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Community ecology of small-mammal pollinated proteas

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Abstract

The floral characteristics of small-mammal pollinated (SMP) *Protea* species have been assessed in a number of previous studies. This study aimed to determine whether the inflorescences of *Protea canaliculata, Protea sulphurea* and *Protea humiflora* possess these traits and are pollinated by small mammal species. An additional aim of this study was to determine whether there is a variation in pollinator efficiency of different animal species. Floral characteristics that may influence plant-pollinator interactions were measured, including floral dimensions, nectar production and spectral reflectance. Live-trapping was conducted using Sherman traps and mean facial and faecal pollen load was determined for the different species caught. Furthermore pollinators were observed through footage from motion sensor cameras placed facing the inflorescences of SMP proteas. The results of this study confirmed that *Protea canaliculata, Protea sulphurea* and *Protea humiflora* are pollinated by small mammal pollinators. The evidence supporting this is that the afore-mentioned species have traits that correspond to those possessed by known small-mammal pollinated proteas including: bowl-shaped inflorescences, high nectar concentrations (ranging between 24.1-42.9%), sucrose-rich nectar composition, a "yeasty" scent, floral colours that are visible to small mammals, and a winter flowering season. These proteas were found to have separated peak flowering times, providing a nectar source throughout winter for small mammals at this site. Fifty-eight small mammals of seven different species, were trapped in *P. canaliculata* and *P. sulphurea* stands over 98 hours. The average night-trapping success was 22.7% and day-trapping success was 5.7%, indicating a relatively abundant nocturnal small-mammal population. A separation in pollinator efficiency was observed for different small mammal species, with *Elephantulus edwardii* identified as the most effective pollinator as it showed the greatest pollen removal (highest faecal pollen load) and spent the longest time foraging on inflorescences (±28 seconds per inflorescence). Another important pollinator was *Aethomys namaquensis* because it visited flowers 75% more frequently than any of the other pollinators. Camera trapping was shown to be a superior method than conventional trapping for assessing pollination by providing insight into pollinator behaviour, identifying new pollinators of 'trap-shy' species and also due to its more animal-friendly disposition.

Introduction

Pollination via small mammals[1] was first studied by Porsch (1934) after which this avenue of research was largely neglected. About 40 years later, pollination by small mammals in South African Proteaceae started receiving more attention with early work by Rourke and Wiens (1977) and Wiens et al. (1983). Rourke and Wiens (1977) discussed this type of pollination making observations and inferences about the convergent evolution of floral traits between the South African and Australian Proteaceae. They also went on to discuss the possible existence of a class of flowers adapted to pollination via small mammals, also referred to as SMP proteas. This class of flowers is defined by the presence of a number of floral traits: flowers occur in floral heads with approximately 100-200 flowers per head, these heads are normally at a ground-level position (geoflorous), sometimes up to 30cm high and deeply hidden within the dense foliage of the shrubby plants and a cup-shaped involucre comprising of a series of overlapping bracts surrounds the flowers (Rourke & Wiens 1977). Rourke and Wiens (1977) also found that many of the species in this pollination class produced large amounts of nectar and had a distinctive yeasty smell. Based on these floral traits, particularly the geoflorous and cryptic positioning of the floral heads as well as their general morphology, Rourke and Wiens (1977) suggested strong convergent evolution between the South African and Australian SMP Proteaceae.

Small-mammal pollinated proteas have evolved certain characteristics that are considered attractive to small mammals. Certain floral structures indicate that the species in this class are likely to have been derived from bird-pollinated species (Rourke & Wiens 1977 and Wiens et al. 1983) and it has been suggested that *Protea* species did not co-evolve with small mammals to form specialised pollination systems, as is the case with the honey possums and *Banksia* in Australia, but rather that these proteas adapted to attract and use small mammals as pollinators (Wiens et al. 1983). Wiens et al. (1983) conducted a number of pollination experiments on various South African Proteaceae. They looked closely at the associated floral traits of rodent and other small-mammal pollination systems established by Rourke and Wiens (1977), and suggested additional traits of SMP proteas. One of these floral features included high levels of sucrose-rich nectar production where the nectar has high volumes of carbohydrates. Another feature was the wiry, flexible styles, which are able to tolerate rough handling and are therefore largely unaffected by the foraging behaviour of small mammals. It was also found that floral heads were normally borne on short, stout peduncles and the nectar presentation to stigma distance was approximately 10mm (Wiens et al. 1983). Species studied and identified by Wiens et al. (1983) as SMP plants were *P. amplexicaulis, P. cryophila, P. effusa, P.*

[1] Small mammals as used in this context include all species of Rodentia, as well as *Elephantulus edwardii* and *Galerella pulverulenta* (Cape gray mongoose) but exclude flying small mammals such as bats.

recondita, P. humiflora and *P. sulphurea*. More recently, other *Protea* species have been identified as being at least partially small-mammal pollinated (e.g. *Protea nana*, Biccard & Midgley 2009, *Protea Witzenbergiana,* Protea Atlas Project; *Protea pendula*, Protea Atlas Project and Balmer 2013; *Protea namaquana,* Balmer 2013) as well as the identification of SMP non-proteoid species (eg. *Massonia depressa*, Johnson et al. 2001; *Colchicum scabromarginatum,* Kleizen et al. 2008; *Whiteheadia bifolia* Pagoda lily, Wester et al. 2009; *Erica hanekomii*, Turner et al. 2011).

Scent has also been identified as a characteristic for attracting small mammals. Wiens et al. (1983) first pointed out that the 'yeasty' odour of certain *Protea* species correlates with small mammal pollination. However, scent has only recently been analysed and separated into its relative chemical components in the hopes of identifying what it is exactly that is attractive to small mammals in the scent of these proteas (Darryn Records, unpublished data) and other SMP plants. Darryn Records (unpublished data), has so far determined that a combination of ethanol and dimethyl sulphide is attractive to small mammals. The significance of this finding is that it has been determined that SMP proteas emit dimethyl disulphide in low concentrations.

Wiens et al (1983) also looked at the pollination from the rodent perspective. In order to provide evidence for small mammal visitation to *Protea* flowering heads expected to be associated with small-mammal pollination, they conducted a series of experimental tests. One such test was to look at the presence of pollen on the rostra and in the gut of small mammals. Although the amounts of pollen per animal were highly variable, they found that *Protea* pollen was present on the rostra and in the faeces of all the small animals captured around these *Protea* species. The authors also noted that the sticky nature of this pollen decreased the likelihood of the pollen being dispersed by wind. To support this, they looked for the presence of pollen on leaf and other plant material around the floral head, which could have accumulated if wind was dispersing the pollen. They found no *Protea* pollen and only the pollen of other plants on the surrounding leaf and plant material.

Another test involved placing fluorescent powders on floral heads of proteas and determining the rodent presence and pathways by looking for powder trails using a shortwave UV lamp (Wiens et al. 1983). The results of this test showed that small mammals visit different floral heads on the same plant and also floral heads on plants up to 15 metres away. The powder was found on rodent pathways between *Protea* plants. This finding along with the large distances of the powder trails and the fact that fluorescing powder was found on trapped small mammals excludes terrestrial insects of transporting the powder. A third test involved looking for evidence of small mammals visiting floral heads through 'artefacts' left behind. Small-mammal faeces were found in the *Protea* heads, with

older floral heads containing more faecal pellets. Furthermore, it was found that pollen was present in these faecal pellets indicating multiple visitation.

Although there was substantial evidence that small mammals were visiting SMP proteas, Wiens et al. (1983) wanted to determine whether this visitation was actually resulting in pollination. One way in which they did this was to observe the foraging behaviour of captive small mammals on *Protea* inflorescences. Another way was to set up selective exclusion experiments, in order to see the effect on seed set of excluding small mammals. They found that seed set was reduced by approximately 50% when small mammals were excluded. Using a similar experimental setup Fleming and Nicolson (2002) found that small mammals were responsible for approximately 50% of the seed set in *Protea humiflora*. Other studies using this method for pollination studies of *Protea* species, include Biccard and Midgley (2009) and Steenhuisen and Johnson (2012). An emerging new method in the observation of pollinator activity is the use of camera trapping where floral heads can be inconspicuously observed. In 2009, Wester et al. used a video camera that constantly recorded for 4.5 hours over two nights to observe potential visiting and pollination of small mammals on *Whiteheadia bifolia*. Motion sensor cameras have the potential to be even more useful and convenient, and are far less battery-limited as they only record when movement or heat is detected. Alice Balmer (2013) used motion sensor cameras with successful results whereby, small-mammal and bird pollinator species were observed foraging on *P. recondita* and *P. pendula*. The number of pollinator species identified from the camera trapping, was greater than was evident from the live small-mammal trapping (Balmer, 2013).

Energy tests, determining how effective nectar is as a food source for small mammals, conducted by Wiens et al. (1983) suggested that the pollination of SMP proteas by small mammals is not a co-evolved system. They proposed the "junk food" hypothesis wherein the nectar provided by these *Protea* species is a bonus for mammals rather than a food source that they are dependent on. Later Fleming and Nicolson (2002) considered whether floral rewards could actually play a role in mammal pollinator reproduction and found that *Acomys subspinosus* was feeding almost primarily on nectar of *Protea humiflora* during the time of breeding which coincided with peak flowering of this plant. This type of finding proposes the question of whether a small mammal population could be sustained or at least partially supported by the nectar provided by SMP proteas. Additionally one can ask whether small mammal populations could be sustained throughout cold winters in areas containing co-occurring SMP *Protea* species with sequential phenologies. In this way *Protea* species could provide a nectar resource that may have the ability to enhance breeding and juvenile survival during the winter months.

This study aims to describe the community ecology of co-occurring small-mammal pollinated *Protea* species and their pollinators. The three species studied were *Protea canaliculata*, *Protea sulphurea* and *Protea humiflora*. The key questions of this study are 1) Do these proteas have morphological, colour, nectar, and scent traits suited for pollination by small mammal pollinators? 2) Which species are pollinating these proteas? 3) Is there a separation in the flowering time of the SMP *Protea* species at this site, and does this benefit the small-mammal population of this site? 4) Do the different small mammal species differ in pollinator effectiveness? and 5) how does camera trapping compare to live small mammal trapping in a pollination study.

Materials and Methods

1) Study site and species

This study was conducted on private land named Kraggashoek (33^0 20' 13" S, 20^0 23' 35" E) in the northern central part of the Western Cape bordering the central Karoo (Figure 1). The study area is a high-lying region with an elevation of 1190 metres above sea level, experiencing hot, dry summers and very cold winters. This site is one of a few patches of *Protea* populations in an otherwise, Renosterbos (*Elytropappus*)-dominated landscape. Four *Protea* species are present at the site, *Protea canaliculata*, *Protea sulphurea*, *Protea humiflora* and *Protea laurifolia*. The species studied were those thought to be small-mammal pollinated which are *P. canaliculata, P. sulphurea* and *P. humiflora* (Fig. 2). The approximate size and distribution of the populations of these species at the study site are shown in Figure 2.

Figure 1: Photograph of the study site (on Kraggashoek farm) showing the three study species, *Protea canaliculata, Protea sulphurea* and *Protea humiflora* populations, with an inset map showing the geographical location of the study site within the Western Cape region (Map source: Google Earth, 2013).

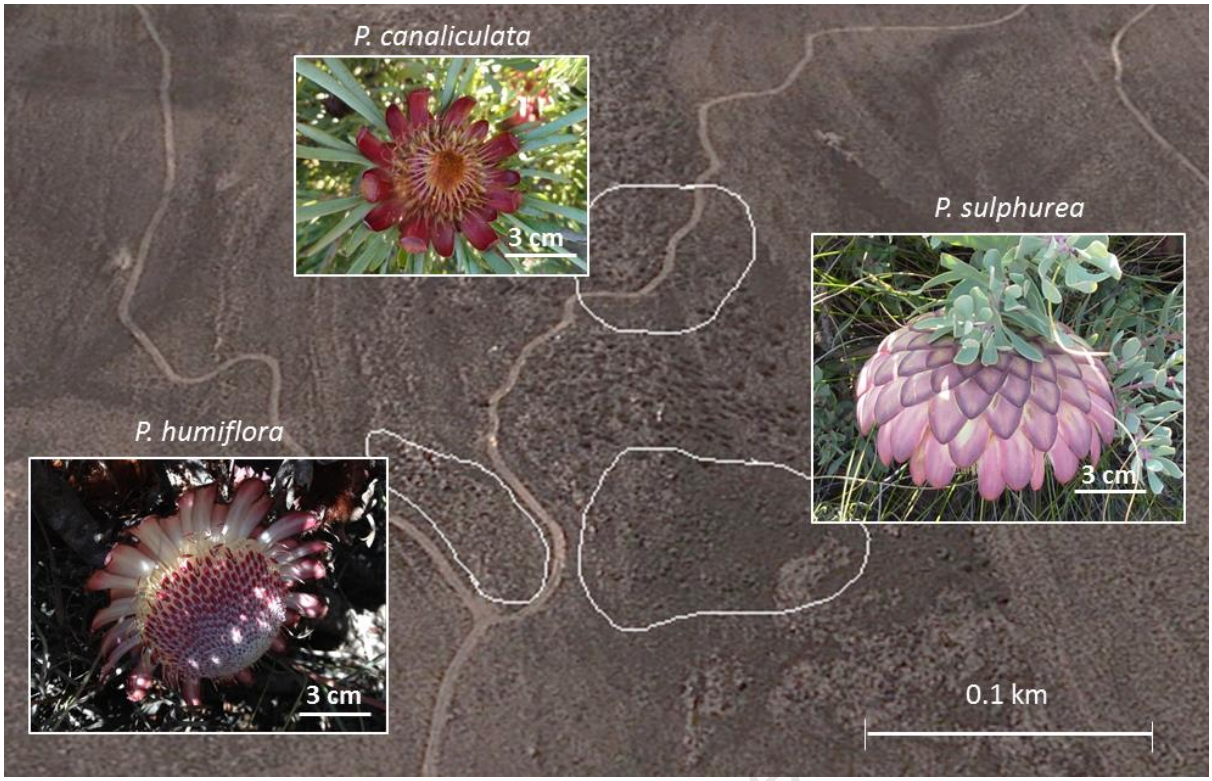

Figure 2: Map of study site with polygons outlining the location and approximate size of the populations of the three study species, *Protea canaliculata*, *Protea sulphurea* and *Protea humiflora* (Map source: Google Earth, 2013). Also included are photograph insets of each of the species.

2) Floral biology

2.1) Morphology

In order to assess the floral morphology of the three *Protea* species in relation to their pollinators, floral dimensions were determined for six inflorescences of each species. Although the floral morphology was not determined for *Protea humiflora* in this study, it was previously determined by Balmer (2013) (n=10) and this data will be used in discussion in order to compare the three *Protea* species. Inflorescence height and diameter was measured in mm. The total number of florets for each inflorescence was counted. Floret height, style length, pollen presenter length, distance from nectar production (ovary) to nectar presentation, distance from nectar presentation to top of stigma and distance from base of floret to nectar presentation measurements were taken for an outer and inner floret for each of the inflorescences. Additionally, the lengths and breadths of six leaves each of *P. canaliculata*, *P. sulphurea* and *P. humiflora* as well as the *P. canaliculata* x *P. sulphurea* and *P. humiflora* x *P. sulphurea* hybrids were taken. The amount of pollen produced per floret was also measured so that a comparison between pollen production and total seed set (as determined by breeding experiments, see point 4) could be made.

2.2)Colour

The colour of different floral parts for *Protea canaliculata* and *Protea sulphurea* was determined by measuring spectral reflectance across the 300-700 nm range using a spectrometer (Ocean Optics S2000) and a fibre optic reflection probe attached to it allowing light to fall on the plant surface at a 45^{o} angle. An Ocean Optics DT-mini deuterium tungsten halogen light was used as the light source (200-1100 nm range) and an Ocean Optics WS-1 diffuse reflectance standard was used for the calibration of the spectrometer (Johnson & Anderson 2002). The floral parts measured included the inner and outer, top and bottom bracts, the outer top perianth, the pollen presenters bearing pollen, the bare styles, the bare stigmas and the leaves. The values obtained for the floral parts thought to be most visible to pollinators (pollen presenters baring pollen, bare stigma, outer top perianth and outer top bract) were averaged and presented as line graphs. Again the data for *P. humiflora* was used from Balmer (2013).

2.3)Nectar

To assess the rewards offered by the plant to the pollinators, nectar samples were collected from 6 open *Protea sulphurea* and *Protea canaliculata* individuals straight after picking (standing crop) and additionally after a 24-hour period which allowed for nectar accumulation while cut inflorescences were placed in water. The nectar production (volume) in µl and concentration (% Brix) of 3 florets per inflorescence was measured. Concentration was determined using an Atago NI 0-50% pocket refractometer. If the concentration was too high to be read by the refractometer, the solution was diluted with water and a correction factor applied to the concentration reading according to the amount of water added. Again, nectar data for *P. humiflora* was used from Balmer 2013, in order to compare the three species.

Nectar from *P. canaliculata* and *P. sulphurea* was also collected for high-pressure liquid chromatography (HPLC) to determine sugar composition. Five µl of nectar from each of three inflorescences was placed onto the same spot on filter paper (Whatman's No. 1), creating a 15µl nectar sample. Three of these samples were made for each of the species. Once these samples had air-dried, the filter paper containing the sample was cut out and placed with 200µl of distilled water into a microcentrifuge tube. In order for the sugars to fully dissolve into the water, the tubes were placed in an oven for two hours at 60^{0}C and vortexed every 15 minutes. This liquid was then extracted and filtered through a 0.45µm nylon filter. The filtered samples were then analysed using a Shimadzu HPLC (LC-20AT) and the sugar composition analysis was done with a Liquid Chromatography post run analysis. The quantities of the sugars sucrose, glucose, fructose and xylose were thus determined as

percentages. The *P. sulphurea* samples are still to be processed at the University of KwaZulu-Natal and thus we incorporate the results from Balmer (2013) for the purposes of discussion in this study.

2.4)Scent

Choice tests have shown that scent influences the attraction of pollinators to inflorescences (Beetle choice tests with *Protea simplex* and *Protea roupelliae,* Steenhuisen et al. 2012). Scent samples were therefore taken to determine the chemical composition of floral scents for *Protea sulphurea* and *Protea canaliculata* by enclosing twelve inflorescences in three polyacetate bags (four in each bag) and drawing air through a scent trap made of a glass tube filled with 1.5mg of Tenax® and 1.5mg of Carbotrap®, held in place by glass wool. These samples were run for four hours using an air pump with a pump rate of 200ml/min. Leaves were also measured for scent in the same way in order to control for compounds released by leaves. A control bag of ambient air was also run at the same time. The scent samples were stored in a freezer before being sent for analysis using gas-chromatography-mass-spectrometry at the University of Kwazulu-Natal, Pietermaritzburg (method described in Steenhusien et al. 2012)

3) Plant phenology

Phenology assessments of the *Protea sulphurea* and *Protea canaliculata* populations were conducted three times in the year, 16th May, 18th June and 29th July 2013. The number of buds, open inflorescences and senesced inflorescences were counted for 25 randomly selected plants in each of the populations. On the 29th July trip, a phenology assessment of the *Protea humiflora* population at this site was conducted for 10 individuals. Fewer individuals were assessed as this population was smaller than the other *Protea* populations, as 10 individuals made up more than three quarters of the total *P. humiflora* population.

4) Breeding system and pollinator effectiveness

On the first fieldtrip to the study site (13-17th May 2013), breeding experiments were set up for 17 randomly selected individuals of the *Protea sulphurea* population and 20 individuals of the *Protea canaliculata* population. Five buds of approximately the same size and maturity were selected from each of the *Protea sulphurea* plants. In order to exclude birds and rodents, one bud was enclosed by a cage made of chicken wire (13mm) (labelled 'cage'). To exclude birds, rodents and insects (all visitors), two buds were enclosed in fine nylon mesh bags as well as a cage over this to prevent damage by animals to the bags. One was left unadjusted for the entire experiment ('bag') to test for autonomous seed production whereas the other was opened and 'selfed' to assess self-compatibility, by moving pollen around its own inflorescence using a toothpick during the flowering period ('self').

Two buds were left open to allow all pollinators access ('open' which was the control), and one was supplemented with cross-pollen collected from other plants in the population ('cross'), to assess plants for pollen or resource limitation. Two inflorescences were selected from each of the *Protea canaliculata* plants and both were enclosed in fine nylon mesh bags, in order to exclude all pollinators. Controls for this experiment were two 'open' or control individuals from each of the plants. Once flowering was over, plants were left to set seed where approximately three months later (November 2013) the experimental inflorescences will be removed and collected. The inflorescences will be cut open and the number of seeds found in each counted.

5) Floral visitor survey

5.1) Bird and small mammal visitors: Camera trapping

The motion sensor cameras used for this experiment are triggered by heat and movement. Four Bushnell, Trophy Cam HD Max-Colour LCD, 119577C cameras and three Bushnell, 119466 cameras were used and the duration and number of camera traps setup at a time was a function of their availability. For *P. canaliculata* 3 cameras were setup over a period of 145 days. For *P. sulphurea,* 6 cameras were setup for 57 days. For *P. humiflora,* 4 cameras were setup for 22 (24-hour) days. Cameras were placed approximately a metre (or more) away from open inflorescences to create optimal camera focus. Once triggered, cameras recorded 60-second videos (with 10 second trigger intervals) which were later analysed for the type of pollinator species, time of the visit, time spent foraging, behaviour and number of inflorescences visited (if there was more than one present in a video frame).

5.2) Small mammal visitors: Sherman trapping

In order to identify the small mammal species present in the area and to determine whether rodents had picked up pollen, small-mammal trapping using Sherman traps was conducted within the *Protea sulphurea* stand on two fieldtrips (animal ethics clearance no. 2012/V46/SS). Trapping was done for two days and two nights (14th night, 15th day and night, 16th day) in May and two days and one night (29th day and night and 30th day) in July. Traps were laid out along five lines approximately 10 metres apart with 10 traps in each line approximately 5 metres from one another. In order to aid in the identification of the rodents, weight (g) and body and tail lengths (mm) were measured (Rodents were identified using De Graaf, 1981). The animal's faces were swabbed with a cube of Fuschin-stained gel (Beattie 1971), which was then placed on a slide, melted and covered with a coverslip. Along three randomly selected transects of the slide, the number of *Protea* pollen grains and the number and type of foreign pollen grains were counted at a 25 x magnification. The pollen counts from the three transects were averaged.

Faecal pellets from each rodent found in the traps were collected and stored in 70 % ethanol to prevent fermentation. Two faecal pellets from each rodent were randomly selected and placed in a microcentrifuge tube with 500 µl of 70% ethanol. The solution was then ground up with a toothpick and vortexed to create a more homogenous solution. From this solution three 5µl-samples were extracted and fixed separately onto slides using melted Fuschin gel, over which three cover slips were placed. The solution was vortexed between each extraction. Pollen was counted, under a 25x magnification, across one transect per sample, of which there were three on a slide. If samples had more than 100 pollen grains, no further counting was done and this was recorded as >100 pollen grains. Pollen counts were averaged across the three samples per slide, with counts of more than 100, being recorded as 100.

The faecal and facial pollen counts were then averaged for each of the species. Pollen counting varied with the different samples due to the different nature of each sample type. This variation was however neutralised because the average pollen counts per species were interpreted as relative to other species.

5.3) Insect visitors

An insect survey was conducted over two afternoons on *Protea sulphurea* and *Protea canaliculata*, where inflorescences were inspected for the presence of insects. Insects found were collected and stored in microcentrifuge tubes in a freezer. Insects were later swabbed with a cube of Fuschin gel which was then melted onto a slide and the total number of pollen grains was counted and then averaged per insect species.

6) Data analysis

In order to determine whether the inner and outer florets differed significantly in their floral dimensions, t-tests of the different variables were conducted. This was done for both *Protea canaliculata* and *sulphurea* and previously for *Protea humiflora* (Balmer, 2013). Using a one-way ANOVA and a post-hoc Tukey test, the difference between overnight accumulation of nectar volume and concentration between the three plant species was analysed. A t-test was used for the standing crop nectar as there was only data for *Protea sulphurea* and *Protea canaliculata.* To determine whether the pollen load was significantly higher for certain small mammal species than others, ANOVAs were run for the facial and faecal pollen count data. Post-hoc Tukey analyses were conducted if there was a significant difference in order to determine which species differed significantly from each other.

Results

1) Floral biology

1.1)Morphology

The placement and position of floral heads on the plant varies considerably between the species as the inflorescences are pendulous in *P. sulphurea*, axillary and near the ground in *P. humiflora* and erect and upward-oriented in *P. canaliculata*. *Protea sulphurea* and *P. humiflora* have larger bowl-shaped inflorescences with diameters of ± 11 and 9 cm and containing an average of 531 and 294 florets respectively, whereas *Protea canaliculata* has a floral diameter of ± 6 cm and contains ± 129 florets (Table 1). As there was no significant difference between the inner and outer florets, measurements were averaged.

Table 1: Mean measurements (± standard deviation) of floral morphological traits of *Protea canaliculata, Protea sulphurea* and *Protea humiflora*. Data for *Protea humiflora* from Balmer (2013).

Part	**Measurement**	***Protea canaliculata***	***Protea sulphurea***	***Protea humiflora***
Inflorescence	Height (mm)	34.46 (± 2.07)	56.71 (± 2.13)	47.49 (± 3.86)
	Diameter (mm)	59.19 (± 8.78)	110.14 (± 11.34)	93.8 (± 7.63)
	No. of florets	128.6 (± 12.50)	531.3 (± 147.14)	294.8 (± 30.00)
Floret	Floret height (mm)	26.03 (±1.50)	35.54 (± 4.42)	27.41 (± 3.92)
	Style length (mm)	23.70 (±1.27)	32.76 (± 4.11)	25.30 (± 3.65)
	Pollen presenter (mm)	3.43 (±0.27)	4.82 (± 0.30)	3.03 (± 0.34)
	Nectar production to presentation (mm)	9.24 (± 1.69)	9.27 (± 1.21)	14.08 (± 2.44)
	Nectar presentation to stigma (mm)	15.91 (±2.01)	24.73 (± 3.54)	13.17 (±2.88)
	Nectar presentation to ovary base (mm)	11.36 (±2.03)	11.72 (± 1.48)	16.49 (± 2.44)

Two hybrid species were found in the *Protea* populations, one being a *P. sulphurea* x *P. canaliculata* hybrid and the other being a *P. sulphurea* x *P. humiflora* hybrid. The leaf length and breadths of the *P. sulphurea* x *P. canaliculata* hybrid are in between those of the original species themselves (Fig. 3). The leaf length for the *P. sulphurea* x *humiflora* hybrid is closer to *P. sulphurea* and the leaf breadth is in between the two original species.

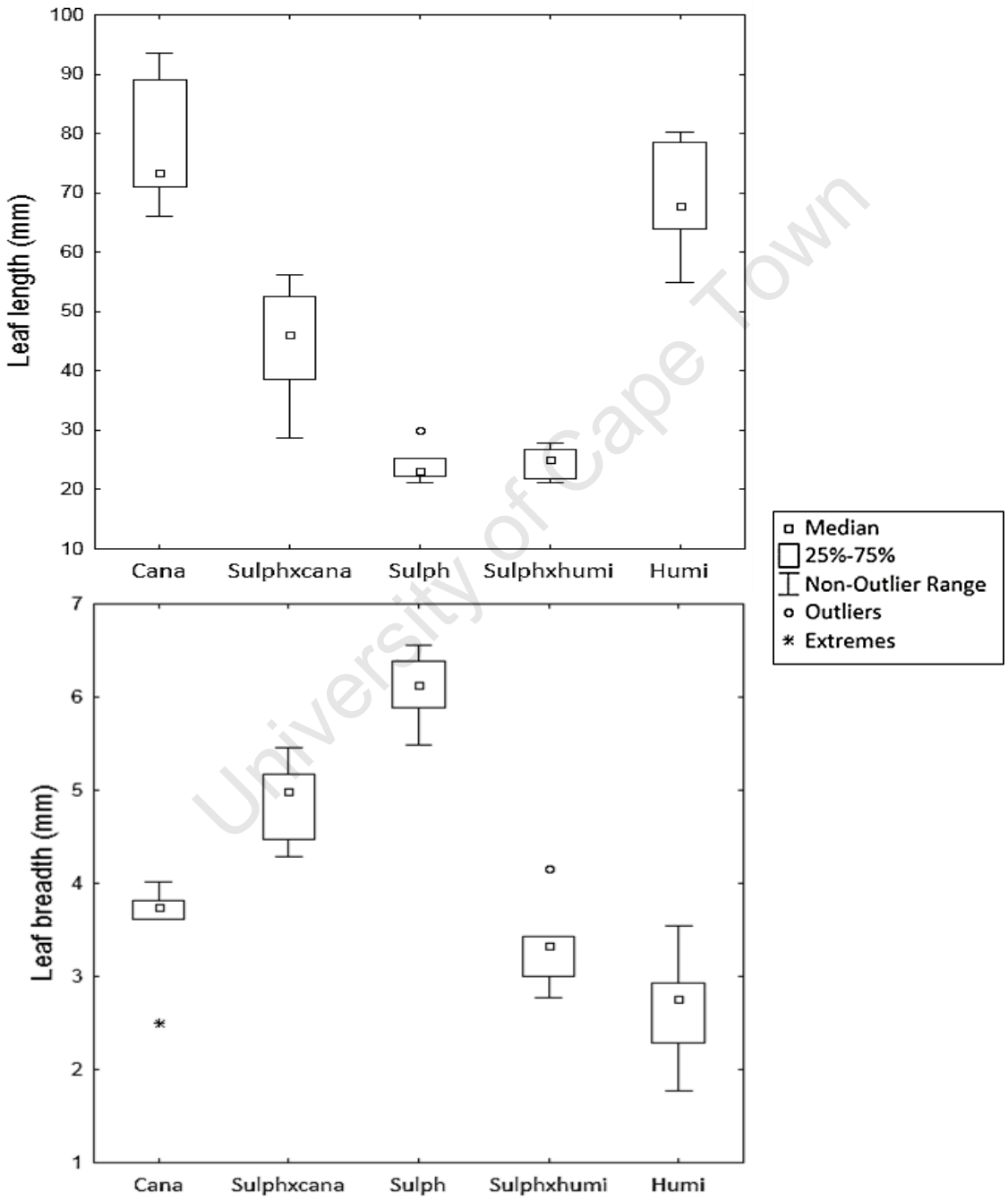

Figure 3: Leaf length (mm) and breadth (mm) of six leaves of *P. canaliculata* (Cana), *P. sulphurea* (Sulph) and *P. humiflora* (Humi) and the hybrids of *P. sulphurea* x *P. canaliculata* (Sulphxcana) and *P. sulphurea* x *P. humiflora* (Sulphxhumi).

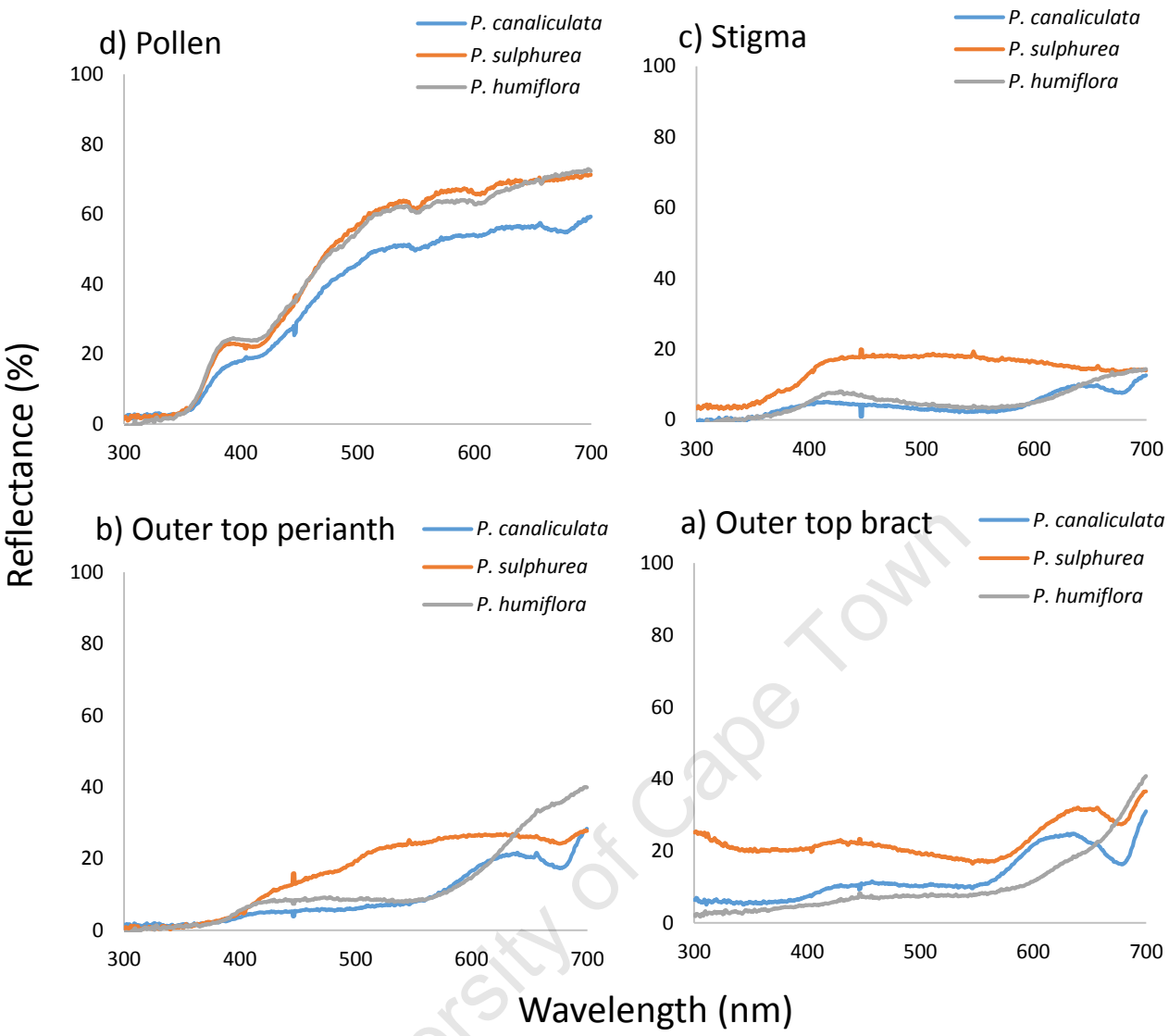

Figure 4: Average spectral reflectance of four floral parts of *Protea canaliculata, Protea sulphurea* and *Protea humiflora. Protea humiflora* data obtained from previous work done by Balmer (2013).

1.2)Colour

To the human eye, the colour of the three study species varies considerably. *Protea canaliculata* is bright red, *P. sulphurea* is more pinky-green and *P. humiflora* is very dark red-brown. The spectral reflectance results indicated that the pollen of *P. canaliculata* had a lower reflectance than the other two proteas (Fig. 4a). The bare stigmas (Fig. 4b) of *P. sulphurea* were more white-coloured whereas the other two proteas had more red-colour in these parts. The outer top perianth was brown in colour for all three species (Fig. 4c). The outer top bracts of *P. humiflora* were dull red whereas the *P. sulphurea* appeared to have had green, yellow-orange and ultra-violet (UV) pigments in the bracts

(Fig. 4d). *Protea canaliculata* had similar pigments in the outer top bracts to *P. sulphurea*, with less of the blue component.

1.3)Nectar

For the standing crop nectar, the volume of nectar produced by *P. canaliculata* was significantly lower than the volume of nectar produced by *P. sulphurea* ($t_{(34)}$= -5.39, p<0.001) (Table 2). The concentration of standing crop nectar, was however not significantly different between these two species. For the overnight accumulation, all three *Protea* species were compared and it was found that both the volume ($F_{(2,95)}$ = 5.023, p=0.008) and the concentration ($F_{(2,95)}$ = 3.749, p=0.0271) was significantly different for the different *Protea* species (Table 2). The Post-hoc Tukey analyses for the overnight accumulation results indicated that the nectar volume (production) of *P. canaliculata* was significantly lower than that of *P. humiflora*. These tests also indicated that *P. humiflora* had a significantly lower nectar concentration than *P. sulphurea* and *P. canaliculata*.

Table 2: Summary of the mean (± standard deviation) nectar production (µl) and concentration (%) of standing crop and overnight accumulation for *Protea canaliculata, Protea sulphurea* and *Protea humiflora. Protea humiflora* data obtained from Balmer (2013).

Species	**Standing crop**		**Overnight accumulation**	
	Production (µl)	**Concentration (%)**	**Production (µl)**	**Concentration (%)**
Protea canaliculata	1.21 (± 0.46)	56.33 (± 15.76)	5.83 (± 3.50)[a]	42.87 (± 21.20)[a]
Protea sulphurea	3.96 (± 2.12)	47.08 (± 19.48)	5.58 (±1.46)[ab]	41.5 (±16.67)[a]
Protea humiflora	-	-	9.62 (± 7.96)[b]	34.1 (± 8.62)[b]

The nectar composition analysis results for *P. sulphurea* were not available when this was written but the nectar composition of *P. canaliculata* (represented in Fig. 5) showed a high proportion of sucrose (48.87%), a low proportion of xylose (7.17%) and glucose and fructose making up the remainder with 19.8% and 24.16% proportions respectively.

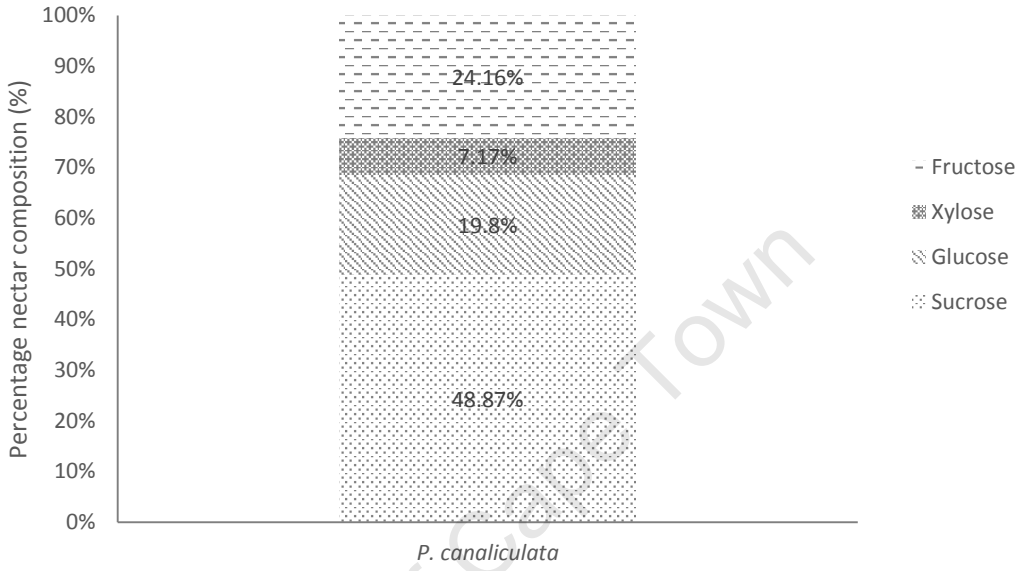

Figure 5: Nectar sugar composition of *Protea canaliculata* where percentage was calculated from the means of three inflorescences.

2) Plant phenology

The peak flowering time of the three *Protea* species' populations at the study site were confirmed to be different through the phenology assessments where Figure 6 shows the percentage of open inflorescences for each of the species at three different times in the year. *Protea canaliculata* and *Protea sulphurea* overlap in flowering time in June. The few hybrid individuals of these two species were also flowering during this time.

3) Breeding system and pollinator effectiveness

Upon inspection of the *Protea sulphurea* breeding experiments it was determined that it was too early to remove the inflorescences to count seed set, as it was likely that the plants had not reached the correct stage of maturity yet. This data is however valuable and will therefore still be collected at a later stage, most likely in November 2013.

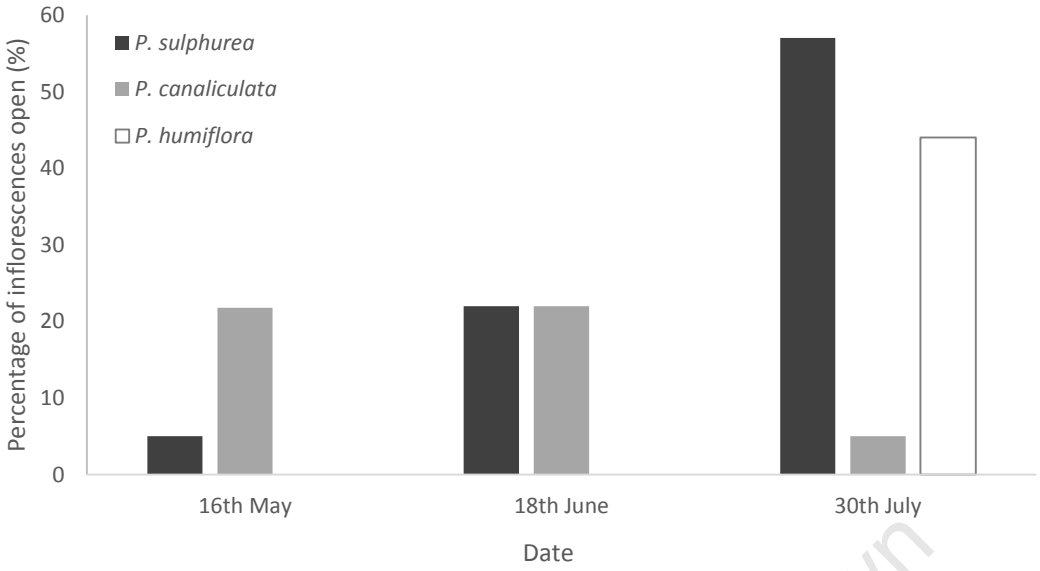

Figure 6: Mean percentage of inflorescences open per plant in the *Protea sulphurea, Protea canaliculata* and *Protea humiflora* populations during three fieldtrips (16th May, 18th June and 30th July).

4) Floral visitor survey

4.1) Bird and small mammal visitors: Camera trapping

Eleven different vertebrate species were found foraging on the *Protea* species by camera traps, eight of which were small mammal species and three of which were birds (Table 3). *Acomys subspinosus* and *Malcothrix typica* were not easily identified through the camera footage as they are of similar size and don't have features that are clearly distinguishable on night camera footage. For this reason they are grouped in Table 3. *Mus minutoides* and *Galerella pulverulenta* (Cape Gray Mongoose) were only found on *P. canaliculata,* and *Dendromys mesomelas* was predominantly found on *P. humiflora* with only one instance on *P. sulphurea*. *Graphiurus ocularis*, a rare mouse species (Graaf, 1981), was found foraging on *P. sulphurea* once and on *P. humiflora* once. In general the small mammal visitors moved around the floral heads, lapping up nectar and where two or more inflorescences were open and visible, visitors were frequently observed moving from one inflorescence to another. The Cape sugarbird appeared not to touch the pollen-presenting stigmas while foraging on the nectar, whereas the smaller-billed sunbirds (Orange-breasted and Southern Double-collared) appeared to do so.

Table 3: Pollinator species visitation (✓= observed visiting, ✖ =not observed visiting) of *P. canaliculata, P. sulphurea* and *P. humiflora* from video footage of camera trapping. Acomys subspinosus and Malacothrix typical are grouped as they were indistinguishable in the video footage.

Pollinator species	***Protea canaliculata***	***Protea sulphurea***	***Protea humiflora***
Acomys subspinosus/ Malacothrix typica	✓	✓	✓
Aethomys namaquensis	✓	✓	✓
Elephantulus edwardii	✓	✓	✖
Rhabdomys pumilio	✖	✓	✓
Dendromys mesomelas	✖	✓	✓
Graphiurus ocularis	✖	✓	✓
Mus minutoides	✓	✖	✖
Galerella pulverulenta (Cape gray mongoose)	✓	✖	✖
Anthobaphes violacea (Orange-breasted sunbird)	✓	✓	✓
Cinnyris chalybeus (Southern double-collared sunbird)	✓	✓	✓
Promerops cafer (Cape Sugarbird)	✓	✓	✓

As a proportion of the total visits to a species, birds visited *Protea humiflora* more often than *Protea sulphurea* and *Protea canaliculata* which had the smallest proportion of bird visits (Fig. 7). A higher plant height above the ground therefore appeared not to have influenced bird visits, as *Protea canaliculata* is taller than *Protea humiflora*.

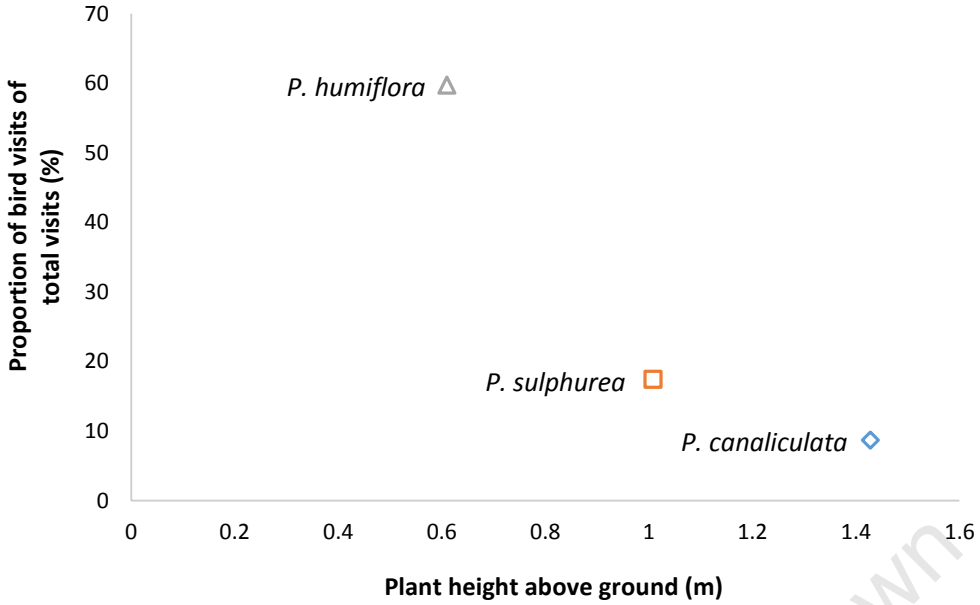

Figure 7: Mean plant height above the ground (m) of *Protea* species plotted against the proportion of bird visits of the total number of animal visitations to the respective *Protea* species as determined from the camera-trapping footage.

4.2) Small mammal visitors: Sherman trapping

Fourty-eight small mammals of seven different species were trapped in the *P. sulphurea* stand over 63 hours of trapping and 10 small mammals of two different species were trapped in the *P. canaliculata* stand over 36 hours of trapping. In total, fifty-eight small mammals of seven different species, were trapped in *P. canaliculata* and *P. sulphurea* stands over 98 hours. The trapping success in the *Protea sulphurea* stand was 13.5% in May and 18% in June and the trapping success in the *P. canaliculata* stand was 14.7% in May. The average night-trapping success for both species was 22.7% and day-trapping success was 5.7%, indicating a relatively abundant nocturnal small-mammal population.

An ANOVA showed that there was a significant difference between the faecal pollen loads of the small mammal species ($F_{(5)}$=2.92, p=0.022). The post-hoc Tukey analysis indicated that the significant difference lay between the faecal pollen loads of *Acomys subspinosus* and *Rhabdomys pumilio,* where *Acomys subspinosus* had a significantly higher load than *Rhabdomys pumilio* ($p<0.05$). All other small mammal species did not significantly differ in faecal pollen loads. The number of facial pollen grains was not found to be significantly different across the different small mammal species.

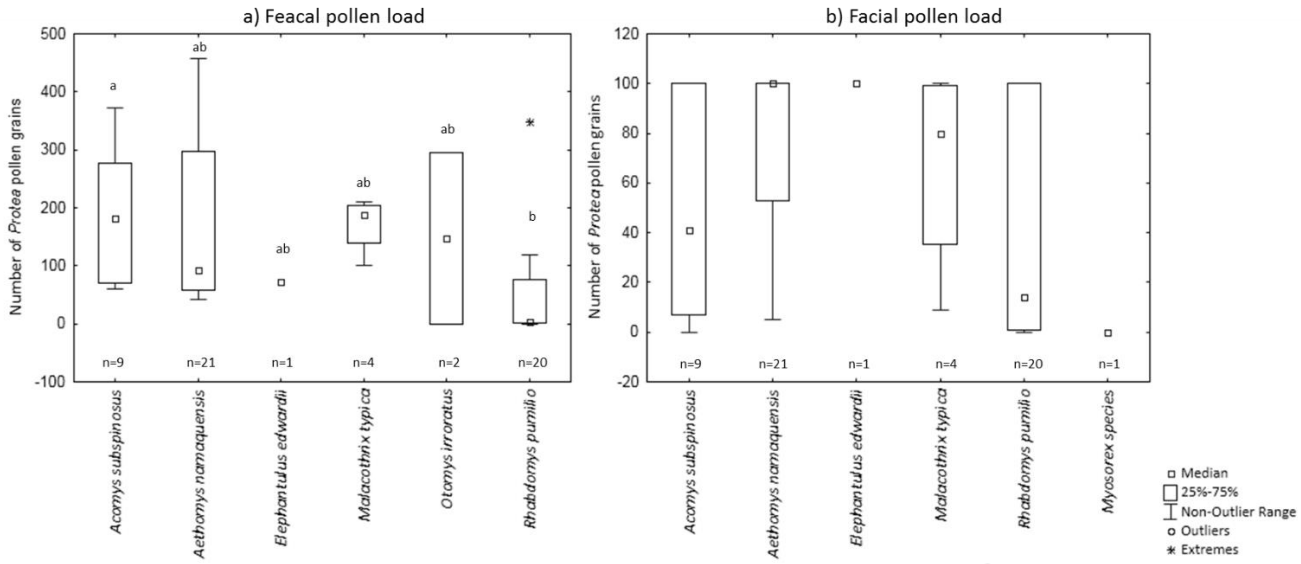

Figure 8: a) Faecal pollen load and b) facial pollen load of different small mammal species caught in the Sherman traps in stands of *Protea canaliculata* and *Protea sulphurea*. The faecal pollen load post-hoc Tukey analysis results are represented by the letters 'a' and 'b' that indicate the significant differences between pollen load of different species. The number of individuals sampled is n.

4.3) Insect visitors

The insect survey indicated that the proteas were not heavily visited by insects. However, on both*, P. canaliculata* and *P. sulphurea* inflorescences, bees were frequently observed moving between flowers in a floral head and also from one floral head to another. Three *Coleoptera* individuals were caught on *Protea canaliculata* inflorescences. The mean number of pollen grains on the body of this species was 154 (±14.17). Four ants were caught on the *Protea sulphurea* inflorescences, but due to the small size and improbable pollinator potential, pollen was not counted.

5) Camera versus Sherman trapping

In comparing the results from the two methods, the data of small mammal visitations for all three *Protea* species was combined. The cameras picked up species that were not caught in Sherman traps (Table 4). *Graphiurus ocularis*, *Galerella pulverulenta*, *Mus minutoides* and *Dendromys mesomelas*, were not caught in Sherman traps but were seen foraging on inflorescences by the camera traps. Furthermore, only one *Elephantulus edwardii* individual was caught in the Sherman traps whereas it was caught 21 times foraging on the inflorescences of the three *Protea* species for long periods at a time on the camera traps.

The mean number of facial pollen grains does not correlate strongly with the mean time spent foraging per inflorescence for species caught by both methods (R^2=0.003) (Fig. 9b), *(Rhabdomys pumilio*,

Elephantulus edwardii, *Acomys subspinosus* and *Rhabdomys pumilio)*. However, the mean number of faecal pollen grains is highly correlated with the time spent foraging per inflorescence for these species (R^2= 0.9937) (Fig. 9a).

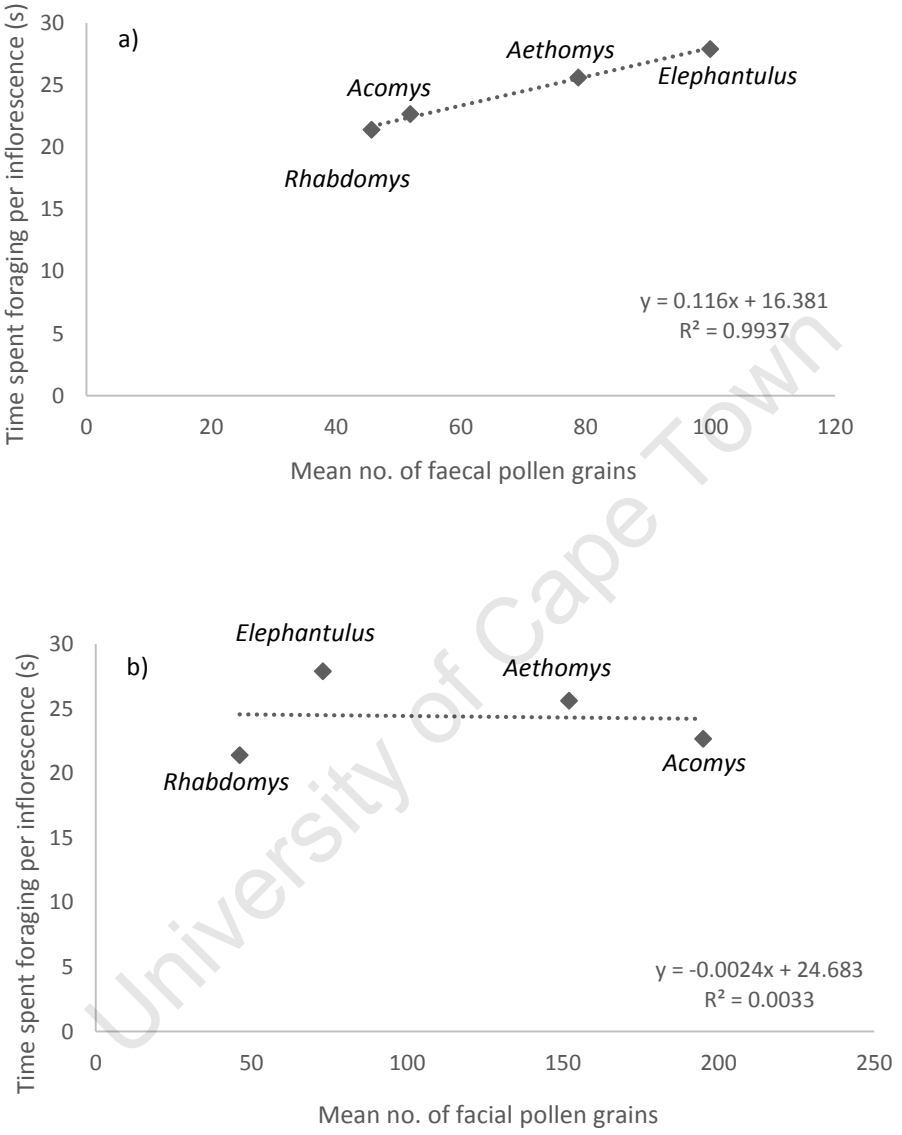

Figure 9: Mean number of a) faecal and b) facial *Protea* pollen grains found on small mammal species plotted against the respective mean time spent foraging per inflorescence (s) on the *Protea* inflorescences.

Table 4: Comparison of the different types of species and the numbers of individuals caught by the two trapping methods as well as a summary of the relative pollinator visitation of the different species in terms of mean (± SD) facial and faecal pollen load values and mean (± SD) time spent foraging per inflorescence. The results are combined for all three *Protea* species, *P. canaliculata, P. sulphurea* and *P. humiflora.*

	Sherman traps			Camera traps	
Species	**# of individuals caught**	**mean # facial pollen grains**	**mean # faecal pollen grains**	**# of individuals caught**	**Mean time spent foraging/ inflorescence (sec)**
Acomys subspinosus	9	195.07 (± 125.76)	51.89 (± 47.09)	3	22.67 (± 9.71)
Aethomys namaquensis	21	152.16 (± 125.74)	78.85 (±32.35)	83	25.62 (± 20.50)
Elephantulus edwardii	1	73	>100	21	27.90 (± 24.90)
Otomys irroratus	2	148.0 (± 209.30)		0	-
Malacothrix typica	4	171.83 (± 48.90)	67.25 (± 42.58)	0	-
Rhabdomys pumilio	20	46.19 (± 85.82)	45.68 (± 46.86)	11	21.41 (± 19.93)
Myoserex species	1	-	0	0	-
Graphiurus ocularis	0	-	-	2	20 (± 19.93)
Galerella pulverulenta	0	-	-	3	5.00 (± 4.36)
Mus minutoides	0	-	-	2	46.50 (± 2.12)
Dendromys mesomelas	0	-	-	15	32.63 (± 21.83)

Discussion

Floral biology: morphology and colour

Geoflorous, bowl-shaped and pendulous inflorescences are typical of small-mammal pollinated *Protea* species (Wiens et al. 1983). All three *Protea* species in this study have aspects of these traits but with slight variations in placement and positioning of their floral heads. *Protea canaliculata* has upright inflorescences with both high and low placement on the plant. *Protea sulphurea* has pendulous and generally low-placed inflorescences and *Protea humiflora* has very low (geoflorous) inflorescences that are placed in the axils of the leaves and are therefore largely hidden beneath dense foliage (cryptic) (Wiens et al. 1983). All three species have bowl-shaped inflorescences, with the largest inflorescences belonging to *Protea sulphurea* (Table 1). While *P. humiflora* has slightly smaller inflorescences than *P. sulphurea*, both these species have considerably larger inflorescences than *P. canaliculata* (Table 1). The nectar-stigma distance of typical small-mammal pollinated *Protea* species is ± 10 mm (Wiens et al. 1983). In this study it was found that this distance was approximately 15.9, 24.7 and 13.2 mm for *P. canaliculata*, *P. sulphurea* and *P. humiflora* respectively (Table 1). Although the nectar-stigma distance was slightly larger for *P. sulphurea*, it is still somewhat lower than the mean nectar-stigma distance for most bird-pollinated species (e.g. approximately 49mm for *P. nitida*) (Balmer 2013). All three *Protea* species in this study appear to possess morphological traits suited to pollination by small mammal pollinators, with *P. humiflora* showing more typical small-mammal pollinated traits than *P. sulphurea* and *P. canaliculata*, in terms of inflorescence placement and stigma-nectar distance.

The main floral parts seen by a pollinator are the pollen, stigma, outer top perianth and outer top bracts. The colour analysis showed that for these traits there was not a very clear separation in colour between the different species with the whiteness of the stigma and outer top perianth of *P. sulphurea* being the only clear differences between the species as these parts of the other species were darker and redder (Fig. 4). Birds have a tetrachromatic visual system with particular sensitivity to red pigments thus, inflorescences with red bracts are therefore commonly associated with an ornithophilous pollination syndrome (Endler, 1990). All three *Protea* species have red components and it is therefore likely that the floral heads of all three *Protea* species would be visible to birds. Although a model of the visual system of small mammals is not yet available, Jacobs (2001) found that rodents have a dichromatic visual system with a sensitivity to ultraviolet light (± 370 nm). The proteas had pink, red and dark red-brown bracts, colours which rodents are not particularly sensitive to. As small mammals were observed visiting all three species, it is suggested that these proteas are not attracting small mammals through colour signals alone.

Floral biology: Nectar production, concentration and composition

The volume of nectar produced by *P. canaliculata* was significantly lower than *P. sulphurea* for the standing crop analysis and *P. humiflora* for the overnight accumulation analysis (Table 2). *Protea humiflora* nectar production (±9.62 µl) was higher than the other two species (both under 6 µl), and was also closer to the mean production of bird-pollinated species found by Balmer (2013) which was 10.02 µl for bird-pollinated species. The nectar concentrations found for *P. sulphurea* (41.5% Brix) were higher than previously found for another population by Balmer (2013) (21.2% Brix) (Table 2). The variation in values was however higher for our study where the standard deviation was 16.67% versus 6.53% for the previous study. The nectar concentration of *P. humiflora* was found to be significantly lower than *P. canaliculata* and *P. sulphurea* in the overnight accumulation analysis (Table 2). The higher production and lower concentration of *P. humiflora* nectar could possibly help to explain the unexpectedly high bird visits to *P. humiflora* found through camera trapping (Fig. 7) as birds prefer less viscous and therefore less concentrated nectar.

The nectar composition of *Protea sulphurea* was found by Balmer (2013) to have a sugar composition of 42 (±3.68)% sucrose, 28.74 (± 2.18)% fructose, 21.58 (± 1.48)% glucose and 7.67 (±2.05)% xylose. *Protea humiflora* had a sugar composition of 56.87 (±15.48) sucrose, 23.75(±10.97)% fructose, 11.83 (±4.89)% glucose and 7.54 (±1.76)% xylose. The nectar composition for *P. canaliculata* was similar to what was previously found for SMP species by Balmer (2013) and the nectar was highly sucrose-rich (Fig. 5) which is typical of SMP plants (Wiens et al. 1983; Johnson et al. 1999; Nicolson & Van Wyk 1998).The sugar preferences of the pollinator, *Aethomys namaquensis*, was found to correspond to the amounts of different sugars in the nectar of *P. humiflora* and *P. amplexicaulis* where sucrose>fructose>glucose>xylose (Johnson et al 1999). This reflects Baker's (1990) proposition that the proportion of sugars in the nectar correlates with the preferences of the plant's pollinator. Although nectar characteristics can vary with the age of a plant, weather, altitude, amount of visitors and the time of the day sampled, our results indicate that the nectar production, concentration and composition of the study species corresponds to known small-mammal pollination systems.

Plant phenology

Although phenology assessments were not conducted on a continuous basis, the peak flowering times of *P. canaliculata* (May to June), *P. sulphurea* (July) and *P. humiflora* (August) appear to correspond with those recorded by the Protea Atlas Project (unpublished data). There is therefore a separation of peak flowering time between the *Protea* species at this site (Fig. 6). Furthermore, *P. laurifolia* is also

present at this site, and has a long flowering time, with the predominant flowering occurring between May and September. The unexpectedly-high levels of bird pollination on *P. humiflora* (Fig. 7) during August as opposed to *P. canaliculata* and *P. sulphurea* earlier in the year, may therefore be as a result of the decline in flowering of *P. laurifolia* at this time. In this way *P. humiflora* may be providing a resource to birds when the *P. laurifolia* resource becomes more limited.

Floral visitors

The *Protea* Atlas Project suggests that the pollination of *P. canaliculata* is 100% by beetles, the pollination of *P. sulphurea* is 33% by birds (orange-breasted sunbird), 33% by mammals and 33% by honeybees and that the pollination of *P. humiflora* is 100% by mammals. The breeding system and pollinator effectiveness experiments will provide evidence for the relative pollinator effectiveness of these different species in pollinating *P. sulphurea* and *P. canaliculata*. Our current results do however indicate that the pollinator proportions are different from those suggested by the *Protea* Atlas Project. *Protea canaliculata* was frequently visited by small mammal species while very few insects were found on this species (Table 3). Although the insect survey was conducted on mild and relatively overcast days, hence not optimal conditions for insects, it is still unlikely that these *Protea* species are solely pollinated by beetles and bees. This is because the flowering season of *P. canaliculata* falls in a time of the year that experiences colder and wetter conditions suggesting that insects that aren't very active in these conditions are unlikely to contribute to pollination very much. Our results suggest that the Protea Atlas data may be under-representing the pollinator contribution of small mammals and over-representing the contribution of birds and honeybees of *Protea sulphurea*. This is however more speculative and will be clarified with the pollinator effectiveness experiment results. *Protea humiflora* was more frequently visited by bird species than expected which suggests that this species is not solely pollinated by small mammals as suggested by the Protea Atlas Project data.

There does not appear to be a separation of the pollinator species between the different *Protea* species as most small mammal and bird species were found foraging on all three proteas (Table 3). Species not found on all three proteas were the rarer individuals of the small-mammal community, for example *Mus minutoides*, *Galerella pulverulenta* and *Graphiurus ocularis* (Table 3). Due to the variation in time of cameras recording on the different *Protea* species, it is highly unlikely that the presence or absence of rarer individuals is a reflection of whether they visit these proteas or not but it is rather a case of chance. Furthermore, the presence of hybrids suggests that the pollinators are generalist and are moving between the different species with overlapping flowering seasons i.e. between *P. canaliculata* and *P. sulphurea* and between *P. sulphurea* and *P. humiflora* (Fig. 3).

Pollinator effectiveness

The Cape sugarbird did not appear to touch the pollen presenting stigmas while foraging on the nectar of the proteas, suggesting that this species is more likely a nectar robber than a pollinator. Sunbirds, are smaller and have shorter beaks and appeared to touch the pollen presenters, indicating a possible role in pollen transfer. Further studies are needed to determine the relative contribution of smaller, shorter-beaked birds to pollination of these proteas.

Pollen load results indicate that *Acomys subspinosus* had significantly more faecal pollen than *Rhabdomys pumilio*, however the facial pollen load did not significantly differ between these two species (Fig. 8). Fleming and Nicolson (2002) found that *P. humiflora* pollen grains constituted approximately 33.5% of the winter scats of *Acomys subspinosus*, which was approximately 30% greater than the other two study species, *Aethomys namaquensis* and *Elephantulus edwardii*. The authors therefore concluded that pollen was a major component of *Acomys subspinosus*' diet and that it was potentially, actively foraging on pollen. This behaviour illustrated by *Acomys subspinosus* is the likely reason for its significant difference in faecal pollen load from *Rhabdomys pumilio*. Camera trapping results show that *Aethomys namaquensis* frequents the inflorescences of the studied *Protea* species a lot more than any of the other small mammal species with approximately 75% more visits than the next most frequent visitor, *Elephantulus edwardii* (83 vs. 21 visits respectively) (Table 4). In general, there appears to be a difference in pollinator efficiency of different small mammal species, in terms of pollen removal and foraging times. Both the faecal pollen load and time spent foraging results indicate that *Elephantulus edwardii* is the most effective pollinator out of the small mammal visitors caught on cameras and in the Sherman traps, followed by *Aethomys namaquensis*, *Acomys subspinosus* and *Rhabdomys pumilio* respectively (Fig. 9a). Nicolson and Fleming (2003) suggested that *Elephantulus edwardii*, being an insectivore, is attracted to SMP proteas due to the abundance of insects found in floral heads. The behaviour of this species, as observed in this study, suggests otherwise. Firstly, the videos showed *Elephantulus edwardii* individuals, sniffing in the direction of inflorescences and following the scent given off by the floral heads. Furthermore, insects are active during the day and these videos were taken during the night, hence the insect presence would be very low, if anything at all. This study provides one of the first accounts of time spent foraging and foraging behaviour of small mammals under natural conditions. Other studies include, Wester et al. (2009) who looked at foraging time and behaviour of small mammal pollinators on *Whiteheadia bifolia* under natural conditions and Balmer (2013) who did the same for *Protea recondita* and *Protea pendula*.

Effectiveness of camera versus live trapping

The small mammal species that were caught by both the Sherman and camera traps were *Acomys subspinosus, Aethomys namaquensis, Elephantulus edwardii* and *Rhabdomys pumilio.* The faecal pollen load of these small mammal species caught in the traps was highly correlated with the mean time spent foraging per inflorescence (R^2=0.99) (Fig. 9a) as found from the camera observations. This suggests that camera trapping is as effective as faecal pollen counting in determining pollinator visitation of small mammal species. Facial pollen load was not correlated with mean time spent foraging per inflorescence and is therefore a poor indicator of pollinator visitation (Fig. 9b). This may be because individuals groom themselves after foraging as was observed in a number of videos, resulting in a variation between species with different grooming habits. Alternatively or additionally, species caught in Sherman traps would have been caught at different times allowing some individuals to have more time in the trap where grooming could possibly take place as opposed to others that were caught just before we examined them.

Due to the similar effectiveness of the two methods in determining pollinator visitation, the question arises of which method is better. Ethically speaking, camera trapping is significantly better than live trapping as it is non-invasive and does not put the small mammals under the stress that they most probably experience with live trapping. Furthermore, the risk of trapped individuals freezing in low winter temperatures or dying of dehydration is completely eliminated. An important factor to consider is that, relating pollen loads to the efficiency of pollination is based on the assumption that the animal is indeed picking up the pollen from the flower and moving it to another inflorescence. Therefore, from a scientific perspective, camera trapping is better than live-trapping because videos from camera trapping provide insight into pollinator behaviour by actually showing the pollinators foraging on inflorescences and moving around and between floral heads in a way that enables pollen to be picked up by fur and deposited onto other flowers. One of the most important benefits of camera trapping is that more species can be identified as pollinators by the cameras than live-trapping. This applies to pollinators that cannot fit into live traps such as *Galerella pulverulenta* (Cape Gray Mongoose) and also to species that are rarely caught by live trapping such as *Elephantulus edwardii*, *Malocathrix typica*, *Dendromys mesomelas* and *Graphiurus ocularis* (Table 4). In this way new pollinators that were not previously thought to visit or pollinate flowers can be identified. Additionally, camera trapping is also a more 'user-friendly' method as it does not require much time in the field and cameras can be left in the field for lengthy periods. Perhaps the most important benefit is that foraging behaviour can be observed under natural conditions. Tank experiments where small mammals and floral heads are purposefully placed together in a confined environment cannot lead to conclusions that small

mammals display this behaviour in the natural environment, whereas camera trapping accurately documents the real-life plant-animal interaction.

Conclusion

This study confirms that *Protea canaliculata, Protea sulphurea* and *Protea humiflora* display floral traits that conform to a small-mammal pollination syndrome and are indeed pollinated by small mammals. The relative extent of these animal's contribution to pollination of *Protea sulphurea* as opposed to other pollinators will later be determined from the breeding and exclusion experiment results. Although we cannot say with confidence that small mammals are dependent on nectar as a food source, the nectar provided by these three *Protea* species at slightly different times in an otherwise resource-limited winter season, could promote the survival and as a result abundance of the small mammal population observed at this site. To provide more insight into this and to determine whether small-mammal population abundance corresponds to peak flowering times of the different proteas, live-trapping could be done in all three *Protea* populations throughout the year. Additionally, live-trapping could be conducted in an area containing no proteas and then compared to the area containing SMP proteas in order to assess the dependence of small-mammal population abundance on SMP proteas. This study found a separation in pollinator efficiency between different small mammal species with *Elephantulus edwardii* identified as the most effective pollinator and *Aethomys namaquensis* as the most frequent floral visitor. The use of camera trapping for both small-mammal and bird-pollination studies appears to be better than live-trapping methods as it provides an ethical way of obtaining more scientifically robust data. Importantly, the identification of new pollinators is possible using this type of method, with this study confirming that the rare species *Graphiurus ocularis,* the large species *Galerella pulverulenta* (Cape Gray Mongoose) and the rarely trapped species of *Elephantulus edwardii* and *Dendromys mesomelas*, all play a role in the pollination of the SMP *Protea* species at this site.

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