Evaluation of the floral rewards of *Aloe greatheadii* var *davyana* (Asphodelaceae), the most important indigenous South African bee plant

by

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For my husband and children

"The larger the island of knowledge, the longer the shoreline of wonder" (Smith, 1996:4)

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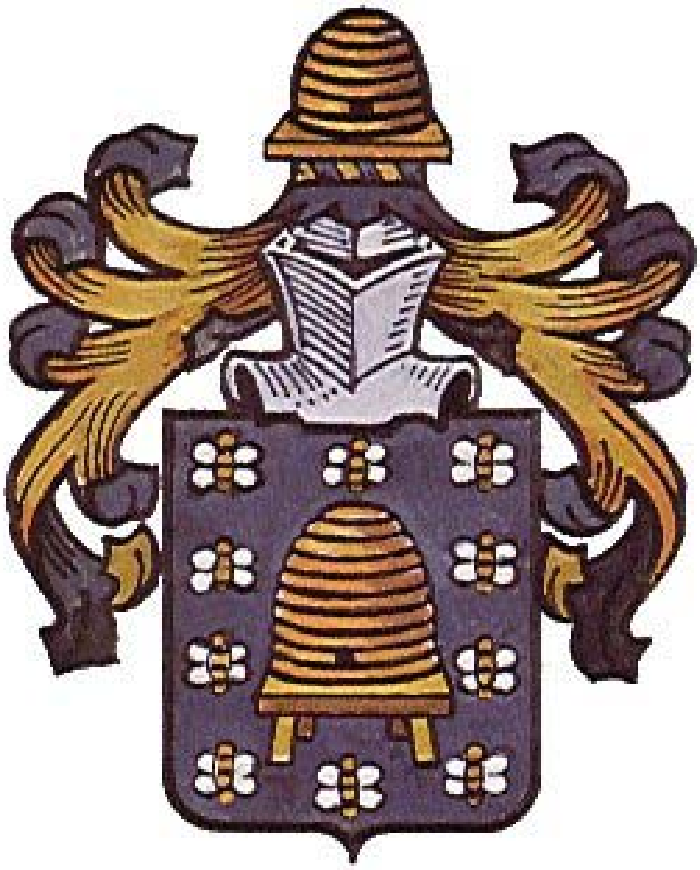

Bezuidenhout coat of arms

(My maiden name was Bezuidenhout)

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Evaluation of the floral rewards of *Aloe greatheadii* var *davyana* (Asphodelaceae), the most important indigenous South African bee plant

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Abstract

The most important indigenous bee plant in South Africa is the winter flowering *Aloe greatheadii* var *davyana,* with a widespread distribution across the summer rainfall region. Beekeepers commonly move their hives to the "aloe fields" during winter, using the strong pollen and nectar flow for colony growth, queen rearing and honey production. In spite of its importance for the bee industry, no complete pollen analysis is available and, except for the popular bee literature, little is known about nectar production or pollinators. The aim of the study was therefore to evaluate the floral rewards of this aloe and to investigate the importance of these resources for honeybees.

We analysed fresh, bee-collected and stored aloe pollen for its nutritional content (not previously done for any plant species). Addition of nectar and glandular secretions leads to an increase in water and carbohydrate content and a decrease in protein and lipid content. All the essential amino acids, except tryptophan, met or exceeded the minimum levels for honeybee development. In worker bees in queenright colonies, ovarian development is greater on aloe than on sunflower pollen, which may be explained by the exceptionally high protein content and high extraction efficiency during digestion.

In assessing the nectar resource, we investigated the nectary structure and nectar presentation of two species belonging to different sections of the genus *Aloe*, *A. castanea* and *A. greatheadii* var *davyana,* but anatomical differences were not related to the nectar production. We looked at variation in nectar volume and concentration of *A. greatheadii* var *davyana* on various levels, from within the flowers to across the summer rainfall area. Nectar was continuously available and, although dilute (mean

concentration 18.6%), the nectar of *A. greatheadii* var *davyana* is more concentrated than that of other *Aloe* species, making it an ideal source of energy and water for honeybees. Utilisation of dilute nectar by bees requires elimination of much excess water. We sampled crop contents of nectar foragers to determine if changes in nectar concentration occurred after collection and before unloading in the hive. Contrary to the common assumption that nectar is either unchanged or slightly diluted during transport, we observed a dramatic increase in concentration and a decrease in volume between the flowers and the hive. Bees may be foraging primarily to get enough water for their physiological needs. Using miniaturised data loggers, we showed that bees are able to adjust nest humidity within sub-optimal limits, in addition to efficient regulation of hive temperature. Humidity levels are influenced by trade-offs with regulation of temperature and respiratory gas exchanges.

Although the dilute nectar and pinkish red tubular flowers are characteristic of bird-pollination, exclusion experiments showed that bees are the primary pollinators of *A. greatheadii* var *davyana*. This contrasts with other *Aloe* species which are pollinated by sunbirds and other passerine birds, but highlights the two-way interaction between the bees and the aloes.

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GENERAL INTRODUCTION

Honeybee flora of South Africa: exotic and indigenous plants

Honeybees visit about 1000 plant species in South Africa for pollen and/or nectar. Only half of these plant species are indigenous (Illgner, 2002). Many South African beekeepers migrate with their hives over distances of hundreds of kilometres to certain crops as they flower, and use minor nectar sources to bridge periods between major nectar flows (Johannsmeier, 2001). For example, in the northern summer rainfall area, the cycle begins in spring with certain *Eucalyptus* species, followed by *Faurea saligna* (boekenhout) and *Fagopyrum esculentum* (buckwheat) in December. In January honeybees are used to pollinate *Phaseolus coccineus* (kidney beans) and *Helianthus annuus* (sunflowers) and in autumn *Cosmos bipinnatus* (cosmos) is available. *Eucalyptus grandis* flowers from April onwards while July and August are the important *Aloe* months (Keats, 1980).

The annual honey crop in South Africa is estimated at 3 500 tons, of which 1 800 tons is derived from *Eucalyptus,* 900 tons from crop plants and the remainder from weeds, indigenous and other plants (Johannsmeier, 2001). Of the exotic bee plants, the single most important nectar source for bees is *Eucalyptus* and beekeeping is considered impossible without it. There are 34 *Eucalyptus* species listed as honey plants in South Africa. These trees are highly attractive nectar and pollen producers, grow under a variety of conditions and have a widespread distribution with a year-round flowering period (Johannsmeier, 2001; Illgner, 2002). In South Africa a timber industry, based on fast growing trees such as pines and eucalypts, was established at the end of the nineteenth century, and by the early twentieth century the majority (80%) of trees grown were *Eucalyptus grandis.* These plantations provided additional and more reliable sources of nectar than the indigenous flora. However, since 1975 *Eucalyptus* nectar flows have declined to about one third of the previous average. Various factors may contribute to this deterioration; *Drosophila flavohirta* larvae utilising the nectar in *Eucalyptus* flowers (Herrmann, 1983; Nicolson, 1994) and the leaf sucking bugs *Thaumastocoris australicus* that cause defoliation, dieback of branches and even death of *Eucalyptus* trees (Jacobs & Neser, 2005). *Thaumastocoris australicus* may even affect the flowering and nectar production of infested *Eucalyptus* trees (D. Jacobs, pers. comm.). Another explanation may be the genetic make up of the trees currently planted in plantations; *Eucalyptus* with fewer flowers are preferred, thus less nectar is available to honeybees (A. Schehle, pers. comm.). Government regulations (the Working for Water Programme) provide for the removal of certain *Eucalyptus* species in water catchment areas and along watercourses, and this presents another threat to beekeepers (Johannsmeier, 2001).

Of the indigenous plants, the major producers of honey are firstly the aloes, of which *A. greatheadii* var *davyana* is the most important species, followed by boekenhout (*Faurea saligna*), wilde peer (*Dombeya rotundifolia*), karee (*Rhus lancea*), wilde sering (*Burkea Africana*), wit-olyf (*Cordia caffra*), as well as several *Acacia* and *Protea* species (Beyleveld, 1969; Fletcher & Johannsmeier, 1978; Schonfeld, 1983; Johannsmeier, 2001). An extensive list of bee plants in South Africa, including their distribution as well as flowering phenology, has since been compiled by Johannsmeier (2001) and Illgner (2002).

The genus *Aloe*

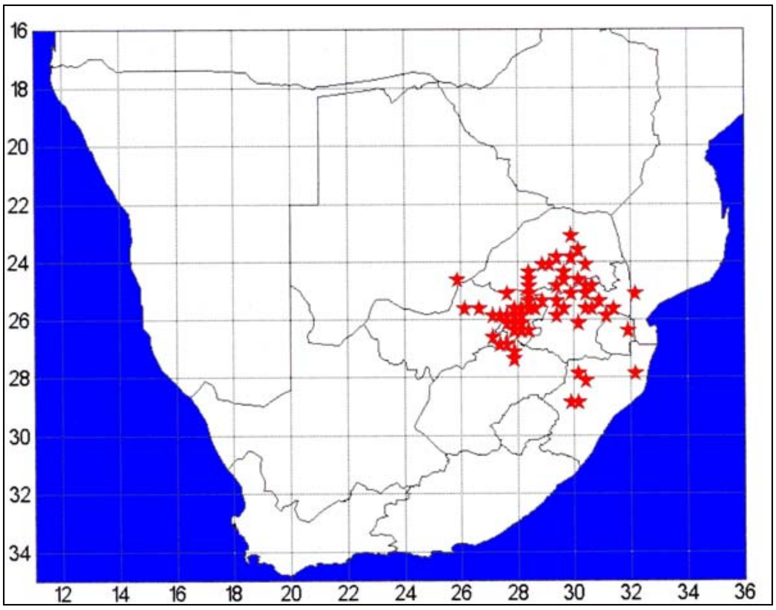
The genus *Aloe*, family Asphodelaceae, occurs across a wide range of habitats, from dry forests to scrublands in Africa, Madagascar, Arabia, the Canary and the Comoro islands. South Africa has the highest diversity of *Aloe* species with more than 100 species (Van Wyk & Smith, 1996; Glen & Hardy, 2000; Smith et al., 2000). These succulent plants grow well in warm climates and can tolerate drought. Few species, however, can withstand frost. The huge variation in size, leaf width, leaf markings, etc., has led to the division of the genus into 26 sections (Reynolds, 1969; Van Wyk & Smith, 1996; Glen & Hardy, 2000). The section Pictae (spotted aloes) is the largest, consisting of 32 species. These aloes are stemless or short-stemmed, have inflorescences that are branched and re-branched and their flowers, with conspicuous basal swellings, often have pale longitudinal stripes. Species are difficult to distinguish from each other e.g. the summer flowering *Aloe zebrina* and winter flowering *A. greatheadii* var *davyana* (Schönland) Glen & D.S. Hardy (Van Wyk & Smith, 1996; Glen & Hardy, 2000).

Aloe greatheadii *var* davyana *and honeybees,* Apis mellifera scutellata

The winter flowering *A. greatheadii* var *davyana* (Fig. 1) has a widespread distribution across the summer rainfall area (Fig. 2) and is very common in the Bushveld and on the Witwatersrand (Glen & Hardy, 2000; Van Wyk & Smith, 1996; Smith & Crouch, 2001). The plants grow well in rocky terrain and on grassy plains and occurring most densely in overgrazed areas (Clark, 1992). Plants are robust and grow singly or in groups of up to fifteen. They flower prolifically in mid-winter, from June to August, with flower colour ranging from pale pink to bright red. Flower abundance may vary throughout the flowering period and from year to year. Pronounced daily temperature changes characterise the winter flowering period with warm days and cold, sometimes frosty, nights.

Figure 1. *Aloe greatheadii* var *davyana*

A



B

Figure 2. (A) Distribution map of *Aloe greatheadii* var *davyana* (redrawn from Glen & Hardy, 2000) and (B) map of South Africa (redrawn from www.safarinow.com) indicating study sites used in this study: **1**. Roodeplaat Nature Reserve, **2**. Rust de Winter, **3**. Marble Hall and **4**. Zeerust.

Aloe greatheadii var *davyana* is a major indigenous beeplant and it is widely known that beekeepers move their hives to the aloe fields north of Pretoria in winter (see Fig.3) to make use of the strong nectar and pollen flow from *A. greatheadii* var *davyana* (Fletcher & Johannsmeier, 1978). The first report on the utilisation of this aloe was that of Mr Krohn from Rustenburg in 1934 (Williams, 2002). However, it was only in 1950 that Mr E.A Schnetler realised the commercial value of *A. greatheadii* var *davyana*. While transporting bees along the Warmbaths (now Bela Bela) road to a new site, his truck broke down and the bees had to be unloaded. When it was time to reload the hives he realised that the bees were collecting pollen and nectar from *A. greatheadii* var *davyana* growing in the vicinity (Short, 1962; Keats, 1980).

Figure 3. Beehives among *A. greatheadii* var *davyana* in the Rust de Winter area in 2005.

Apparently honeybees become particularly aggressive and unmanageable during this nectar flow (Fletcher & Johannsmeier, 1978). Doull (1976) believed that this behaviour might be caused by certain properties of the pollen; he considered *A. greatheadii* var *davyana* to be a good source of pollen but a poor source of nectar. He observed few bees collecting nectar during the day, in spite of nectar being readily available, and suggested that the aggressive behaviour of honeybees is the result of the amount of food available and natural behavioural patterns of bees. On the other hand, Johannsmeier (2001) considers the nectar to be of medium to good quality. The best nectar and pollen is apparently produced from approximately July 17 to August 25 each year, and thereafter the quality deteriorates; after this period beekeepers move their hives to the next available food source e.g. *Eucalyptus* or *Citrus* (J. Williams, pers. comm.).

Currently the entire beekeeping industry, as well as the agricultural industry in South Africa that depends on pollination services of *Apis mellifera scutellata* honeybees, is at threat by *A. mellifera capensis* bees. Prior to the translocation of *A. mellifera capensis* in 1991 into the interior of South Africa, *A. mellifera capensis* (Cape honeybees) and *A. mellifera scutellata* (African honeybees) remained separate races of honeybees. *Apis mellifera capensis* were only found along the Cape coast, their distribution roughly corresponding to that of the fynbos vegetation, but they are now distributed throughout the country. These two races of bees are incompatible since *A. mellifera scutellata* queens are unable to control and prevent *A. mellifera capensis* workers from reproducing. *Apis mellifera capensis* workers rapidly become laying workers and as soon as they start laying eggs, the African bees start looking after these bees as though they were queens, neglecting their own queen, which eventually dies. The new "queens" are not able to manipulate the colony with pheromones, thus causing the colony to dwindle and eventually die. The rich nectar and pollen flow from *A. greatheadii* var *davyana* seems to promote the *A. mellifera capensis* take-over. When *A. mellifera scutellata* beehives are moved to the aloes in winter, *A. mellifera capensis* are able to spread between these hives and apiaries (Allsopp, 1998; Kryger et al., 2000). Pollen of the aloes also activates the ovaries of *A. mellifera capensis* workers even in the presence of the queen (Kryger, et al., 2000).

In an attempt to eliminate and control the problem, the government divided the country into two sectors and prohibited movement of the two races of bees between these sectors (Johannsmeier, 2001). All *A. mellifera capensis* colonies and infested colonies north of the dividing line were legally required to be destroyed. Thousands of colonies have been lost due to this infestation, and many commercial beekeepers have been forced out of business. Beekeepers that lost their stock were financially supported in order to re-establish *A. mellifera scutellata* beekeeping but attempts to manage this problem have been unsuccessful and research will have to provide a permanent solution (Johannsmeier, 1997, 2001; Allsopp, 1998). Unfortunately, some wild populations of *A. mellifera scutellata* have also become infested with *A. mellifera capensis* (Johannsmeier, 1997).

Is there anything special about Aloe greatheadii var davyana pollen and nectar?

Beekeepers use the strong nectar and pollen flow of *A. greatheadii* var *davyana* not only for honey production but also to build up colonies, rear queens and increase colony numbers by division (Jackson, 1979; Williams, 2002). Pollen quality and quantity have a direct effect on the productivity of a bee colony. Proteins and amino acids are important for the growth and development of bees and insufficient quantities of protein (< 20% dry mass) may affect reproduction, brood rearing and longevity of honeybees and subsequently honey production (Kleinschmidt & Kondos, 1978; Moritz & Crailsheim, 1987). Pollen lipids are a source of energy and are important for the synthesis of reserve fat and glycogen as well as for the production of royal jelly (Singh et al., 1999; Loidl & Crailsheim, 2001; Manning, 2001).

Aloe greatheadii var *davyana* aloes are a major pollen source, and since the anthers are exserted beyond the floral tubes the orange pollen is readily available to honeybees. Very little is known about the pollen except that it has a high protein content (33.8% on a dry mass basis, based on a single measurement; Johannsmeier, 2001), and aloes in general are starchless according to Franchi et al. (1996). Beekeepers describe *A. greatheadii* var *davyana* pollen as “dry” with a sweet taste to it and the nectar as “reasonably dense and sweet” (Doull, 1976; Schönfeld, 1983; Williams, 2002).

It is possible that substances such as protein in the pollen may have a direct effect on the ovarian development of workers honeybees (Kryger, P., Wossler, T.C., Crewe, R.M., Moritz, F.A. & Johannsmeier, M.F., unpublished data) who are able to start reproducing in the absence of a queen (Velthuis, 1970). The relationship between dietary protein and ovarian development in adult workers has been well documented. Protein-rich diets promote ovarian development and oogenesis is restricted by a lack of protein (Hoover et al., 2006). Ovarian development is not only influenced by the quality of the diets but may also be affected by the time of year (Hoover et al., 2006). In the summer rainfall areas, cold winter nights (often below freezing) and low ambient temperatures early in the mornings result in overcrowding of the brood nest as well as delayed foraging; thereby aggravating the swarming tendency (a period with little or no brood) on the aloes (Steinhobel, 1976) thus allowing workers to use food reserves for development of their ovaries instead of taking care of the brood.

The other floral reward is nectar. Nectar concentrations can vary between 7% and 70% and great variation exists not only between species but also within species (Nicolson, 1998; Nepi et al., 2001). The mean nectar concentration tend to be less in flowers from the tropics and higher in hot and dry climates (Willmer & Stone, 2004). Composition and production rates of nectar vary with time of day, flower age, nutritional status of the plant and even location of the flower on the plant, and are also influenced by environmental parameters such as temperature and relative humidity (Corbet et al., 1979; Nicolson, 1994; Vesprini et al., 1999; Nepi et al., 2001).

Nectar of bird-pollinated flowers is usually relatively dilute. Birds are closely associated with aloes (Oatley & Skead, 1972) such as *A. ferox,* which has nectar with low concentrations (12.5%) and large volumes per flower (180 µl) (Hoffman, 1988). *Aloe* species produce very dilute (10-15%), hexose-dominant nectars (Van Wyk et al., 1993; Nicolson, 2002). The average nectar concentrations of bee-pollinated flowers tend to exceed 35% (Nicolson, 1998) and although honeybees collect nectar with a wide range of sugar concentrations (from 12-65% w/w, or 0.5 to 2.5M) they prefer nectar with 30-50% sugar content (Southwick & Pimentel, 1981). However, when honeybees need to cool the hive (through evaporation) they will collect nectar with lower concentrations or collect water. Honeybees are known to collect more dilute nectars during the dearth period in Israel (Eisikowitch & Masad, 1982). Since *A. greatheadii* var *davyana* flowers during the dry winter months the dilute aloe nectar can thus also serve as a source of moisture (Van Wyk et al., 1993; Tribe & Johannsmeier, 1996). This nectar contributes substantially to the honey crop (Williams, 2002); therefore large quantities of the dilute nectar must enter the hive and consequently may affect humidity regulation in the hive. Transforming nectar into ripe honey requires elimination of excess water. Utilisation of the dilute nectar of *A. greatheadii* var *davyana* (with a water content of 77%; Human and Nicolson, unpublished data) will thus require significant evaporation. Bees could begin this process en route to the hive, prior to the unloading of their crop contents. However, since the study by Park (1932), it has generally been assumed that changes in nectar concentration only occur in the hive during storage and the honey ripening process.

Pollination ecology

Animal pollinated flowers possess certain floral features such as colour, structure and scent that are believed to reflect the preferences of their pollinators. These associations were described by Faegri and Van der Pijl (1979) and became known as "pollination syndromes". They included nectar volume in their descriptions while Baker and Baker (1983) extended the whole concept to include nectar composition. Pollination syndromes have been helpful in understanding plant-pollinator interactions. Recognition of certain floral features and reward types can help to predict pollinators but has to be applied critically otherwise it can be misleading. Pollinators are not restricted to visiting only one kind of flower; birds may sometimes visit flowers that are not typical bird flowers, while bees and butterflies may visit ornithophilous flowers (Robertson et al., 2005). As a result, flowers may be visited by a wide variety of pollinator types but may actually only be effectively pollinated by some visitors (Robertson et al., 2005). Most aloes appear to be typical bird pollinated plants, with red-orange tubular flowers with dilute nectar, but they may also be pollinated by bees and other insects (Stokes & Yeaton, 1995).

Few studies are available on pollination ecology of aloes (Holland, 1978) and little is known about nectar secretion rates, time of anthesis or visitors to most *Aloe* species. Although bees are noted visitors to aloes their contribution to pollination of *Aloes* has seldom been investigated as aloes were classically considered to be bird pollinated. Studies by Stokes and Yeaton (1995) and Ratsirarson (1995) showed that birds and not insects, were the primary pollinators of *A. candelabrum* and *A. divaricata* respectively while Tribe and Johannsmeier (1996) consider sunbirds and honeybees as the major pollinators of three species of tree aloes, *A. dichotoma, A. pillansii* and *A. ramosissima*. The red tubular flowers of *A. ferox* indicate sunbird pollination but a study by Hoffman (1988) showed that both birds and bees may be pollinators of this aloe. The pinkish-red colour, tubular structure and lack of scent of *A. greatheadii* var *davyana* flowers, as well as the copious and relatively dilute nectar, fits the bird pollination syndrome (Faegri & Van der Pijl, 1979). However, since honeybees are known to utilise *A. greatheadii* var *davyana* pollen and nectar extensively they may also contribute to the pollination of this aloe.

Thesis organisation

The aim of this study was to evaluate the floral rewards of *Aloe greatheadii* var *davyana* (Asphodelaceae). In spite of the importance of *A. greatheadii* var *davyana* for the beekeeping industry, no complete analysis of its pollen is available and except for the popular bee literature little is known about its nectar concentration and production. It is also unknown whether honeybees, *Apis mellifera scutellata,* are the primary pollinators of *A. greatheadii* var *davyana*.

Each chapter is presented as a research article and consequently there is some overlap of information and references. I did not write the thesis in the first person but used the term "we" throughout the thesis due to the fact that some of the chapters are already published and that I were unable to do all the bee fieldwork on my own.

Chapter one (published as Human & Nicolson, 2006, *Phytochemistry*) deals with the nutritional value of fresh, bee-collected and stored pollen of *A. greatheadii* var *davyana,* examining whether there is anything special about the pollen that causes the rapid build-up of colonies when feeding on this aloe. Chapter two investigates the influence of pollen of *A. greatheadii* var *davyana* and sunflower, *H. annuus,* on ovarian development in normal queenright colonies in the field and compares the extraction efficiency of the two types of pollen. Chapter three (published as Nepi et al., 2006, *Plant Systematics and Evolution*) compares the nectary structure and nectar presentation in *A. castanea* and *A. greatheadii* var *davyana.* Chapter four deals with nectar production patterns of *A. greatheadii* var *davyana* and the dilute nectar as a resource for honeybees, *A. mellifera scutellata,* during dry winters. Chapter five investigates whether honeybees, *A. mellifera scutellata,* eliminate excess water from the dilute nectar of *A. greatheadii* var *davyana* before returning to the hive. Chapter six (published as Human et al., 2006, *Naturwissenschaften*) tries to answer the question whether honeybees, *A. mellifera scutellata,* regulate humidity in their nest and whether the dilute *A. greatheadii* var *davyana* nectar affects it. Chapter seven investigates the importance of birds and bees as pollinators of *A. greatheadii* var *davyana,* which exibits an ornithophilous pollination syndrome. The general conslusion synthesises the main finding of the above mentioned chapters and provides ideas for future research.

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