaceae ^{AD}	Physalis	viscosa L.*			40, D, E	1	1	1	1	1	1					1	1	1	1
Lamiaceae ^{MBG}	Physostegia	virginiana (L.) Benth.*	1		19, 20														
Phytolaccaceae ^{AD}	Phytolacca	dioica L.*	1	1	19, 29, 41, B, C	1	1	1						1	1	1	1	1	1
Phytolaccaceae ^{AD}	Phytolacca	octandra L.	1		19, B, D, E	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Asteraceae ^{AD}	Picris	echioides L.*	1	1	19, E	1	1	1			1								1
Pinaceae	Pinus	spp.*		1	1														
Fabaceae ^{AD} (Leguminosae) ^{FE}	Pisum	sativum L.*			19														
Pittosporaceae ^{MBG}	Pittosporum	eugenioides A. Cunn.*	1	1	19, B										1	1	1	1	1
Pittosporaceae ^{AD}	Pittosporum	undulatum Vent.* ¹	1	1	19, 41, B									1	1	1			
Plantaginaceae ^{AD}	Plantago	lanceolata L.*			19, 22, B, D, E	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Platanaceae ^{FE}	Platanus	acerifolia (Aiton) Willd.*			19, B										1				
Cunoniaceae ^{AD}	Platylophus	trifoliatius (L. f.) D. Don	1	1	1, 18, 38, A	1	1												1
Lamiaceae ^{AD}	Plectranthus	ecklonii Benth.		1	46, D, E			1	1	1	1								
Lamiaceae ^{AD}	Plectranthus	neochilus Schltr.	1	1	19, 20, 46, B, D, E	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Fabaceae ^{AD}	Podalyria	calyptrata (Retz.) Willd.	1		19, B									1	1	1	1		
Fabaceae ^{AD}	Podalyria	microphylla E. Mey.			10														
Fabaceae ^{AD}	Podalyria	sericea (Andr.) R. Br. ex Ait. f.	1	1	19, B						1	1	1	1					
Euphorbiaceae ^{MBG}	Poinsettia	pulcherrima (Willd. ex Klotzsch) Graham*		1	29, C		1	1	1						1	1	1	1	1
Polygalaceae ^{AD}	Polygala	myrtifolia L.	1		19, B		1	1	1	1	1	1	1	1	1	1	1	1	1
Polygalaceae ^{AD}	Polygala	virgata Thunb.	1		19, B, D, E		1	1	1	1	1	1	1	1	1	1	1	1	1
Polygonaceae ^{AD}	Polygonum	aviculare L.*	1	1	19, B, E		1	1	1	1						1	1	1	1
Mesembryanthemaceae ^{AD}	Polymita	albiflora (L. Bol.) L. Bol.		1	47														

[illegible]

Fagaceae ^{AD}	Quercus	robur L.*	1	1	3, 19, 22, 34, 35, 41, B								1	1			
Ranunculaceae ^{FE}	Ranunculus	asiaticus L.*		1	19, 20, B								1	1	1		
Myrsinaceae ^{AD}	Rapanea	melanophloeos (L.) Mez		1	19, B, E					1	1	1	1	1	1	1	1
Brassicaceae ^{AD}	Raphanus	raphanistrum L.*	1	1	1, 9, 19, A, B, E	1	1	1	1	1	1	1	1	1	1	1	1
Brassicaceae ^{AD}	Rapistrum	rugosum (L.) All.*	1	1	19, B, E								1	1	1	1	1
Apocynaceae ^{AD}	Rauvolfia	caffra Sond.	1		29, 41, C, E			1	1				1	1	1	1	1
Resedaceae ^{FE}	Reseda	odorata L.*	1	1	19, B			1	1	1							1
Rhamnaceae ^{AD}	Rhamnus	prinoides L'Hérit. ^B			51, E			1	1	1	1	1	1			1	1
Bignoniaceae ^{AD}	Rhigozum	obovatum Burch.			31, E								1		1	1	
Bignoniaceae ^{AD}	Rhigozum	trichotomum Burch. ^B			8												
Ericaceae	Rhododendron	spp.*	1		19												
Vitaceae ^{AD}	Rhoicissus	tomentosa (Lam.) Wild & Drum.		1	22, E			1	1						1	1	1
Anacardiaceae ^{AD}	Rhus	laevigata L.	1		19												
					1, 3, 18, 19, 20, 29, 36, 41, A, B, C, E												
Anacardiaceae ^{AD}	Rhus	lancea L. f. ^B	1	1							1	1	1	1	1	1	1
Anacardiaceae ^{AD}	Rhus	leptodictya Diels		1	41, E			1	1	1	1						
Anacardiaceae ^{AD}	Rhus	lucida L. ^B	1	1	19, B, E			1	1	1	1	1	1	1	1		
Anacardiaceae ^{MBG}	Rhus	succedanea L.*		1	19												
Anacardiaceae ^{AD}	Rhus	tomentosa L.		1	19, B, E			1	1	1	1	1	1		1	1	1
					1, 3, 19, 29, 41, A, B, C, E												
Fabaceae ^{AD}	Robinia	pseudoacacia L.* ³	1	1											1	1	1
Iridaceae ^{AD}	Romulea	rosea (L.) Eckl.		1	19, B								1	1	1	1	1
Brassicaceae ^{AD}	Rorippa	nasturtium-aquaticum (L.) Hayek* ³	1	1	19, B, E			1	1	1					1	1	1
Rosaceae	Rosa	spp.*		1	19												
Lamiaceae ^{(PNI)(IK)}	Rosmarinus	lavandulaeus Noe. ex Debeaux*	1	1	19, 20												
Lamiaceae ^{AD} (Labiateae) ^{FE}	Rosmarinus	officinalis L.*	1	1	19, 20, B			1	1	1	1	1	1	1	1	1	1
Rubiaceae ^{AD}	Rothmannia	capensis Thunb.	1		29, C, E			1	1	1	1				1	1	1
Rosaceae ^{FE}	Rubus	idaeus L.*	1	1	19, B										1	1	1
Asteraceae ^{AD} (Compositae) ^{FE}	Rudbeckia	hirta L.*	1	1	19												
Polygonaceae ^{AD}	Rumex	sagittatus Thunb.			40, D, E			1	1	1	1				1	1	1
Mesembryanthemaceae ^{AD}	Ruschia	elineata L. Bol.		1	47												
Mesembryanthemaceae ^{AD}	Ruschia	lineolata (Haw.) Schwant.			52												
Mesembryanthemaceae ^{AD}	Ruschia	robusta L. Bol.		1	47												
Rutaceae ^{AD}	Ruta	graveolens L.*	1	1	19												
Acanthaceae	Ruttya	sp.	1		1												
Poaceae ^{AD} (Gramineae) ^{FE}	Saccharum	officinarum L.		1	1, 16, A 1, 3, 19, 41, A, B, E			1			1	1	1	1	1	1	1
Salicaceae ^{AD}	Salix	babylonica L.* ³	1	1										1	1		
Salicaceae ^{AD}	Salix	caprea L.*	1	1	19, 20, B									1	1		
Salicaceae ^{AD}	Salix	mucronata Thunb.		1	19, B, E			1	1	1	1	1		1	1	1	1
Chenopodiaceae ^{AD}	Salsola	sp.	1		43												
Lamiaceae ^{AD}	Salvia	africana-lutea L.	1		19, B							1	1	1	1	1	1
Lamiaceae ^{AD}	Salvia	chamelaegnea Berg.	1	1	19, B			1	1	1	1	1				1	1
Lamiaceae ^{MBG}	Salvia	leucantha Cav.*	1	1	19												
Lamiaceae ^{AD} (Labiateae) ^{FE}	Salvia	officinalis L.*	1		19, 20												
Lamiaceae ^{MBG}	Salvia	splendens Sellow ex Roem. & Schult.*	1	1	19, B			1	1	1	1						1
Rosaceae ^{AD}	Sanguisorba	minor Scop.		1	19												
Geraniaceae ^{AD}	Sarcocaulon	crassicaule Rehm		1	19, B			1	1	1	1	1	1	1	1	1	1
Lamiaceae	Satureia	spp.*	1	1	19, 20												
Dipsacaceae ^{AD}	Scabiosa	africana L.	1		19, B								1	1	1	1	1
Dipsacaceae ^{FE}	Scabiosa	atropurpurea L.*	1	1	19, B								1	1	1	1	1
Dipsacaceae ^{AD}	Scabiosa	columbaria L.			40, D, E			1	1	1	1	1	1	1	1	1	1

Goodeniaceae ^{AD}	<i>Scaevola</i>	<i>plumieri</i> (L.) Vahl	1	19, B, D	1	1	1	1	1	1	1	1	1	1	1
				1, 3, 19, 20, 29,											
Anacardiaceae ^{AD}	<i>Schinus</i>	<i>molle</i> L.*	1	1	1	1	1	1	1	1	1	1	1	1	1
Anacardiaceae ^{AD}	<i>Schinus</i>	<i>terebinthifolius</i> Raddi* ³	1	1	19, B			1	1						
Fabaceae ^{AD}	<i>Schotia</i>	<i>afra</i> (L.) Thunb.	1	1	18, 19, 20, B	1	1					1	1	1	1
Fabaceae ^{AD}	<i>Schotia</i>	<i>brachypetala</i> Sond.	1	1	3, 18, 29, 41, C, E							1	1	1	1
Fabaceae ^{AD}	<i>Schotia</i>	<i>capitata</i> Bolle	1	1	29, C, E	1	1	1				1	1	1	1
Fabaceae ^{AD}	<i>Schotia</i>	<i>latifolia</i> Jacq.	1		19, B, E	1							1	1	1
Anacardiaceae ^{AD}	<i>Sclerocarya</i>	<i>birrea</i> (A. Rich.) Hochst.	1	1	1, 7, 18, 41, A, E							1	1	1	
				1, 5, 9, 18, 19, 42,											
				A, B, E	1	1	1	1				1	1	1	1
Rhamnaceae ^{AD}	<i>Scutia</i>	<i>myrtina</i> (Burm. f.) Kurz	1	1											
Crassulaceae ^{FE}	<i>Sedum</i>	<i>acre</i> L.*	1	1	19										
Crassulaceae ^{FE}	<i>Sedum</i>	<i>dasyphyllum</i> L.*	1		19										
Crassulaceae ^{MBG}	<i>Sedum</i>	<i>spectabile</i> Boreau*	1	1	19										
Crassulaceae ^{FE}	<i>Sedum</i>	<i>spurium</i> M.Bieb.*	1	1	19										
Selaginaceae ^{AD}	<i>Selago</i>	<i>corymbosa</i> L.	1	1	19										
Asteraceae ^{AD}	<i>Senecio</i>	<i>apiifolius</i> (DC.) Benth. & Hook. f. ex O. Hoffm.	1	1	1, 3, 16, A, E	1	1	1	1	1	1	1	1	1	1
Asteraceae ^{AD}	<i>Senecio</i>	<i>arenarius</i> Thunb.		1	47, E				1						
Asteraceae ^{MBG}	<i>Senecio</i>	<i>cruentus</i> (Masson ex L'Hér.) DC.*	1	1	19, B						1	1	1		
Asteraceae ^{AD}	<i>Senecio</i>	<i>elegans</i> L.	1	1	19, B	1	1	1			1	1	1	1	1
Asteraceae ^{AD}	<i>Senecio</i>	<i>halimifolius</i> L.	1	1	19, B	1								1	1
Asteraceae ^{AD}	<i>Senecio</i>	<i>juniperinus</i> L. f.	1	1	1, A								1	1	1
Asteraceae ^{AD}	<i>Senecio</i>	<i>lineatus</i> (L. f.) DC.	1	1	19, B	1	1	1	1	1	1				
Asteraceae ^{AD}	<i>Senecio</i>	<i>tamoides</i> DC.	1	1	19, B, D, E	1	1	1	1	1	1		1	1	1
Fabaceae ^{AD}	<i>Senna</i>	<i>corymbosa</i> (Lam.) Irwin & Barneby*		1	29, C, E	1	1	1	1	1	1				
Fabaceae ^{AD}	<i>Senna</i>	<i>didymobotrya</i> (Fresen.) Irwin & Barneby*		1	29, C, E	1	1	1	1		1	1	1	1	1
Proteaceae ^{AD}	<i>Serruria</i>	<i>aitonii</i> R. Br.	1		19, B							1	1	1	1
Proteaceae ^{AD}	<i>Serruria</i>	<i>fasciflora</i> Salisb. ex Knight	1		19, B	1	1	1	1	1	1	1	1	1	1
Proteaceae ^{AD}	<i>Serruria</i>	<i>foeniculacea</i> R. Br.	1		19, B								1	1	
Fabaceae ^{AD}	<i>Sesbania</i>	<i>punicea</i> (Cav.) Benth.* ¹		1	19, B, E	1	1	1	1			1	1	1	1
Sapotaceae ^{AD}	<i>Sideroxylon</i>	<i>inermis</i> L.	1	1	19, B, E	1	1	1	1	1			1	1	1
Caryophyllaceae ^{AD}	<i>Silene</i>	<i>gallica</i> L.*		1	19, B	1	1						1	1	1
Asteraceae ^{AD}	<i>Silybum</i>	<i>marianum</i> (L.) Gaertn.*	1	1	19, E									1	
Ericaceae ^{AD}	<i>Simochilus</i>	<i>depressus</i> (Licht.) Benth.	1	1	19, B				1						
Brassicaceae ^{AD}	<i>Sinapis</i>	<i>alba</i> L.*	1	1	19										
Brassicaceae ^{AD}	<i>Sinapis</i>	<i>arvensis</i> L.*	1	1	19, B, E	1	1	1		1	1	1	1	1	1
Brassicaceae ^{AD}	<i>Sisymbrium</i>	<i>capense</i> Thunb.	1	1	19, B	1	1	1	1				1	1	1
Zygophyllaceae ^{AD}	<i>Sisymbrium</i>	<i>sparteum</i> E. Mey. ex Sond.			10										
Solanaceae ^{AD}	<i>Solanum</i>	<i>nigrum</i> L.*		1	19, B, E	1	1	1	1	1	1		1	1	1
Solanaceae ^{AD}	<i>Solanum</i>	<i>pseudocapsicum</i> L.*			10, E	1	1	1	1	1			1	1	1
Asteraceae	<i>Solidago</i>	spp.*	1	1	19, 20										
Asteraceae ^{AD}	<i>Sonchus</i>	<i>oleraceus</i> L.*		1	19, B, E	1	1	1	1	1	1	1	1	1	1
					19, 20, 29, 41, B,										
					C, E	1	1								1
Fabaceae ^{AD}	<i>Sophora</i>	<i>japonica</i> L.*	1	1											
Iridaceae	<i>Sparaxis</i>	spp.	1	1	19										
Tiliaceae ^{AD}	<i>Sparrmannia</i>	<i>africana</i> L. f.		1	19, B					1	1	1	1	1	1
Bignoniaceae ^{MBG}	<i>Spathodea</i>	<i>campanulata</i> P. Beauv.		1	41										
Caryophyllaceae ^{AD}	<i>Spergula</i>	<i>arvensis</i> L.*	1		19, B, E	1	1	1	1	1	1	1	1	1	1
Lamiaceae ^{AD}	<i>Stachys</i>	<i>aethiopica</i> L.	1	1	19, 40, B, D, E	1	1	1	1	1	1	1	1	1	1
Lamiaceae ^{AD}	<i>Stachys</i>	<i>arvensis</i> L.*	1		19, B	1	1	1	1	1	1	1	1	1	1
Lamiaceae ^{AD}	<i>Stachys</i>	<i>aurea</i> Benth.			10										
Lamiaceae ^{AD}	<i>Stachys</i>	<i>rugosa</i> Ait.	1		19, B								1	1	1
Asteraceae ^{AD}	<i>Steirodiscus</i>	<i>tagetes</i> (L.) Schltr.	1	1	19, B							1	1	1	
Caryophyllaceae ^{AD}	<i>Stellaria</i>	<i>media</i> (L.) Vill.*	1	1	19, B, E				1	1	1	1	1	1	

Sterculiaceae ^{AD}	<i>Sterculia</i>	<i>murex</i> Hemsl.	1	29, 41, C, E						1	1	1	1	
Asteraceae	<i>Stoebe</i>	spp.		19										
Strelitziaceae ^{AD}	<i>Strelitzia</i>	<i>alba</i> (L. f.) Skeels	1	19, B						1	1	1	1	1
Strelitziaceae ^{AD}	<i>Strelitzia</i>	<i>reginae</i> Ait.	1	19, 20, B, D	1	1	1	1	1	1	1	1	1	1
Scrophulariaceae ^{AD}	<i>Sutera</i>	<i>caerulea</i> (L. f.) Hiern	1	19, B	1	1	1	1	1	1	1	1	1	1
Scrophulariaceae ^{AD}	<i>Sutera</i>	<i>floribunda</i> (Benth.) Kuntze		40, D, E	1	1	1	1	1					
Fabaceae ^{AD}	<i>Sutherlandia</i>	<i>frutescens</i> (L.) R. Br.	1	19, B, E	1	1				1	1	1	1	1
Boraginaceae ^{FE}	<i>Symphytum</i>	<i>officinale</i> L.*	1	19										
Asteraceae ^{AD}	<i>Syncarpha</i>	<i>paniculata</i> (L.) B. Nord.	1	19, B	1	1	1	1	1	1	1	1	1	1
Myrtaceae ^{APNI}	<i>Syncarpia</i>	<i>glomulifera</i> (Sm.) Nied.	1	41										
Ericaceae ^{AD}	<i>Syndesmanthus</i>	<i>viscosus</i> (H. Bol.) N.E. Br.	1	19, 43, B	1	1							1	1
Myrtaceae ^{AD}	<i>Syzygium</i>	<i>cordatum</i> Hochst.	1	18, 41, 51, E	1	1	1	1	1		1	1	1	1
Myrtaceae ^{APNI}	<i>Syzygium</i>	<i>paniculatum</i> Gaertn.	1	41										
Asteraceae ^{AD}	<i>Tagetes</i>	<i>erecta</i> L.*	1	19, B, E	1	1	1	1	1				1	1
Asteraceae ^{AD}	<i>Tagetes</i>	<i>minuta</i> L.*	1	34, D, E	1	1	1	1	1	1	1	1	1	1
Asteraceae ^{MBG}	<i>Tagetes</i>	<i>patula</i> L.*	1	19, B	1	1	1	1					1	1
Tamaricaceae ^{MBG}	<i>Tamarix</i>	<i>aphylla</i> (L.) H. Karst.*	1	19										
Tamaricaceae ^{FE}	<i>Tamarix</i>	<i>gallica</i> L.*	1	19, 20										
Tamaricaceae ^{FE}	<i>Tamarix</i>	<i>hispida</i> Willd.*	1	19										
Asteraceae ^{AD}	<i>Taraxacum</i>	<i>officinale</i> Weber sens. lat.*	1	19, B, D, E	1	1	1	1	1	1	1	1	1	1
Asteraceae ^{AD}	<i>Tarchonanthus</i>	<i>camphoratus</i> L. ^B	1	19, B, E	1	1	1	1	1	1	1	1	1	1
Bignoniaceae ^{MBG}	<i>Tecoma</i>	<i>stans</i> (L.) Juss. ex Kunth*. ¹	1	3, 19, 20, 29, B, C	1	1	1	1	1	1	1	1	1	1
Bignoniaceae ^{AD}	<i>Tecomaria</i>	<i>capensis</i> (Thunb.) Spach	1	19, 20, 29, B, C, E	1	1	1	1	1	1	1	1	1	1
Aizoaceae ^{AD}	<i>Tetragonia</i>	<i>decumbens</i> Mill.	1	19, B	1	1	1			1	1	1	1	1
Aizoaceae ^{AD}	<i>Tetragonia</i>	<i>fruticosa</i> L.		19, B	1							1	1	1
Aizoaceae ^{AD}	<i>Tetragonia</i>	<i>spicata</i> L. f.		19, B						1	1	1	1	
Restionaceae ^{AD}	<i>Thamnochortus</i>	<i>insignis</i> Mast.		22										
Santalaceae ^{AD}	<i>Thesium</i>	<i>aggregatum</i> A.W. Hill	1	19, B	1						1	1	1	1
Lamiaceae ^{AD} (Labiatae) ^{FE}	<i>Thymus</i>	<i>serpyllum</i> L.*	1	19, 20										
Fabaceae ^{MBG}	<i>Tipuana</i>	<i>tipu</i> (Benth.) Kuntze*. ³	1	3, 19, 20, 41, B									1	1
Asteraceae ^{AD}	<i>Tithonia</i>	<i>rotundifolia</i> (Mill.) Blake*. ¹	1	19, 20, B, D, E	1	1	1	1	1	1				1
Asphodelaceae ^{AD}	<i>Trachyantha</i>	<i>divaricata</i> (Jacq.) Kunth	1	19, B	1						1	1	1	1
Asphodelaceae ^{AD}	<i>Trachyantha</i>	<i>falcata</i> (L. f.) Kunth		10										
Asphodelaceae ^{AD}	<i>Trachyantha</i>	<i>hirsutiflora</i> (Adamson) Oberm.	1	19, B						1	1	1	1	
Ulmaceae ^{AD}	<i>Trema</i>	<i>orientalis</i> (L.) Blume	1	29, C, E	1	1	1	1			1	1	1	1
Zygophyllaceae ^{AD}	<i>Tribulus</i>	<i>cristatus</i> Presl		10										
Zygophyllaceae ^{AD}	<i>Tribulus</i>	<i>terrestris</i> L.	1	19, 22, B, D, E	1	1	1	1	1			1	1	1
Meliaceae ^{AD}	<i>Trichillia</i>	<i>dregeana</i> Sond.		23, E									1	1
Meliaceae ^{AD}	<i>Trichillia</i>	<i>emetica</i> Vahl	1	29, 41, C, E							1	1	1	1
Boraginaceae ^{AD}	<i>Trichodesma</i>	<i>africanum</i> (L.) Lehm.		10										
Fabaceae ^{AD} (Leguminosae) ^{FE}	<i>Trifolium</i>	<i>balansae</i> Boiss. (provisional)*	1	19, B							1	1	1	
Fabaceae ^{AD} (Leguminosae) ^{FE}	<i>Trifolium</i>	<i>fragiferum</i> L.*	1	19										
Fabaceae ^{AD}	<i>Trifolium</i>	<i>pratense</i> L.*	1	19, E	1	1	1						1	1
Fabaceae ^{AD}	<i>Trifolium</i>	<i>repens</i> L.*	1	19, 20, B, E	1	1	1				1	1	1	1
Fabaceae ^{AD}	<i>Trifolium</i>	<i>resupinatum</i> L.*	1	19, B							1	1	1	
Fabaceae ^{AD}	<i>Trifolium</i>	<i>subterraneum</i> L.*	1	19, B							1	1	1	
Fabaceae ^{AD} (Leguminosae) ^{FE}	<i>Trifolium</i>	<i>vesiculosum</i> Savi*	1	19										
Tiliaceae ^{AD}	<i>Triumfetta</i>	<i>sonderi</i> Ficalho & Hiern		2, E	1	1	1	1					1	1
Tropaeolaceae ^{FE}	<i>Tropaeolum</i>	<i>majus</i> L.*	1	19, 20, B				1			1	1	1	
Typhaceae ^{AD}	<i>Typha</i>	<i>capensis</i> (Rohrb.) N.E. Br.		19, B, D, E	1	1	1	1				1	1	1
Fabaceae ^{AD}	<i>Ulex</i>	<i>europaeus</i> L.*. ¹	1	19, B, E	1	1	1	1	1	1	1	1	1	1
Ulmaceae ^{AD}	<i>Ulmus</i>	<i>parvifolia</i> Jacq.*		19, 20, 41, B, E	1	1	1						1	
Ulmaceae ^{AD}	<i>Ulmus</i>	<i>procera</i> Salisb.*		19										
Poaceae	<i>Urochloa</i>	sp.		1										

Asteraceae ^{AD}	<i>Ursinia</i>	<i>anethoides</i> (DC.) N.E. Br.	1	19, B						1	1				
Asteraceae ^{AD}	<i>Ursinia</i>	<i>anthemoides</i> (L.) Poir.		1	19, B					1	1	1	1	1	1
Asteraceae ^{AD}	<i>Ursinia</i>	<i>nana</i> DC.	1	1	19, E			1	1	1	1	1	1	1	1
Asteraceae ^{AD}	<i>Ursinia</i>	<i>sericea</i> (Thunb.) N.E. Br.		1	19, B			1					1	1	1
Vahliaceae ^{AD}	<i>Vahlia</i>	<i>capensis</i> (L. f.) Thunb.	1	1	19, B, E			1	1	1	1			1	1
Scrophulariaceae ^{FE}	<i>Verbascum</i>	<i>thapsus</i> L.*		1	19										
Verbenaceae ^{AD}	<i>Verbena</i>	<i>bonariensis</i> L.*	1	1	19, D, E			1	1	1	1	1	1	1	1
Verbenaceae ^{AD}	<i>Verbena</i>	<i>officinalis</i> L.*	1	1	19, E			1	1	1	1	1	1	1	1
Scrophulariaceae ^{AD}	<i>Veronica</i>	<i>persica</i> Poir.*	1	1	19, E					1	1	1	1		
Caprifoliaceae ^{FE}	<i>Viburnum</i>	<i>tinus</i> L.*	1	1	19, 20, B						1	1			
Fabaceae ^{AD}	<i>Vicia</i>	<i>angustifolia</i> L.*	1	1	19, B						1	1	1		
Fabaceae ^{AD}	<i>Vicia</i>	<i>benghalensis</i> L.*	1	1	1, 2, 19, A, E						1	1	1	1	
Fabaceae ^{AD} (Leguminosae) ^{FE}	<i>Vicia</i>	<i>faba</i> L.*	1	1	19, 20, B					1	1	1	1	1	
Fabaceae ^{AD}	<i>Vicia</i>	<i>sativa</i> L.*			19, E			1	1	1	1			1	1
Fabaceae ^{AD} (Leguminosae) ^{FE}	<i>Vicia</i>	<i>villosa</i> Roth*	1	1	19, E			1	1	1	1			1	1
Fabaceae ^{AD}	<i>Virgilia</i>	<i>oroboides</i> (Berg.) Salter	1	1	19, B			1	1	1	1		1	1	1
Viscaceae ^{AD}	<i>Viscum</i>	<i>combreticola</i> Engl.			25, E			1	1	1	1	1	1	1	1
Verbenaceae ^{MBG}	<i>Vitex</i>	<i>agnus-castus</i> L.*	1		19										
Vitaceae ^{FE}	<i>Vitis</i>	<i>vinifera</i> L.*		1	1, 19, 20, A, B							1	1	1	
Haemodoraceae ^{AD}	<i>Wachendorfia</i>	<i>brachyandra</i> W.F. Barker			28										
Haemodoraceae ^{AD}	<i>Wachendorfia</i>	<i>paniculata</i> Burm.	1		19, B					1	1	1	1	1	
Haemodoraceae ^{AD}	<i>Wachendorfia</i>	<i>thyrsiflora</i> Burm.	1		19, 37, B							1	1	1	1
Campanulaceae ^{AD}	<i>Wahlenbergia</i>	<i>prostrata</i> A. DC.		1	47										
Selaginaceae	<i>Walafrida</i>	spp.	1		18										
Iridaceae ^{AD}	<i>Watsonia</i>	<i>meriana</i> (L.) Mill.			37										
Asteraceae ^{MBG}	<i>Wedelia</i>	<i>trilobata</i> (L.) Hitchc.*	1	1	19, 20, B			1	1	1	1	1	1	1	1
Fabaceae ^{AD}	<i>Wiborgia</i>	<i>monoptera</i> E. Mey.			19, B					1	1	1			
Hydrophyllaceae ^{MBG}	<i>Wigandia</i>	<i>urens</i> (Ruiz & Pav.) Kunth*	1	1	19, B						1	1	1		
Restionaceae	<i>Willdenowia</i>	spp.		1	19										
Asteraceae ^{AD}	<i>Xanthium</i>	<i>strumarium</i> L.* ¹		1	19, E				1	1	1	1	1	1	
Araceae ^{AD}	<i>Zantedeschia</i>	<i>aethiopica</i> (L.) Spreng.		1	19, 20, B, D, E			1	1	1	1	1	1	1	1
Poaceae ^{AD} (Gramineae) ^{FE}	<i>Zea</i>	<i>mays</i> L.*		1	1, 19, 20, A, B			1	1	1					1
Commelinaceae ^{FE}	<i>Zebrina</i>	<i>pendula</i> Schnizl.*		1	19, B			1	1	1	1	1	1	1	1
Asteraceae ^{MBG}	<i>Zinnia</i>	<i>elegans</i> Jacq.*	1	1	19, B			1	1	1	1				1
Asteraceae ^{MBG}	<i>Zinnia</i>	<i>linearis</i> Benth.*	1	1	19, 20, B			1	1	1					1
					1, 9, 18, 35, 36,										
Rhamnaceae ^{AD}	<i>Ziziphus</i>	<i>mucronata</i> Willd.	1	1	41, 51, A, E			1	1	1	1			1	1
Zygophyllaceae ^{AD}	<i>Zygophyllum</i>	<i>flexuosum</i> Eckl. & Zeyh.	1		43										
Zygophyllaceae ^{AD}	<i>Zygophyllum</i>	<i>meyeri</i> Sond.		1	47										
Zygophyllaceae ^{AD}	<i>Zygophyllum</i>	<i>prismatocarpum</i> E. Mey. ex Sond.			10										

REFERENCES

1. Anderson, R.H., Buys, B. and Johannsmeier, M.F. 1983. Beekeeping in South Africa. Bulletin 394, Department of Agricultural Technical Services, Pretoria, 207pp.
2. Anon. 1981. Research being carried out by the Plant Protection Research Institute. South African Bee Journal, 53, 6, 4-16.
3. Beylveid, G.P. 1968. Detailed list of nectar and pollen producing plants of economic importance in the Transvaal. South African Bee Journal, 40, 6, 13-14.
4. Botes, A.J. and Birch, E.B. 1984. Byebestuur vir sonneblombestuiwing (Bee management for sunflower pollination). South African Bee Journal, 56, 3, 64-69.
5. Challen, M. and Scharf, H. 1987. Beekeeping in the Eastern Cape. South African Bee Journal, 59, 4, 74-77.
6. Coetzee, J.H. and Giliomee, J.H. 1985. Insects in association with the inflorescence of *Protea repens* (L.) (Proteaceae) and their role in pollination. Journal of the Entomological Society of South Africa, 48, 2, 303-314.
7. Crisp, W.F. 1957. About South African honey flora. South African Bee Journal, 32, 3, 12-13.
8. Eksteen, J.K. and Johannsmeier, M.F. 1991. Oor bye en byepiante van die Noord-Kaap (On bees and bee plants of the northern Cape). South African Bee Journal, 63, 6, 128-136.
9. Fletcher, D.J.C. and Johannsmeier, M.F. 1978. The status of beekeeping in South Africa. South African Bee Journal, 50, 4, 5-20.
10. Gess, F.W. & Gess, S.K. Unpublished data. Personal communication. Albany Museum, Grahamstown, South Africa.
11. Goldblatt, P. and Bernhardt, P. 1999. Pollination of *Moraea* species (Iridaceae) with a staminal column. Annals of the Missouri Botanical Garden, 86, 47-56.
12. Goldblatt, P., Manning, J.C. and Bernhardt, P. 1995. Pollination biology of *Lapeirousia* subgenus *Lapeirousia* (Iridaceae) in southern Africa; floral divergence and adaptation for long-tongued fly pollinators.

13. Hattingh, V. and Giliomee, J.H. 1989. Pollination of certain *Leucadendron* species (Proteaceae). South African Journal of Botany, 55, 4, 387-393.
 14. Herrmann, J.M. 1985. Die bloekom-nektarvlieg *Drosophila flavohirta* in Oos-Transvaal (The *Eucalyptus* nectar fly *Drosophila flavohirta* in the eastern Transvaal). South African Bee Journal, 57, 1, 8-14.
 15. Hoffman, M.T. 1988. The pollination ecology of *Aloe ferox* Mill.. South African Journal of Botany, 54, 4, 345-350.
 16. Johannsmeier, M.F. 1975. Commercial beekeeping in the Transvaal in relation to honeyplants. Proc. I Congr. ent. Soc. sth. Afr., 181-184.
 17. Johannsmeier, M.F. 1984. A "new" honey plant of the potato family: *Lycium*. South African Bee Journal, 56, 5, 108-112.
 18. Johannsmeier, M.F. 1988. Beekeeping potential of native flora of South Africa. South African Bee Journal, 60, 5, 98-108.
 19. Johannsmeier, M.F. 1995. Beeplants of the South-Western Cape: nectar and pollen sources of honeybees. Plant Protection Research Institute, Department of Agriculture, Pretoria, 59pp.
 20. Johannsmeier, M. and Allsopp, M. 1995. Beeplants for South African suburban gardens. South African Bee Journal, 67, 3, 70-75.
 21. Kennard, R. 1988. "Hlalwane" in Natal. South African Bee Journal, 60, 6, 122-125.
 22. Köttner, M. 1991. *Apis mellifera capensis* Escholtz; Bienenhaltung, Pollenfallenversuche und pollenanalytische Untersuchungen (*Apis mellifera capensis* Escholtz; beekeeping, pollen trap experiments & pollen analysis).
 23. le Roux, P.J. 1985. The need for selection and breeding of non-commercial tree species. South African Forestry Journal, 135, 81-85.
 24. Lear, E. 1995. Cover photograph. South African Bee Journal, 67, 3, cover and 69.
 25. Lear, E. 1996a. Cover photograph. South African Bee Journal, 68, 3, cover and 67.
 26. Lear, E. 1996b. Cover photograph. South African Bee Journal, 68, 4, cover and 99.
 27. Loock, E.E.M. 1983. Eucalypts suitable for honey production. South African Bee Journal, 55, 2, 42-46.
 28. Manning, J. and Goldblatt, P. 1999. Busy bodies: the power of pollinators. Africa - Environment & Wildlife, 7, 3, 50-57.
 29. May, A.F. 1961. Beekeeping in southern Africa. Haum, Cape Town, 210pp..
 30. McDonald, D.J. and van der Walt, J.J.A. 1992. Observations on the pollination of *Pelargonium tricolor*, section *Campylia* (Geraniaceae). South African Journal of Botany, 58, 5, 386-392.
 31. Milton, S.J. & Dean, W.R.J. 1988. Flower and fruit production of *Rhigozum obovatum* (Bignoniaceae) in road reserves and grazing land. South African Journal of Science, 84, 798-799.
 32. Mostert, D.P. 1974. The biology of *Promerops cafer* with special reference to the role of the nectar and satellite insect fauna of *Protea repens* in the reproductive cycle. MSc (Stellenbosch).
 33. Mostert, D.P., Siegfried, W.R. and Louw, G.N. 1980. Protea nectar and satellite fauna in relation to the food requirements and pollinating role of the Cape Sugarbird. South African Journal of Science, 76, 409-412.
 34. Murless, P. 1994a. Beekeeping potential in the Estcourt area: Natal. South African Bee Journal, 66, 3, 64-69.
 35. Murless, P. 1994b. Two and a half years of beekeeping in King William's Town, South Africa. South African Bee Journal, 66, 5, 100-105.
 36. Murless, P.H. 1995. Beekeeping as a Conservation Clubs activity. South African Bee Journal, 67, 3, 80-83.
 37. Nicolson, S.W. and W.-Worswick, P.V. 1990. Sodium and potassium concentrations in floral nectars in relation to foraging by honey bees. South African Journal of Zoology, 25, 2, 93-96.
 38. Phillips, J.F.V. 1925. *Platylophus trifolius* D. Don: a contribution to its ecology. South African Journal of Science, 22, 144-160.
 39. Phillips, J.F.V. 1927. *Ekebergia capensis* Sparrm. ("Essenhout") in the Knysna region: a preliminary ecological note. South African Journal of Science, 24, 216-224.
 40. Pooley, E. 1998. A field guide to wild flowers KwaZulu - Natal and the Eastern Region. Natal Flora Publications Trust, Durban, 630pp.
 41. Poynton, R.J. 1973. 200 selected indigenous and exotic species: how to recognize and grow them. In Our Green Heritage: The South African Book of Trees, Immelman, W.F.E., Wicht, C.L. and Ackern
 42. Scharf, H.T. 1986. Honey Dawn Bee Farm. South African Bee Journal, 58, 6, 133-134.
 43. Smith, C.A. 1966. Common names of South African plants. Botanical Survey Memoirs 35, Department of Agricultural Technical Services, 642pp.
 44. Steiner, K.E. 1990. The *Diascia* (Scrophulariaceae) window: an orientation cue for oil-collecting bees. Botanical Journal of the Linnean Society, 102, 175-195.
 45. Stirton, C.H. 1977a. The pollination of *Canvalia virosa* by Xylcopid and Megachilid bees. Bothalia, 12, 2, 225-227.
 46. Stirton, C.H. 1977b. Broad-spectrum pollination of *Plectranthus neochilus*. Bothalia, 12, 2, 229-230.
 47. Struck, M. 1994. Flowers and their insect visitors in the arid winter rainfall region of southern Africa: observations on permanent plots. Insect visitation behaviour. Journal of Arid Environments, 28, 51-74.
 48. Struck, M. 1997. Floral divergence and convergence in the genus *Pelargonium* (Geraniaceae) in southern Africa: ecological and evolutionary considerations. Plant Systematics and Evolution, 208, 71-97.
 49. Taylor, F. 1937. Times and intensities of South African honey flows. South African Bee Journal, 12, 4, 4-5.
 50. van Steenis, C.G.G.J. 1978. Gregarious flowering in the monocarpic genus *Isoglossa* (Acanthaceae). Bothalia, 12, 553.
 51. Venter, F. and Venter, J.-A. 1996. Making the most of indigenous trees. Briza Publications, Pretoria, 305pp.
 52. Wise, A. 1985. Wheelchair beekeeping. South African Bee Journal, 57, 6, 135-137.
 53. Zietsman, P.C. 1993. Pollination in *Pelargonium dolomiticum* Knuth (Geraniaceae). South African Journal of Botany, 59, 2, 259-264.
 54. Zietsman, P.C. 1998. Pollination biology of *Cotyledon orbiculata* L. var. *dactyloopsis* Toelken (Crassulaceae). Navorsinge van die Nasionale Museum Bloemfontein, 14, 4, 81-96.
- A. Anderson *et al.* (1983) (See above, Ref. # 1).
- B. Johannsmeier (1995) (See above, Ref. # 19).
- C. May (1961) (See above, Ref. # 29).
- D. Pooley (1998) (See above, Ref. # 40).
- E. Retief, E. and Herman, P.P.J. 1997. Plants of the northern provinces of South Africa: keys and diagnostic characters. Strelitzia 6, 1-681.

Appendix 6A. Areas (cm²) of comb utilised per colony per observation day in the Andries Vosloo Kudu Reserve (1992-1993) (Observations = J. Katanga, unpublished data).

[illegible]

4	1993	2	24	14450.63	203.19	4594.35	80.79	2692.20	1675.00	1017.20	2589.54	0.00	0.00	0.00	1.00
4	1993	2	2	14450.63	33.00	5130.70	357.58	559.56	308.55	251.01	2589.54	0.00	0.00	0.00	1.00
7	1993	2	11	10443.15	1750.20	4129.02	226.83	2778.86	1298.19	1480.67	1189.53				
7	1993	2	24	10605.37	1986.48	2391.68	441.86	2891.47	1442.25	1449.22	1189.53	0.00	0.00	0.00	1.00
9	1993	2	24	14542.84	6880.87	1600.79	570.70	1250.51	950.59	299.92	481.42	0.00	0.00	0.00	5.00
9	1992	2	11	14542.84	7093.39	1481.56	422.78	1567.68	839.12	728.56	481.42	0.00	0.00	0.00	1.00
10	1993	2	24	6879.24	473.02	45.19	114.97	319.80	169.53	150.27	599.33	0.00	0.00	0.00	7.00
10	1992	2	11	6879.24	579.51	539.75	95.76	24.08	24.08	0.00	599.33	0.00	0.00	0.00	7.00
11	1993	2	11	6746.67	63.66	454.30	112.25	1086.86	677.36	409.50	546.29	0.00	0.00	0.00	7.00
11	1993	2	24	6746.67	36.92	816.73	88.33	1257.76	737.35	520.41	546.29	0.00	0.00	0.00	3.00
14	1993	2	24	6775.05	61.10	507.40	49.30	1019.60	508.75	510.85	437.95	0.00	0.00	0.00	4.00
14	1993	2	11	6775.05	2.53	1131.14	119.63	0.00	0.00	0.00	437.95	6.67	6.67	0.00	1.00
1993.1	1993	2	24	8755.96	1714.38	779.94	149.36	3753.29	2174.75	1578.54	922.17	375.11	204.84	170.27	1.00
1993.1	1993	2	11	7217.24	2325.85	638.33	660.26	2092.10	1019.32	1072.78	469.46	0.00	0.00	0.00	1.00
1993.2	1993	2	11	7285.68	687.76	2021.16	259.64	1956.78	443.89	1512.89	782.89	118.25	0.00	118.25	4.00
1993.2	1993	2	24	8880.92	501.29	1373.69	57.82	3124.21	2393.38	730.83	861.67	288.42	288.42	0.00	4.00
1993.5	1993	2	24	7085.47	556.98	653.69	207.97	2820.39	1693.56	1126.83	244.56	35.26	35.26	0.00	1.00
P1	1992	2	11	11041.83	13.90	1578.99	642.94	1140.65	410.12	730.53	1850.48	0.00	0.00	0.00	16.00
P1	1993	2	24	11041.83	125.92	946.76	304.44	2546.37	1561.30	985.07	1850.48	0.00	0.00	0.00	16.00
4	1993	3	24	14450.63	57.09	3437.26	140.03	591.24	173.33	417.91	2589.54	0.00	0.00	0.00	2.00
4	1993	3	10	14450.63	168.59	1675.37	10.26	65.54	65.54	0.00	2589.54	0.00	0.00	0.00	2.00
7	1993	3	10	10693.03	1841.16	2909.42	170.00	1523.40	1066.38	457.02	1189.53				
7	1993	3	24	10693.03	1365.63	2504.41	94.52	1400.33	381.23	1019.10	1189.53	0.00	0.00	0.00	1.00

9	1993	3	10	14542.84	5844.95	1308.79	445.43	614.51	21.85	592.66	481.42	0.00	0.00	0.00	5.00
9	1993	3	24	14542.84	5359.89	483.42	355.03	617.63	120.65	496.98	481.42	0.00	0.00	0.00	6.00
10	1993	3	10	6879.24	181.71	388.30	11.02	152.00	152.00	0.00	599.33	0.00	0.00	0.00	7.00
10	1993	3	24	6879.24	0.00	209.01	0.00	0.00	0.00	0.00	599.33	0.00	0.00	0.00	7.00
11	1993	3	10	6746.67	4.20	205.33	12.27	86.26	86.26	0.00	546.29	0.00	0.00	0.00	7.00
11	1993	3	24	6746.67	0.00	0.00	0.00	0.00	0.00	0.00	546.29	0.00	0.00	0.00	7.00
14	1993	3	24	6775.05	0.00	0.00	0.00	0.00	0.00	0.00	437.95	0.00	0.00	0.00	1.00
14	1993	3	10	6775.05	53.67	642.22	85.55	371.95	118.81	253.14	437.95	0.00	0.00	0.00	2.00
1993.1	1993	3	24	8755.96	0.00	40.55	0.00	0.00	0.00	0.00	922.17	0.00	0.00	0.00	1.00
1993.1	1993	3	10	8755.96	739.84	151.41	57.98	422.45	422.45	0.00	922.17	3.69	3.69	0.00	1.00
1993.2	1993	3	10	8880.92	208.03	57.82	4.01	573.18	573.18	0.00	861.67	0.00	0.00	0.00	5.00
1993.2	1993	3	24	8880.92	0.00	1460.42	0.00	0.00	0.00	0.00	861.67	0.00	0.00	0.00	5.00
1993.5	1993	3	24	7085.47	0.00	2619.77	2.50	0.00	0.00	0.00	244.56				
1993.5	1993	3	10	7085.47	333.87	470.19	3.57	40.75	40.75	0.00	244.56				
P1	1993	3	24	11041.83	0.00	179.02	209.56	7.50	7.50	0.00	1850.48	0.00	0.00	0.00	15.00
P1	1993	3	10	11041.83	36.29	426.52	503.27	675.96	675.96	0.00	1850.48	0.00	0.00	0.00	16.00
4	1993	4	7	14450.63	11.28	1977.64	33.73	679.82	230.27	449.55	2589.45	0.00	0.00	0.00	2.00
4	1993	4	21	14450.63	0.00	1171.78	74.58	268.66	0.00	268.66	2589.54	0.00	0.00	0.00	2.00
7	1993	4	21	10783.03	513.76	536.43	104.20	591.39	257.44	333.95	1189.53				
7	1993	4	7	10783.03	928.63	785.48	33.88	456.03	403.96	52.07	1189.53	0.00	0.00	0.00	1.00
9	1993	4	7	14542.84	4768.18	0.00	221.62	928.32	654.75	273.57	481.42	0.00	0.00	0.00	6.00
9	1993	4	21	14542.84	3852.00	171.98	204.20	699.20	205.39	493.81	481.42	0.00	0.00	0.00	6.00
10	1993	4	7	6879.15	0.00	0.00	0.00	0.00	0.00	0.00	599.33	0.00	0.00	0.00	7.00
93.6	1993	4	21	8065.16	1267.42	784.75	309.28	1176.82	631.45	545.37	976.20				

[illegible]

7	1993	6	17	10783.03	0.00	0.00	136.66	439.99	154.62	285.37	1189.53	0.00	0.00	0.00	1.00
7	1993	6	2	10783.03	44.66	134.55	173.95	717.16	208.32	508.84	1189.53	0.00	0.00	0.00	1.00
9	1993	6	2	14542.84	891.72	0.00	185.43	49.94	49.94	0.00	481.42				
93.13	1993	6	17	13894.80	124.57	2663.72	253.37	930.75	179.38	751.37	1726.10				
93.13	1993	6	2	13894.80	142.15	2348.57	185.80	349.63	71.47	278.16	1726.10				
93.14	1993	6	17	12307.06	0.00	422.14	12.13	0.00	0.00	0.00	71.40				
93.14	1993	6	2	12307.06	0.00	0.00	36.15	0.00	0.00	0.00	71.40				
93.15	1993	6	2	12225.28	134.19	252.13	44.24	364.00	50.38	313.62	956.93				
93.15	1993	6	17	12225.28	11.55	518.43	16.38	0.00	0.00	0.00	956.93				
93.6	1993	6	2	8065.16	818.55	410.62	39.77	0.00	0.00	0.00	976.20				
93.6	1993	6	17	8065.16	527.85	591.25	147.27	272.98	41.42	231.56	976.20				
4	1992	7	14	8623.96	528.38	1096.20	348.75	312.45	11.45	0.00	363.30	0.00	0.00	0.00	1.00
4	1992	7	29	8623.96	505.86	0.00	557.00	652.83	647.28	5.55	363.30	0.00	0.00	0.00	1.00
5	1992	7	29	8791.07	1128.28	2080.58	112.25	724.52	525.17	199.35	185.24				
5	1992	7	14	8746.36	1457.57	1147.50	146.75	130.73	0.00	130.73	185.24				
7	1993	7	5	10783.03	0.00	566.98	167.02	779.91	358.45	421.46	1189.53	0.00	0.00	0.00	1.00
7	1992	7	14	7850.94	1398.96	800.67	503.50	2197.73	1131.79	1065.94	349.97	332.54	164.61	167.93	
7	1992	7	29	8526.24	1491.78	827.95	171.50	3357.04	2264.68	1092.36	349.97	6.25	6.25		
7	1993	7	21	10783.03	0.00	625.66	45.13	586.59	289.18	297.41	1189.53	0.00	0.00	0.00	1.00
8	1992	7	29	7415.03	631.56	2546.60	249.00	437.94	437.94	0.00	130.73	0.00	0.00	0.00	2.00
8	1992	7	14	7415.03	513.75	2602.11	253.75	888.46	685.13	203.33	130.73	0.00	0.00	0.00	1.00
9	1992	7	14	8199.79	828.51	1610.61	197.00	1141.58	545.98	595.60	159.10				
9	1992	7	29	8199.79	851.68	1382.35	219.00	1947.32	1254.43	692.89	159.10				
93.13	1993	7	21	13894.80	37.85	972.00	250.16	1325.50	821.77	503.73	1726.10	40.18	40.18		

93.13	1993	7	5	13894.80	72.94	1545.51	153.36	1252.48	605.20	647.28	1726.10	96.58	22.15	74.43	
93.14	1993	7	5	12307.06	0.00	0.00	4.88	0.00	0.00	0.00	71.40				
93.15	1993	7	21	12225.28	0.00	240.15	118.51	259.22	108.94	150.28	956.93				
93.15	1993	7	5	12225.28	0.00	885.42	37.38	151.46	40.94	110.52	956.93				
93.6	1993	7	21	8065.16	285.32	711.69	222.10	858.22	213.85	644.37	976.20				
93.6	1993	7	5	8065.16	362.95	415.92	232.55	718.70	332.02	386.68	976.20				
I	1992	7	14	6841.79	0.00	1165.98	216.50	0.00	0.00	0.00	790.41	0.00	0.00	0.00	6.00
I	1992	7	29	6841.79	0.00	1334.05	210.50	0.00	0.00	0.00	790.41	0.00	0.00	0.00	5.00
II	1993	7	14	8481.04	745.37	1581.09	747.75	984.33	800.73	183.60	51.64	0.00	0.00	0.00	29.00
II	1993	7	29	8481.04	437.54	524.17	538.75	184.43	184.43	0.00	51.64	0.00	0.00	0.00	17.00
III	1992	7	29	5880.96	450.86	770.29	159.00	348.45	293.21	55.24	1605.67				
III	1992	7	14	5880.96	469.70	516.85	71.75	132.54	0.00	132.54	1605.67				
P1	1992	7	29	6383.23	558.03	829.45	21.00	687.05	572.18	114.87	502.31	0.00	0.00	0.00	1.00
P1	1992	7	14	6383.23	802.26	1214.20	66.50	394.92	271.99	122.93	502.31				
P2	1992	7	14	6871.82	18.15	552.17	127.28	422.67	311.29	111.38	635.94	0.00	0.00	0.00	3.00
P2	1992	7	29	6871.82	16.27	535.43	142.00	512.84	413.60	99.24	635.94	0.00	0.00	0.00	3.00
4	1992	8	26	8849.30	59.19	506.88	297.75	1548.15	838.12	710.03	589.53	16.74	14.06	2.68	2.00
4	1992	8	12	8623.96	344.61	0.00	534.75	798.32	454.92	343.40	363.30	0.00	0.00	0.00	1.00
5	1992	8	26	9052.53	272.59	1231.41	159.75	1876.23	1001.44	874.79	636.61				
5	1992	8	12	8846.84	1204.12	771.30	328.75	1073.59	588.78	484.81	185.24				
7	1993	8	25	10783.03	0.00	51.15	193.91	444.60	305.67	138.93	1189.53	0.00	0.00	0.00	1.00
7	1992	8	12	8626.24	1047.58	479.56	274.00	2118.05	1351.47	766.58	349.97	232.37	232.37		
7	1992	8	26	8906.79	144.56	1798.57	391.75	2258.11	1094.07	1164.04	1189.53	821.01	77.19	743.82	2.00
7	1993	8	12	10783.03	0.00	101.88	109.96	459.02	204.37	254.65	1189.53	0.00	0.00	0.00	2.00

8	1992	8	12	7415.03	523.98	1565.89	188.25	431.17	51.23	379.94	130.73	0.00	0.00	0.00	5.00
8	1992	8	26	7486.37	400.65	2126.34	226.75	440.16	110.47	329.69	130.73	0.00	0.00	0.00	4.00
9	1992	8	12	8458.32	702.72	715.09	175.50	1729.34	1344.18	385.16	159.10				
9	1992	8	26	8967.41	379.51	2543.76	255.25	2506.40	1622.91	883.49	221.06				
93.13	1993	8	12	13894.80	9.57	122.62	305.88	339.65	117.23	222.42	1726.10				
93.13	1993	8	25	13894.80	0.00	0.00	170.96	0.00	0.00	0.00	1726.10				
93.15	1993	8	12	12225.28	0.00	75.58	16.13	1.13	1.13	0.00	956.93				
93.15	1993	8	25	12225.28	0.00	0.00	78.37	1.13	1.13	0.00	956.93				
93.6	1993	8	25	8065.16	59.12	393.92	93.99	131.20	0.75	130.45	976.20				
93.6	1993	8	12	8065.16	150.36	661.13	165.24	254.99	55.28	199.71	976.20				
I	1992	8	12	6841.79	0.00	0.00	294.50	0.00	0.00	0.00	790.41	0.00	0.00	0.00	7.00
I	1992	8	26	6841.79	0.00	0.00	339.25	234.80	23.08	211.72	790.41	122.79	15.90	106.89	7.00
II	1992	8	12	8481.04	394.50	0.00	670.25	10.54	10.54	0.00	51.64	0.00	0.00	0.00	17.00
II	1992	8	26	8531.39	282.50	511.36	496.25	471.88	291.37	180.51	187.75	0.00	0.00	0.00	19.00
III	1992	8	26	5880.96	405.34	247.01	35.75	642.26	303.90	338.36	1605.67				
III	1992	8	12	5880.96	671.20	0.00	211.25	357.19	221.23	135.96	1605.67				
P1	1992	8	12	6383.23	440.51	0.00	450.75	963.41	521.15	442.26	502.31	0.00	0.00	0.00	1.00
P1	1992	8	26	6423.23	121.12	1248.07	186.75	2251.82	1182.58	1069.24	502.31				
P2	1992	8	12	6871.82	0.00	0.00	120.50	429.29	267.08	162.21	635.94	0.00	0.00	0.00	3.00
P2	1992	8	26	6871.82	0.00	0.00	30.00	656.38	236.08	420.30	635.94	0.00	0.00	0.00	2.00
4	1992	9	23	9897.34	0.00	0.00	370.25	4746.93	1877.06	2869.87	1754.13	547.57	200.27	347.30	1.00
4	1992	9	9	9897.34	0.00	258.42	206.96	4184.16	2277.28	1906.88	1754.13	261.85	207.77	54.08	2.00
5	1992	9	9	9052.53	40.53	643.01	318.45	4433.05	2022.79	2410.26	636.61	160.69	141.01	19.68	
5	1992	9	23	9052.53	18.25	44.93	169.75	4702.53	1733.25	2969.28	636.61	71.73	71.73		

7	1993	9	8	10783.03	0.00	12.63	147.13	940.33	196.05	744.28	1189.53	0.00	0.00	0.00	1.00
7	1992	9	9	8906.79	564.09	918.36	581.85	4043.05	2452.42	1590.63	1189.53	559.50	559.50	0.00	5.00
7	1992	9	23	8906.79	774.67	1419.80	67.00	3571.24	1020.97	2550.27	1189.53	70.62	70.62	0.00	8.00
8	1992	9	23	7486.37	168.07	659.81	239.72	244.69	54.27	190.42	130.73	0.00	0.00	0.00	5.00
8	1992	9	9	7486.37	270.41	737.49	404.72	410.14	80.88	329.26	130.73	0.00	0.00	0.00	4.00
9	1992	9	9	10269.42	178.20	2661.06	606.98	3560.33	2222.25	1338.08	221.06				
9	1992	9	23	10633.98	228.80	2014.81	62.25	5026.68	2842.22	2184.46	221.06				
93.13	1993	9	8	13894.80	0.00	0.00	102.82	846.73	0.00	846.73	1726.10	209.21	0.00	209.21	9.00
93.15	1993	9	8	12225.28	0.00	0.00	29.64	1.13	1.13	0.00	956.93				
93.6	1993	9	8	8065.16	0.00	0.00	78.35	0.00	0.00	0.00	976.20				
I	1992	9	23	6841.79	0.00	0.00	227.00	8.01	8.01	0.00	790.41	11.70	11.70	0.00	6.00
I	1992	9	9	6841.79	0.00	168.72	348.89	34.34	27.81	6.53	790.41	66.10	37.07	29.03	5.00
II	1992	9	23	8531.39	106.53	506.43	335.36	191.01	151.39	39.62	187.75	0.00	0.00	0.00	9.00
II	1992	9	9	8531.39	219.27	735.21	388.99	187.14	112.85	74.29	187.75	0.00	0.00	0.00	17.00
III	1992	9	23	6037.30	35.27	83.19	220.75	350.66	350.66	0.00	1605.67	132.31	132.31	0.00	5.00
III	1992	9	9	5880.96	53.37	0.00	135.14	896.43	762.67	133.76	1605.67	171.63	53.53	118.10	
P1	1992	9	9	6749.13	1.33	493.00	223.55	3151.75	1963.76	1187.99	736.18	204.59	9.33	195.26	1.00
P1	1992	9	23	8759.72	67.93	93.58	207.50	5094.34	2550.12	2544.22	1349.53	522.74	351.40	161.34	3.00
P2	1992	9	23	6871.82	0.00	0.00	69.75	973.69	483.81	489.88	635.94	0.00	0.00	0.00	1.00
P2	1992	9	9	6871.82	0.00	217.59	115.17	1019.21	763.44	255.77	635.94				
4	1992	10	21	9897.34	181.54	1158.64	741.39	2713.12	1751.68	961.44	1754.13	1237.48	738.14	499.34	4.00
4	1992	10	7	9897.34	599.72	538.01	1500.83	2999.07	1574.19	1424.88	1754.13	695.26	486.89	208.37	3.00
5	1992	10	7	9107.25	478.02	724.86	554.96	3442.92	1756.32	1686.60	636.61	182.12	0.00	182.12	1.00
5	1992	10	21	9374.98	42.20	686.61	411.38	4508.46	2522.21	1986.25	904.31	591.14	591.14	0.00	5.00

7	1992	10	21	8906.79	418.48	1268.57	977.38	1920.42	825.36	1095.06	1189.53	122.71	86.01	36.70	5.00
7	1992	10	7	8906.79	538.05	2091.51	517.71	518.86	0.00	518.86	1189.53	3.11	3.11		5.00
8	1992	10	7	7486.37	165.22	602.00	233.89	185.21	0.00	185.21	130.73	0.00	0.00	0.00	4.00
9	1992	10	21	11582.75	363.39	3631.53	759.73	2654.19	1867.73	786.46	221.06	75.99	75.99	0.00	2.00
9	1992	10	7	11217.71	470.63	3123.85	366.72	3827.51	2689.16	1138.35	221.06	78.63	0.00	78.63	3.00
10	1992	10	21	6879.24	0.00	0.00	305.87	3312.32	1831.61	1480.71	599.33	108.32	108.32	0.00	1.00
11	1992	10	21	5142.69	0.00	0.00	129.02	1793.02	1029.69	763.33	16.11				
13	1992	10	21	6314.25	0.00	0.00	229.83	2354.76	1680.55	674.21	429.38	94.10	0.00	94.10	1.00
14	1992	10	21	4736.12	0.00	320.03	75.25	1045.00	388.33	656.67	202.38				
15	1992	10	21	6324.51	0.00	1287.38	445.30	1923.04	1402.22	520.82	181.82				
16	1992	10	21	6069.22	0.00	88.17	217.43	824.17	226.93	597.24	383.09				
I	1992	10	21	6841.79	0.00	0.00	153.22	0.00	0.00	0.00	790.41	0.00	0.00	0.00	6.00
I	1992	10	7	6841.79	0.00	35.67	302.00	0.00	0.00	0.00	790.41	3.35	3.35	0.00	6.00
II	1992	10	7	8531.39	0.00	80.96	219.75	158.16	158.16	0.00	187.75	0.00	0.00	0.00	16.00
II	1992	10	21	8531.39	0.00	0.00	160.25	84.08	84.08	0.00	187.75	0.00	0.00	0.00	18.00
III	1992	10	21	6037.30	15.80	0.00	197.92	99.33	99.33	0.00	1605.67	30.12	30.12	0.00	3.00
III	1992	10	7	6037.30	15.83	1221.09	374.10	333.78	24.13	309.65	1605.67	239.70	13.29	218.71	2.00
P1	1992	10	7	10516.83	1331.34	1237.47	157.62	4026.92	2674.65	1352.27	1746.93	485.22	137.69	347.53	11.00
P1	1992	10	21	11014.09	955.15	483.95	291.45	3053.29	2156.05	897.24	1746.93	667.59	527.50	140.09	16.00
P2	1992	10	21	6871.82	0.00	0.00	146.64	67.68	34.56	33.12	635.94	0.00	0.00	0.00	7.00
P2	1992	10	7	6871.82	0.00	0.00	140.84	430.44	196.19	234.25	635.94	5.59	5.59	0.00	6.00
4	1992	11	18	14292.70	3192.37	1304.73	1003.90	2767.17	2000.81	766.36	2589.54	867.81	623.24	244.57	
5	1992	11	18	12959.83	3279.30	1270.87	373.13	3320.78	2201.78	1119.00	2335.40	510.09	305.56	204.53	1.00
7	1992	11	18	8906.79	126.19	1645.59	715.93	2511.93	1212.26	1299.67	1189.53	12.34	12.34	0.00	5.00

9	1992	11	18	12392.26	1823.31	3055.76	839.66	3610.18	2650.82	959.36	221.06	0.00	0.00	0.00	2.00
10	1992	11	18	6879.24	0.00	277.37	40.85	3822.59	2455.43	1367.16	599.33	349.69	349.69	0.00	5.00
11	1992	11	18	6424.67	0.00	319.70	186.54	2076.06	1304.85	771.21	308.07	44.76	44.76	0.00	1.00
13	1992	11	18	7602.31	1110.14	123.51	28.28	2934.78	2356.24	578.54	429.38	174.80	174.80	0.00	8.00
14	1992	11	18	6775.06	504.94	1209.76	60.35	2004.27	1566.32	437.95	437.78	6.96	6.96		
15	1992	11	18	7594.32	1682.74	98.97	238.16	3108.00	2510.29	597.71	643.12	479.39	451.26	28.13	
16	1992	11	18	7209.65	2372.11	6.81	212.40	2823.23	2236.53	586.70	663.22	263.26	263.26		
III	1992	11	18	6037.30	12.45	0.00	250.37	458.20	303.25	154.95	1605.67	0.00	0.00	0.00	4.00
P1	1992	11	18	11041.83	253.25	98.24	213.75	0.00	0.00	0.00	1850.48	0.00	0.00	0.00	15.00
P2	1992	11	18	6871.82	0.00	0.00	109.56	11.04	11.04	0.00	635.94	0.00	0.00	0.00	3.00
4	1992	12	2	14450.63	2019.20	664.63	947.22	3447.63	2424.74	1022.89	2589.54	4.02	4.02	0.00	1.00
4	1992	12	16	14450.63	195.85	53.06	104.37	3044.23	1556.08	1488.15	2589.54	0.00	0.00	0.00	1.00
4	1992	12	30	14450.63	17.42	48.19	17.78	1394.13	1394.13	0.00	2589.54	5.04	5.04	0.00	1.00
5	1992	12	16	12959.83	457.54	0.00	120.64	881.93	114.40	767.53	2335.40				
5	1992	12	2	12959.83	2282.37	139.92	573.17	2529.25	1299.96	1229.29	2335.40				
5	1992	12	30	12959.83	0.00	0.00	167.16	2086.50	1441.38	645.12	2335.40	3.97	3.97	0.00	1.00
7	1992	12	16	9217.63	255.33	1206.47	633.59	2956.77	1701.08	1255.69	1189.53	0.00	0.00	0.00	3.00
7	1992	12	30	9754.01	825.54	933.17	489.22	2665.91	1740.19	925.72	1189.53	0.00	0.00	0.00	1.00
7	1992	12	2	8906.79	44.11	1410.21	711.24	3352.71	1883.24	1469.47	1189.53	0.00	0.00	0.00	3.00
9	1992	12	2	13772.16	2065.33	3389.76	1192.76	3539.97	2272.40	1267.57	481.42	0.90	0.90	0.00	2.00
9	1992	12	30	14542.84	7787.93	1859.58	454.01	1185.15	952.97	232.18	481.42	0.00	0.00	0.00	1.00
9	1992	12	16	14542.84	5521.25	1789.79	337.58	3396.92	3044.65	352.27	481.42	151.44	151.44	0.00	2.00
10	1992	12	16	6879.24	170.82	670.06	212.30	66.28	66.28	0.00	599.33	0.00	0.00	0.00	11.00
10	1992	12	30	6879.24	730.65	1433.91	181.04	400.95	244.81	156.14	599.33	0.00	0.00	0.00	9.00

10	1992	12	2	6879.24	0.00	24.20	213.10	516.60	516.60	0.00	599.33	0.00	0.00	0.00	9.00
11	1992	12	16	6746.67	26.02	699.32	301.11	1733.25	1077.36	655.89	546.29	0.00	0.00	0.00	3.00
11	1992	12	2	6746.67	0.00	747.52	347.71	1921.90	1215.08	706.82	546.29	0.00	0.00	0.00	1.00
11	1992	12	30	6746.67	71.21	643.55	283.76	1559.72	1177.01	382.71	546.29	0.00	0.00	0.00	6.00
13	1992	12	16	7602.31	0.00	0.00	0.00	0.00	0.00	0.00	429.38	0.00	0.00	0.00	5.00
13	1992	12	2	7602.31	0.00	0.00	4.33	0.00	0.00	0.00	429.38	0.00	0.00	0.00	4.00
14	1992	12	30	6775.06	0.00	0.00	14.50	0.00	0.00	0.00	437.78				
14	1992	12	16	6775.06	26.23	0.00	0.00	0.00	0.00	0.00	437.78				
14	1992	12	2	6775.06	133.48	0.00	7.85	0.00	0.00	0.00	437.78				
15	1992	12	2	7594.32	425.94	0.00	216.90	397.18	397.18	0.00	643.12	0.86	0.86		
15	1992	12	16	7594.32	0.00	0.00	69.36	477.44	0.00	477.44	643.12				
15	1992	12	30	7594.32	0.00	0.00	7.57	1717.28	1304.81	412.47	643.12				
16	1992	12	30	7209.65	0.00	0.00	32.99	2416.30	1760.29	656.01	663.22	135.64	135.64		
16	1992	12	16	7209.65	0.00	0.00	111.01	1120.79	563.47	557.32	663.22				
16	1992	12	2	7209.65	840.88	0.00	263.73	333.76	333.76	0.00	663.22				
III	1992	12	2	6037.30	0.00	0.00	174.88	188.91	77.79	111.12	1605.67	0.00	0.00	0.00	4.00
III	1992	12	16	6037.30	0.00	0.00	0.00	0.00	0.00	0.00	1605.67	0.00	0.00	0.00	4.00
P1	1992	12	30	11041.83	0.00	0.00	272.47	439.76	277.38	162.38	1850.48	0.00	0.00	0.00	16.00
P1	1992	12	16	11041.83	0.00	446.39	358.07	662.12	117.74	544.38	1850.48	0.00	0.00	0.00	16.00
P1	1992	12	2	11041.83	159.65	663.38	612.49	944.87	520.81	424.06	1850.48	0.00	0.00	0.00	16.00

Appendix 8.A. A list of the key results obtained in this study and others selected from the literature.

Chapter	Key results of this study	Notes
HONEYBEE FORAGE PLANTS		
Two: Location	1. Documents the location of 39 scale-hive records. These locations lie within the fynbos, grassland, nama karoo, savanna, succulent karoo and thicket biomes. None occur within the forest biome.	Known scale-hive studies: Canada (Mitchener, 1955; Szabo, 1982 & 1996), Germany (Gerlach, 1985), South Africa (Schnettler, 1946; Johannsmeier, 1988), Tanzania (Smith, 1960), United Kingdom (McLellan, 1977) and United States (Hambleton, 1925; Munro, 1929; Jorgensen & Markham, 1946; Moffett & Parker, 1953).
		Scale-hive records provide the best combined spatial and temporal phenological data coverage for honeybees in South Africa.
Three: Taxonomy & Distribution	<p>1. Floristic composition.</p> <p>a. Known honeybee flora (number of indigenous families in brackets) = 137 (91) families, 532 (241) genera and 944 (464, excl. hybrids) species (incl. hybrids).</p> <p>b. Best represented families by genus (indigenous & exotic) (number of genera in brackets) = Asteraceae (58), Fabaceae (54), Mesembryanthemaceae (19), Rosaceae (17), Lamiaceae (15) and Myrtaceae (15).</p> <p>c. Best represented families by species (indigenous & exotic) (number of species in brackets) = Fabaceae (119), Myrtaceae (104), Asteraceae (96), Proteaceae (50) and Rosaceae (31).</p> <p>d. Orchidaceae are the largest family with no recorded honeybee forage plants.</p> <p>e. The five best represented indigenous genera (number of species in brackets) are <i>Erica</i> (15), <i>Aloe</i> (14), <i>Pelargonium</i> (14), <i>Aspalathus</i> (13) and <i>Protea</i> (12).</p> <p>f. The largest genera on the subcontinent not recorded as honeybee forage plants in South Africa (number of species in brackets) are <i>Conophytum</i> (301), <i>Delosperma</i> (159), <i>Haworthia</i> (153), <i>Restio</i> (113) and <i>Stapelia</i> (88).</p> <p>2. Reward category (number of species).</p> <p>a. Indigenous. Nectar & Pollen = 203, Nectar = 104, Pollen = 63, Unknown = 94, Total = 464.</p> <p>b. Exotic. Nectar & Pollen = 330, Nectar = 58, Pollen = 74, Unknown = 18, Total = 480.</p>	The most important sources of information with regard to the rewards offered by honeybee forage plants in South Africa are May (1961), Anderson <i>et al.</i> (1983), Johannsmeier (1995) and Johannsmeier & Allsopp (1995).

c. Total. Nectar & Pollen = 533, Nectar = 162, Pollen = 137, Unknown = 112, Total = 944.

3. Nectar composition.

a. The overwhelming majority of species have nectar sugar compositions which are either hexose-dominant (50.6 %) or sucrose-dominant (40.7 %). These percentages include species which may fall into more than one category.

The sugar composition is possibly the least significant of the tripartite combination of features by which honeybees evaluate the quality of a nectar source. Free (1993) suggested the other two, concentration and volume were the most important factors governing the value of nectar to honeybees.

Comparative tests have shown that sucrose is preferred by honeybees to other sugars (Wykes, 1952; Waller & Buchman, 1981).

4. Distribution.

The simple arithmetic conclusion is that 334 genera native to and pandemic in Africa are closely associated with honeybees, against about 35 lacking the honeybee connection. The argument is circumstantial but the odds strongly favour the idea that bee plant distribution and bees themselves tend to go hand in hand. (Hepburn & Radloff, 1998 p.17)

a. The overwhelming majority (> 80%) of indigenous forage plant families are cosmopolitan or pantropic in nature.

b. More than half of the 21 best represented indigenous genera (number of genera in brackets) have their centre of diversity within the fynbos (13), with the rest centred within the savanna (6), grassland (2), succulent karoo (1) and nama karoo (1) biomes. *Aloe* has no centre of diversity. *Asclepias*, *Heliophila*, *Lycium* and *Rhus* are centred on two biomes.

5. Conservation status (*sensu* Hilton-Taylor, 1996a&b).

Probably extinct in wild = *Podalyria microphylla*,
Endangered = *Protea pudens*, Vulnerable = *Erica bauera*, *Leucadendron daphnoides*, *Mimetus hirtus*, *Otholobium fruticans*, *Paranomus reflexus* and *Podalyria sericea*.

Four: Flowering Phenology

1. Phenology of the null flora.

a. Seasonality.

Weakly bimodal. Major peak = October, minor peak = March. Low = May. Significantly correlated with indigenous and exotic species offering both rewards, indigenous Asteraceae and indigenous and exotic Fabaceae ($p < 0.01$).

Thomson (1980) hypothesised that positively skewed flowering regimes may be due to competition for pollinators, delayed flowering by individuals located in marginal habitats or a large initial response to a flowering cue.

Limited dispersion in the flowering regime of a *species* is thought to facilitate cross-pollination (Rathcke & Lacey, 1985).

A positively skewed distribution of the flowering regime has been attributed to an environmental stimulus (Rathcke & Lacey, 1985).

Kochmer & Handel (1986) hypothesised that families should flower in the same order independent of their location if phylogenetic constraint exerted a dominant influence on flowering regimes. In contrast, they suggested that if pollinator-limitation was an important factor in the evolution of flowering phenologies "*...there should be considerable selection pressure for species of a family to spread flowering times throughout the year*" (p.305).

Divergent inter-specific flowering regimes within a plant community have been ascribed to both pollinator-limitation and inter-specific pollination (Rathcke & Lacey, 1985).

b. Duration.

Mean duration of flowering = 6.7 months. Distribution of flowering durations are positively skewed and platykurtic. The indigenous Asteraceae and Ericaceae flower for longer, but the indigenous Fabaceae for shorter periods than the null flora.

The duration of flowering is inclined to be shorter in species capable of self-pollination (Rathcke & Lacey, 1985).

A spatial or temporal dearth of resources necessary for seed development may lead to prolonged flowering (Rathcke & Lacey, 1985).

2. Reward phenologies.

a. Seasonality (Indigenous forage plants).

Flowering peak: Nectar = September, Pollen = November, Nectar & Pollen = October. Flowering low: Nectar = March, Pollen = May to June, Nectar & Pollen = May to June. All indigenous reward categories are significantly correlated at the 0.05 level. Seasonality (exotic forage plants), Flowering peak: Nectar = October & January, Pollen = October, Nectar & Pollen = October. All exotic reward categories are significantly correlated at the 0.05 level.

b. Duration.

Indigenous sources of nectar and pollen flower for the longest (6.9 months) and exotic sources of pollen (5.4 months) for the shortest period. For every reward category indigenous plants flower on average longer than the exotic species. All the distributions for flowering duration are positively skewed and platykurtic. The indigenous nectar plants are the least positively skewed and most platykurtic, whereas the exotic nectar plants are the most positively skewed and least platykurtic.

3. Family phenologies.

a. Seasonality (Indigenous forage plants).

Unimodal = Asteraceae & Fabaceae, Bimodal = Ericaceae.
 Flowering peak: Asteraceae = September-October, Fabaceae = October, Ericaceae = April and secondary peak in October-November. Flowering low: Asteraceae = May, Fabaceae = April to June, Ericaceae = August. The flowering phenologies of the indigenous Asteraceae and Fabaceae are significantly correlated at the 0.01 level. Seasonality (exotic forage plants) Flowering peak: Asteraceae = December, Fabaceae = October. Flowering low: Asteraceae = June to August, Fabaceae = May. The flowering phenologies of the indigenous and exotic Asteraceae are not significantly correlated, while the indigenous and exotic Fabaceae are significantly correlated with each other at the 0.01 level.

b. Duration.

Asteraceae & Fabaceae. Indigenous Asteraceae flower on average for the longest (7.8 months) and exotic Fabaceae for the shortest (5.2 months) period. The indigenous species of the two families flower on average for longer than their exotic counterparts. The flowering durations of the indigenous Ericaceae and Fabaceae are normally distributed, while that for the indigenous Asteraceae is not. The distribution of flowering durations for the Asteraceae are positively skewed and leptokurtic.

4. Indigenous species pairs.

Sympatry = 23, Allopatry = 5, possible Parapatry = 2. Significant correlations ($p < 0.05$): Sympatry = 7 (+) & 2 (-), Allopatry = 4 (+), Parapatry = 2 (+). In most (21) of the species pairings the species flowering for a shorter duration only flowered for 75% or less as long as the longer flowering species.

Interspecific differences in the time of flower production and fruit availability in the sympatric and myrmecochorous *Agathosma stenopetala* and *A. apiculata* have been attributed to past competition for agents of pollination and dispersal (Pierce, 1984).

5. *Eucalyptus* in South Africa.

a. Seasonality.

Flowering peak: December. Flowering low: June. The flowering peak in the *Eucalyptus* species lags that for the indigenous honeybee flora (all rewards) and null flora by two months and the flowering low by a month. There is no significant correlation ($p < 0.05$) between the flowering phenology of the *Eucalyptus* species and either the indigenous honeybee forage plants (all rewards) or the null flora.

b. Duration.

Eucalyptus flower on average for 7.9 months per annum. The distribution of the flowering durations deviates significantly from normal ($p < 0.01$), positively skewed and platykurtic.

c. Species pairs.

Significant correlations ($p < 0.05$): *E. calophylla*, *E. salubris* and *E. torquata*. Insignificant correlations: *E. cornuta*, *E. gomphocephala* and *E. platypus*. In all the species above flowering was longer in South Africa than Western Australia, with the exception of *E. platypus* which flowered longer in Australia.

Five: Land Management

1. Impact of landuse strategies on honeybees.

Habitat modification in South Africa is most likely to result from alien plant invasions, bush clearing, fire, monoculture, overgrazing and urbanization.

Habitat destruction can influence pollination in a number of ways, including the loss of food plants, mating or nesting sites (Kevan, 1999).

At Towoomba Research Station, within Sourish Mixed Bushveld, an increase in the density of aloes (*Aloe transvaalensis*) was attributed to increased grazing pressure (Smit & Rethman, 1992). No grazing can lead to the same effect if grasses become "moribund"; likewise the absence of fire (Smit & Rethman, 1992).

Owen-Smith & Danckwerts (1997) have suggested that goats can hinder regrowth of *Portulacaria afra* and can have a greater impact on it than indigenous browsers.

The frequencies, intensities and seasonalities of fires in the fynbos biome may affect species composition (Bond, 1997) and hence the quality of honeybee forage. Similarly, fire could have a negative impact on honey yield in savanna regions as trees are likely to be better sources of nectar than the grasses. In the savanna biome fires may help prevent encroachment by trees (Bond, 1997). Fire could also have contributed to the scarcity of trees within the fynbos biome (Stock *et al.*, 1992).

Flowering by *Graderia scabra* is largely confined to the post-fire period, while flowering by *Agapanthus africanus* and *Protasparagus compactus* is more common after fires than other periods (Frost, 1984).

Crop monocultures cover extensive areas in some parts of the country such as the western Cape, where they may represent virtual deserts to honeybees. For example, barley which is automatically self-pollinated, covered 132 000 ha, while oats and wheat, which are wind-pollinated, covered 703 000 ha and 1 382 000 ha respectively in 1997 within South Africa (Crane & Walker, 1984; Anonymous, 2001).

Exotic plants could also decrease the attractiveness of an area to honeybees, especially if they offer little or no rewards, by obscuring indigenous honeybee forage plants or increasing the distance between them for the flower-constant honeybees (Rebelo, 1987).

2. Honeybees and plant conservation in South Africa.

a. Pollination.

Facilitate spread of exotics via pollination. Depending on the flowering phenologies and relative attractiveness of the exotic forage plants pollination may involve a cost (decreased visitation, increased distance between conspecifics, shielding) or benefit (asynchronous flowering = enhanced carrying capacity) to the indigenous flora and indirectly the community of seed dispersers.

b. Increased colony density.

Managed colonies of honeybees could be used to augment the number of feral colonies within an area and so enhance seed set within the wide range of indigenous forage plants visited by honeybees. However, hived colonies overwintered in indigenous plant communities could also pose a risk to the survival of feral colonies with whom they must compete, with unknown effects on the pollination of their indigenous forage plants in the summer (Rebello, 1987).

Commercial beekeeping activities may pose a threat to indigenous plant-pollinator associations, for example during 1985 c. 52 000 hives were required for deciduous fruit pollination in the southwestern Cape (Rebello, 1987).

Rebello (1987) speculated that honeybees could via pollination of oligophiles increase the levels of hybridization between species or decrease seed viability.

It is possible that elevated population densities of honeybees may be inversely related to numbers of competing oligotrophs, leading to decreased levels of pollination amongst the latter oligophilic forage plants (Rebello, 1987).

Hived colonies overwintered in indigenous plant communities could also pose a risk to the survival of feral colonies with whom they must compete, with unknown effects on the pollination of their indigenous forage plants in the summer (Rebello, 1987).

3. Honeybees in the service of man.

Honeybee pollination enhances both commercial cultivation of fruit and seeds as well as rural food security.

At least 15 000 to 20 000 hives are required for the production of sunflower seed alone in South Africa (Johannsmeier, 1996).

In one study carried out on lucerne seed yields near Oudtshoorn, the Cape honeybee (*Apis mellifera capensis*) was more than twice as successful as a pollinator than the Highveld honeybee (*Apis mellifera scutellata*) and associated with yields more than eight times that obtained in the control experiment (Hepburn & Jacot Guillarmod, 1991).

More than three quarters of the households (n = 67 families, 31 villages) investigated by Arnold & Musil (1983) in Gazankulu cultivated watermelons, a crop which has been associated with honeybee facilitated yield enhancement in the past (Crane & Walker, 1984).

GEOGRAPHICAL VARIATION IN HONEY YIELD

Six: Spatiotemporal variability

1. Scale-hive records.

a. Site-specific intra-annual variation and correlation.

Site specific inter-annual differences in flowering time and spatial variation in the suite of pollinators and competitors for pollination only serve to further confound the interpretation of flowering regimes (Rathcke & Lacey, 1985).

Procedure 1

Statistically significant correlations ($p < 0.05$): Inter-site (1 of 8 pairs) viz. High Bank vs Dunnottar, Intra-site (1 of 2 pairs) Duiwelskloof No. 2.1 vs Duiwelskloof No. 2.2.

Procedure 2

Statistically significant correlations ($p < 0.05$): (2 of 15 pairs) viz. Dunnottar vs High Bank and Dunnottar vs Prinsrivier.

Honey flow seasons

None = Boschfontein, 4 months = Compton Ranch & Helshoogte, 5 months = Dunnottar and 6 months = High Bank & Prinsrivier.

Mean annual gain/loss in honey reserves

Gain = Compton Ranch, Helshoogte, High Bank & Prinsrivier.
Loss = Boschfontein & Dunnottar.

b. Biome specific intra-annual variation and correlation.

Statistically significant correlations ($p < 0.05$) between savanna, fynbos & grassland.

None.

Mean annual gains in weight

Savanna = 1.46 kg, Fynbos = 1.11 kg, Grassland = 0.86 kg.

Greatest monthly gains

Savanna = 44.84 kg, Grassland = 28.90 kg, Succulent Karoo = 19.73 kg & Fynbos = 14.66 kg.

Greatest monthly losses

Savanna = -15.55 kg, Fynbos = -10.54 kg, Grassland = -7.90 kg and Succulent Karoo = -4.99 kg.

Annual range in monthly hive weights

Savanna = 60.39 kg, Grassland = 36.80 kg, Fynbos = 25.20 kg and Succulent Karoo = 24.72 kg.

Maximum monthly ranges in hive weight

Savanna = September (48.92 kg), Grassland = November (31.17 kg) and Fynbos = October (19.83 kg).

Minimum monthly ranges in hive weight

Savanna = August (9.84 kg), Grassland = April (5.44 kg) and Fynbos = May (1.56 kg).

Most frequently occurring month amongst the 20 greatest monthly gains in hive weight

Savanna = September ($n = 8$), Grassland = January ($n = 4$) & February ($n = 4$) and Fynbos = December ($n = 5$) and January ($n = 5$).

Most frequently occurring month amongst the 20 greatest monthly losses in hive weight

Savanna = December (n = 4), Grassland = September (n = 4) and Fynbos = November (n = 7).

Mean monthly maxima

Savanna = September (9.51 kg), Fynbos = January (6.22 kg) and Grassland = July (6.24 kg).

Mean monthly minima

Grassland = July (-3.09 kg), Fynbos = June (-1.88 kg) and Savanna = August (-1.48 kg).

Honey flow seasons

Savanna = (2 X 4 months) = 15.22kg & 5.36 kg, Grassland = 6 months = 14.04 kg, Fynbos = 5 months = 16.32 kg.

c. Rainfall.

Greatest monthly gain in hive weight

650 - 750 mm rainfall class (44.84 kg, Boschfontein, September 1945)

Smallest monthly gain in hive weight

< 300 mm rainfall class (12.47 kg, Prinsrivier, December 1948)

Greatest monthly loss in hive weight

650 - 750 mm rainfall class (-15.55 kg, Boschfontein, October 1942)

Smallest monthly loss in hive weight

< 300 mm rainfall class (-5.22 kg, Prinsrivier, June 1948)

Greatest range in monthly hive weights

650 - 750 mm rainfall class (60.39 kg, Boschfontein)

Smallest range in monthly hive weights

< 300 mm rainfall class (17.69 kg, Prinsrivier).

d. Extreme monthly hive weight variations for all records combined.

Statistically significant correlations ($p < 0.05$) between the extreme monthly highs and lows.

None.

Greatest monthly gain in hive weight

September 1945 (44.84 kg, Boschfontein)

Smallest monthly gain in hive weight

June 1933 (7.01 kg, Port Durnford)

Greatest monthly loss in hive weight

October 1942 (-15.55 kg, Boschfontein)

Smallest monthly loss in hive weight

April 1948 (-3.63 kg, Dunnottar)

Greatest range in monthly hive weights

September (52.74 kg)

Smallest range in monthly hive weights

June (14.02 kg)

2. Colony demography. Andries Vosloo Kudu Reserve.

a. Total comb area.

Mean annual monthly maximum

May (11 798 cm²)

Mean annual monthly minimum

October (7 997.55 cm²)

Statistically significant correlations (p<0.05).

Positive: None Negative: pollen cells, sealed worker brood, unsealed worker brood, sealed drone brood and total drone brood.

Hepburn et al. (1984) have demonstrated that the presence of a queen is necessary for comb construction in colonies of *Apis mellifera scutellata*.

Hepburn (1998) reported that a limited comb area hampered brood production. He also suggested that the construction of new comb was dependent on the duration and intensity of nectar flows when nectar holding space is limited.

b. Honey.

Mean annual monthly maxima

Uncapped: February (1 621.85 cm²) Capped: February (1 320.52 cm²) Total Honey: February (2 942.37 cm²)

Mean annual monthly minima

Uncapped: September (486.17 cm²) Capped: September (113.61 cm²) Total Honey: September (599.78 cm²)

Statistically significant correlations (p<0.05).

Positive: Uncapped: total honey Capped: total honey, drone comb
Negative: None

The storage of honey is a heritable trait of particular importance to the survival of colonies at colder, higher-latitudes (Danka *et al.*, 1987).

Danka *et al.* (1987) found that in Venezuela more nectar was stored by colonies under low (pollen present, no brood), rather than high (no pollen, brood present) incentive conditions. Check paper.

It would appear that nectar foraging behaviour is at least partially governed by queen pheromones (Jaycox, 1970a, citing Jaycox, 1970b) and "...comb volatiles..." (Hepburn, 1998 p.59).

Fewell & Winston (1996) have suggested that different mechanisms govern the collection of nectar and pollen, although demand for the former may influence foraging for the latter and vice versa via the foragers which collect both food types.

Fewell & Winston (1996) found that the extent of honey reserves had little or no effect on colony and individual flight activity, the flower handling times, the nectar loads of foragers, the amount of pollen stored or quantities of brood present.

c. Pollen.

Mean annual monthly maximum

October (384.42 cm²)

Mean annual monthly minimum

April (61.75 cm²)

Statistically significant correlations (p<0.05).

Positive: % comb in use, unsealed worker brood, sealed worker brood, total worker brood, sealed drone brood and total drone brood
Negative: total comb area

Pollen plays an important role in the brood cycle of workers of both temperate and tropical races, with brood development dependent on pollen stores in the former, but pollen income in the latter (Hepburn & Radloff, 1998).

d. Worker brood.

Mean annual monthly maximum

Unsealed Worker Brood: September (1 027.60 cm²)

Sealed Worker Brood: November (1 600.74 cm²) Total

Worker Brood: November (2 265.25 cm²).

Mean annual monthly minimum

Unsealed Worker Brood: March (161.84 cm²) Sealed

Worker Brood: June (68.68 cm²) Total Worker Brood:

June (284.04 cm²)

Statistically significant correlations (p<0.05).

Positive: Unsealed Worker Brood: % comb in use, pollen, sealed worker brood, total brood, unsealed drone brood, sealed drone brood, total drone brood. Sealed Worker Brood: % comb in use, pollen, unsealed worker brood, total brood, unsealed drone brood, sealed drone brood, total drone brood. unsealed drone brood, sealed drone brood, total drone brood. Total Worker Brood: % comb in use, pollen, unsealed worker brood, sealed worker brood, Negative: Unsealed Worker Brood: none Sealed Worker Brood: total comb area Total Worker Brood: none.

Brood-rearing, swarming and the flowering phenology of honeybee forage plants are correlated in sub-equatorial Africa (Hepburn & Radloff, 1998).

For *Apis mellifera capensis* and *Apis mellifera scutellata* an increase in worker brood production lags the extra-colonial availability of nectar, a phenomenon known as "follow-flow brood rearing" (Hepburn, 1992).

e. Drone brood.

Mean annual monthly maximum

Drone comb: January (1 133.62 cm²) Unsealed Drone Brood:

October (90.28 cm²) Sealed Drone Brood: November

(171.68 cm²) Total Drone Brood: October (220.02 cm²)

Mean annual monthly minimum

Drone comb: July (666.12 cm²) Unsealed Drone Brood: Absent

(December & March to June) Sealed Drone Brood: Absent (April to June) Total Drone Brood: Absent (April to June).

Statistically significant correlations (p<0.05).

Positive: Drone Comb: capped honey Unsealed Drone Brood: % comb in use, pollen, unsealed worker brood, sealed worker brood, total worker brood, sealed drone brood, total drone brood. Sealed Drone Brood: % comb in use, pollen, unsealed worker brood, sealed worker brood, total worker brood, unsealed drone brood, total drone brood. Total Drone Brood: % comb in use, pollen, unsealed worker brood, sealed worker brood, total worker brood, unsealed drone brood and sealed drone brood. Negative: Drone Comb: none Unsealed Drone Brood: total comb area, Sealed Drone Brood: total comb area, Total Drone Brood: total comb area.

f. Number of queen cells

Mean annual monthly maximum

January (6.36 cells)

Mean annual monthly minimum

June (1 cell)

Statistically significant correlations ($p < 0.05$).

None.

Aird (1943) more than 50 years ago suggested that the age of queens may have been responsible for variable honey yields in the Cradock area, South Africa.

h. Intra-African correlations ($p < 0.05$).

Cape Peninsula

Positive: worker brood and drone brood.

Sudan (Medani & Shambat)

Positive: worker brood (Shambat)

1. Scale-hive records

Seven:
Bioclimatology:
University of
Pretoria
Experimental Farm

a. Annual mean monthly maxima and minima (only $n \geq 3$ months)

Maxima: September (14.784 kg, H42), November (12.51 kg, H47) Minima: January (-1.76, H42), February (-0.99 kg, H47).
<3 monthly values: H42 (October & November), H47 (January, May, June, August, September, October & December).

b. Statistically significant correlations (Spearman Rank Order, $p < 0.05$)

Positive: None Negative: rainfall (H42)

c. Autocorrelations

H42 (1 & 2 months), H47 (1, 2, 3, 4 & 5 months)

d. Cross-correlation (>0.5 or <-0.5)

None.

e. Single series Fourier analysis

H42 (252, 126, 28, 16.8 & 14.82 months); H47 (230, 115, 76.67, 57.5 & 38.33 months).

f. Cross-spectrum analysis

H42: 12 (air pressure at 14h00, daily sunshine hours, rainfall Pretoria (Forum), maximum temperature, minimum temperature), 28 (daily sunshine hours, rainfall Pretoria (Forum)), 63 (air pressure at 14h00, rainfall Pretoria (Forum)) and 252 (air pressure at 14h00, SOI, minimum temperature).

H47: 12.11 (maximum temperature, minimum temperature), 15.33 (maximum temperature, minimum temperature), 17.69 (daily sunshine hours, minimum temperature), 19.17 (air pressure at 14h00, daily sunshine hours), 32.86 (daily sunshine hours, rainfall Pretoria (Forum), 38.33 (daily sunshine hours, rainfall Pretoria (Forum)), 57.50 (air pressure at 14h00, SOI, maximum temperature, minimum temperature), 115 (air pressure at 14h00, rainfall Pretoria (Forum)), 230 (air pressure at 14h00, daily sunshine hours, rainfall Pretoria (Forum), SOI, maximum temperature).

2. Air pressure (hPa) at 14h00

a. Annual mean monthly maximum and minimum

Maximum: July (875.53 hPa) Minimum: January (868.95 hPa)

b. Statistically significant correlations (Spearman Rank Order, $p < 0.05$)

Positive: daily sunshine hours Negative: cloud cover, evaporation, rainfall, relative humidity, maximum and minimum daily temperature.

Esler (1999) has speculated that changes in air pressure associated with passing cold fronts may be related to flowering in certain geophytes.

3. Cloud cover (octas) at 14h00

a. Annual mean monthly maximum and minimum

Maximum: December (4.33 octas) Minimum: July (0.40 octas)

b. Statistically significant correlations (Spearman Rank Order, $p < 0.05$)

Positive: evaporation, rainfall, relative humidity, maximum and minimum daily temperature Negative: air pressure at 14h00 and daily sunshine hours.

Moffett & Parker (1953) found in a study covering many summers (May to August) that the 10 years with the strongest nectar flows had fewer cloud-free days than the 10 years with the weakest flows. They speculated that the lower transpiration rates associated with cloudy conditions were more conducive to nectar secretion than those on clear days.

Jorgensen & Markham (1946) provide evidence which indicates that the best days for honey production were associated with twice the number of clear days and half the number of cloudy days than for the worst days of honey production. They suggested that elevated temperatures may mitigate the effects of cloud cover on honey production.

If "...dappled shade..." (Acutt, 1988 p.61) can be equated with cloud cover then a similar situation appears to prevail in KwaZulu-Natal, South Africa. Acutt (1988) suggested that hives below *Eucalyptus* sp. trees produced less honey than colonies in the sun.

4. Daily sunshine (hours/day)

a. Annual mean monthly maximum and minimum

Maximum: August (9.521 hours/day) Minimum: March (7.875 hours/day)

b. Statistically significant correlations (Spearman Rank Order, $p < 0.05$)

Positive: cloud cover at 14h00 Negative: air pressure at 14h00, rainfall, relative humidity and minimum daily temperature.

Krishnamurti (1939) and Gerlach (1985) both noted a degree of coincidence in the changes in hive weight and the duration of sunshine.

5. Evaporation (mm/day)

a. Annual mean monthly maximum and minimum

Maximum: October (7.90 mm/day) Minimum: June (3.24 mm/day)

b. Statistically significant correlations (Spearman Rank Order, $p < 0.05$)

Positive: cloud cover at 14h00, rainfall, maximum and minimum daily temperature Negative: air pressure at 14h00.

Evaporation is believed to influence both the concentration and quantity of nectar available from plants (Cruden *et al.*, 1983) and to facilitate the transformation of nectar to honey within a hive (Gerlach, 1985).

Gerlach (1985) ascribed a fall in hive weight at night to evaporation.

6. Rainfall (mm/month)

a. Annual mean monthly maximum and minimum

Maximum: January (138.30 mm, Pretoria (Forum); December (126.40 mm, University of Pretoria Experimental Farm)
Minimum: July (2.81 mm, Pretoria (Forum); 3.25 mm, University of Pretoria Experimental Farm)

b. Statistically significant correlations (Spearman Rank Order, $p < 0.05$)

Positive: cloud cover at 14h00, evaporation, rainfall (Pretoria (Forum)), relative humidity, maximum and minimum daily temperature Negative: air pressure at 14h00 and daily sunshine hours.

1. Plants

Phillips (1926), in an early paper on the Knysna forests, suggested limited periods of both anomalously wet and dry conditions may be associated with flowering.

Moisture stress can retard nectar secretion (Vogel, 1983), while rainfall can dilute nectar or flush it from flowers (Cruden *et al.*, 1983; Szabo & Mueller, 1996).

Rainfall has been known to affect the flowering phenology of a number of honeybee forage plants *inter alia* *Osteospermum sinuatum* and *Lycium cinereum* (Milton, 1992).

Smith-Ramírez & Armesto (1994) found a negative correlation between monthly rainfall and flowering in the temperate rain forests on the eastern side of Chiloé Island, Chile.

On a continental scale flowering is coincident or nearly so with rainfall in Africa (Hepburn & Radloff, 1995).

Moisture stress has an effect on some Namaqualand ephemerals such as the honeybee forage plants *Dimorphotheca sinuata* and *Senecio arenarius* (Steyn *et al.*, 1996a).

2. Honeybees

Honeybees may be prevented from flying by rain, while wet hive boxes may complicate the interpretation of scale-hive records (Hambleton, 1925).

As flight has been recorded at low rainfall intensities (Fletcher, 1978) it would appear that it only becomes a limiting factor above an unknown threshold and if coincident with potential foraging activity (Jorgensen & Markham, 1946).

Statistically significant positive correlations between rainfall for periods of varying duration and intervals preceding honey flows and honey production have been reported by a number of researchers *inter alia* Moffett & Parker (1953), Crane (1975) and Hepburn & Radloff (1996).

7. Relative humidity (%)

a. Annual mean monthly maximum and minimum

Maximum: January (55.33%) Minimum: September (35.55%)

b. Statistically significant correlations (Spearman Rank Order, $p < 0.05$)

Positive: cloud cover at 14h00, rainfall, maximum and minimum daily temperature Negative: air pressure at 14h00 and daily sunshine hours.

1. Plants

In general, researchers appear to associate an increase in relative humidity with an increase in volume (Cruden *et al.*, 1983), but a decrease in concentration of the available nectar (Park, 1929; Scullen, 1940; Oertel, 1946; Cruden *et al.*, 1983). This has been ascribed to atmospheric water absorption by the nectar (Cruden *et al.*, 1983).

Smith-Ramírez & Armesto (1994), working in Chile, found a statistically significant negative correlation between the monthly flowering intensity of the plant community and relative humidity.

2. Honeybees

Nectar secretion and concentration are positively related to increases in temperature (Oertel, 1946; Percival, 1965; Vogel, 1983).

In some African plant species nectar secretion reportedly occurs preferentially in the cooler periods of the diurnal cycle (Fletcher, 1978).

2. Honeybees

An anecdotal account from Natal appears to indicate that the minimum threshold for foraging lay between 10°C and 11°C (Fletcher, 1978).

The minimum thresholds for flight appear to vary with the time of year, being lower in spring (12°C to 14°C) than summer (16°C to 18°C) (Kevan & Baker, 1983).

Garin (1931) reporting on honey yields at Morokwen in the early part of the twentieth century was of the opinion that *"the average temperature of every month does not seem to have much influence on the honey crop"* (p.18).

Szabo (1980) found statistically significant positive correlations between temperature and both flight activity and changes in hive weight.

