Geographical variation in insect pollinators of generalist Asteraceae

Stephen Gibson
UCT Botany Honours 1999
Supervisor: Mike Picker

Abstract

Pollination syndromes for four species of widespread Namaqualand daisies are described. The flowers are not specialized and are not visited by specialized insects, rather, they have a generalist disc shape and are visited by numerous species of insect. Pollinator efficiency for each species of insect caught we is also evaluated, revealing that only some of the visitors contribute significantly to pollen transfer. Pollen load was analysed with the help of a centrifuging method. The most common and frequently the most efficient pollinators are various species of monkey beetles (Scarabaeidae, Rutelinae, tribe Hopliini) and bee fly (Bombyliidae). These pollinator sets vary with geographical location and each species' set is compared across three regions: Niewoudtville, Northern Cederberg and Darling.

Introduction

Approximately 83% of the Cape Flora is insect pollinated (Johnson 1992). In pollination biology studies focus has been on very specific pollination interactions. Or example the oil collecting bees (Vogel 1974, Whitehead et al 1984) and long-tounged fly pollination (Whitehead et al 1987, Johnson 1994).Such specific interactions have been well studied elsewhere, with well known examples like *Ficus* plants and their associated fig wasps (Ramirez 1969) and *Yucca* plants and the *Yucca* moth (Powell 1992). There is, however, growing evidence that such close interactions are not the norm and that pollination studies which deal with them are somewhat biased in terms of representing the world's flora.

Indeed it is the generalist strategy that seems to predominate (Faegri 1978). Robertson (1928) conducted a vast pollination survey of the angiosperm flora in Carlinville, Illinois, USA. He found that 91% of all species surveyed had more than one animal species visiting it, and were thus, in some way, generalized. Waser et al (1996) summarised and presented information on European flora of the Ranunculaceae, Orchidaceae and Polemoniaceae. They showed that the proportions of flowers species in these families that were visited by more than one species of insect were 95%, 100% and 83% respectively (the median number of visitors per plant species was approximately five).

The generalist plant does not depend on one insect to secure pollination. Rather, a set of visitors to the flower contributes to the transfer of pollen. This set may include a variety of insect families and may be in excess of 50 species in 29 genera, in a Ranuculaceaen example in Waser et al (1996). A flower with a specific pollinator usually has characteristics that attract only that pollinator or ensure that only that insect can pollinate it effectively. The generalist on the other hand attracts a wide range of insects and is morphologically suited to this. Motten (1986) describes pollination ecology for a site in North Carolina that is dominated by generalist visitors. This situation of a generalist visitor must be distinguished from that of a generalist flower. A generalist flower attracts a wide range of visitors that are either highly host specific or are not host specific at all. A generalist visitor visits a wide range of flowers that are either specialized with respect to it or generalized. One does not require the other. In the case of Motten (1986) where generalist visitors dominate there is the implication that the flowers are generalists too.

Generalist flowers frequently have disc or cup shaped inflorescences and provide both nectar and pollen rewards. The disc is a form of inflorescence that a number of families have evolved convergently, such as the Asteraceae and Mesembryanthemaceae. In the Asteraceae it is a bisexual capitulum of florets making up one functional flower head, surrounded by an involucre of protective bracts (Heywood 1985). The central disc florets are bisexual and protandrous. They are short, tubular and regular florets that provide the nectar and pollen rewards. The irregular ray florets on the circumference of the disc form the petals that attract pollinators. These can be sterile or pistillate. In the case of the Mesembryanthemaceae disc the attractive 'petals' are made up of modified stamens. There are usually five central stigmas and numerous fertile stamens (Heywood 1985) Pollen and nectar are offered as rewards (Hammer et al 199x). Cups are found in numerous families around the world and are highly variable in size and construction, but share functionality. Cups and discs are well suited to a generalist strategy because they do not limit visitors the way a more specialized flower does. They function merely as a target or landing site for its set of pollinators.

For the Cape Flora few examples of generalist pollinator syndromes have been studied. Robertson (1980) found that *Erica viridipurpurae* and *E. parviflora* have cup shaped flowers and a wide range of visitors, mostly bees and flies. Two species of bee that visited both these flowers were identified as the most important pollinators and were evaluated in terms of their effectiveness as pollinators. *Apis mellifera* (Apidae) had a higher pollen load, but was considered a less important pollinator than *Allodapula acutigera* (Anthophoridae), which visited the flowers far more frequently. Also in the Cape Flora, Gess (1968), Mostert et al (1980) and Coetzee and Giliomee (1985) all describe the wide range of insect visitors, mostly beetles, of *Protea repens*.

Disc Asteraceae provide visual cues to attract pollinators and colour plays a very important role in determining what the set of pollinators will be. Picker and Midgely (1996) showed that the monkey beetles (Scarabaeidae, Rutelinae, tribe Hopliini) can be grouped into guilds that are attracted to particular colours irrespective of flower phylogeny. Bee-flies (Bombyliidae), which are very frequent visitors to Asteraceae, can possibly be grouped into similar kinds of guilds (M. Picker, personal comm.). Colours of the discs vary across the visual spectrum but do not include green, brown or black. Yellow is, however, the predominant colour of Asteraceae and is considered a generalist colour in pollination ecology (Valentine 1975).

Few detailed pollination studies have been done on Asteraceae. Johnson and Midgley's (1997) work on *Gorteria diffusa* is an example, but even this has focused on a more specialized member of the Asteraceae. *G. diffusa* has spots on some of its ray florets that mimic the Bombyliid flies that pollinate it in order to attract them. No other detailed studies on detailed studies on generalist Asteraceae appear to have been carried out.

Apart from colour determining the set of pollinators, another determinant of pollinator~~s~~ sets is geographical locality. Different possible pollinators may be present in different areas, resulting in turnover of pollinators for a particular species of flower. Some species of disc daisies from Namaqualand are very widespread, occurring from the most northern reaches to the West Coast to Cape Town in the South. The best example of this is *Dimorphotheca pluvialis*, the rain daisy, which is found even to the East towards Riversdale on the South Coast of South Africa (Manning and Goldblatt, 1996). It seems unlikely that this plant and others like it, rely on the same insects to pollinate it across this entire range. Geographical variation in pollinators in South Africa is poorly represented in the literature. Elsewhere in the world similar studies are also rare. Robertson and Wyatt (1990) mentioned this point in their report on geographical variation in the pollinators of an orchid in the South Eastern United States. Cruden (1976) also found that pollinators were different for subspecies of *Nemophila menziesii* in California.

This project asks the following questions:

1) Which insects visit these widespread species of Asteraceae and which of these are effective pollinators?
2) Are different sets of pollinators found on the same species in different regions?

3) If so, do widespread species rely on pollinators from the same families, or are their pollinators very different in different areas?
4) With respect to 1, 2 and 3: how do annual and perennial species compare? Annual species are weedy species that regenerate from seed each season and perennial species are those whose plants live throughout the year. The prediction is that annual species would have a wider range of generalist pollinators compared to those found on perennial species.

The generalist pollination strategy and the pollination biology of Asteraceae have been somewhat neglected by detailed pollination studies in South Africa and this project aims contribute to the knowledge in this field.

Methods

1. Study sites and species chosen.

The goal was to describe and compare pollination for at least three annual and three perennial Asteraceae species in three different regions. These regions were 1) the Niewoudtville plateau (31°22'30"S 19°06'30"E), 2) the Northern Cederberg, in the region of the Pakhuis Pass and Biedouw valley (32°04'00"S 19°04'00"E) and 3) the surrounds of the town of Darling in the South Western Cape (33°22'45"S 18°23'00"). These localities are marked on Figure 1. Unfortunately the stated goal could not be achieved because only four of the initial species chosen could be found in all the study sites.

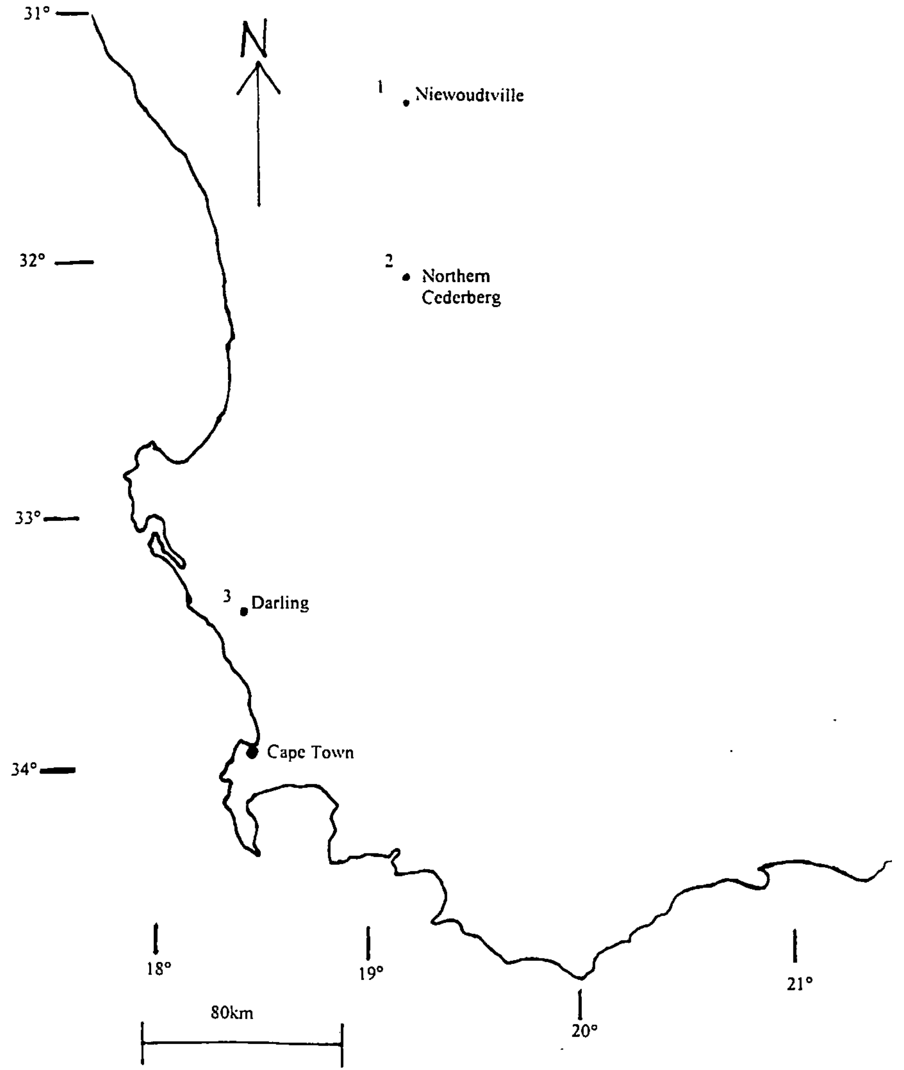

Figure 1: Map of the Western Cape, showing study regions

The four species of widespread Asteraceae chosen are listed below (Table 1). Before the sampling trips the distribution of the chosen species was confirmed by checking herbarium records of collection localities.

Table 1: List of study species

Species	**Annual/Perennial**
Dimorphotheca pluvialis (L.) Moench FP	A
Senecio arenarius Thunb. FP	A
Ursinia anthemoides (L.) Poir	A
Gazania krebsiana Less.	P

Trials for self pollination were not conducted with these species because the main emphasis was on visitors of generalist flowers. It has also been shown that pollination of autogamous species such as *Ursinia cakelifolia* often improves seed set (Smuts 1994). Thus, the importance of the visitors is not necessarily diminished if the species studied here are autogamous.

2. Pollinator sampling procedures

Sampling at Niewoudtville was conducted on the 15th and 16th August 1999. Sampling in the Cederberg was conducted between the 8th and 12th of September 1999 and sampling at Darling was conducted on the 29th of September 1999.

At each study site a patch of the target plant species was chosen and all insects found on the flowers within one hour were caught and placed in Eppendorf vials. Direct handling was avoided as this removes some or all of the pollen load. Insects were either caught directly with the vials or caught in a net and then guided into the vials. In the case of sites 1 and 2, after collection the vials were filled with 96% ethanol to preserve both the insect and the pollen before the pollen removal process. Collections from site 3 were brought back from the field and placed in xylene within 6 hours of collection, avoiding pollen damage. The former two sites were sampled on extended field trips and the pollen centrifuging was conducted days later. The collections from the latter site could be placed directly in xylene as the pollen centrifuging was conducted on the same day (see below for centrifuging method).

At each study site a pollen reference library was created. This involved collecting pollen from all the most common flowers in the general region of the study species. This pollen was processed and mounted on microscope slides in the same way as the pollen from the pollinators. This library was used for comparative identification of pollen found on insects caught.

3. Pollen analysis procedure

The procedure followed was essentially that described MacGillivray (1987), with some modification to allow for equipment and chemical availability. Pollen from site 3 that was placed directly into xylene was processed almost exactly as described by MacGillivray. This involved vibrating pollen off the insect into suspension using a vortex mixer. The insect was removed and pinned and dried for later identification. A small blob (30μl) of glycerol gelatin was then added to the centrifuge vial of xylene with pollen. The pollen was then centrifuged into the blob of gelatin. After the excess xylene was removed the gelatin was removed with a piece of fine, hooked wire to a preheated microscope slide. Once it had melted a coverslip was placed on top of it and the slide was allowed to set. The pollen, from sites 1 and 2, that was preserved in alcohol was treated slightly differently. This is because the alcohol interacts with the gelatin to a small extent, appearing to dissolve it slightly. After the insect was removed the pollen was centrifuged to the bottom of the vial and the excess alcohol carefully siphoned off. This left some alcohol in the tube, but not enough to affect the gelatin. Xylene was then added to this tube. The gelatin was added next and the procedure then followed the course described above for pollen from site 3.

The amount of pollen carried by each insect could now be counted and the pollen from surrounding plants catalogued into a reference library. This was done at 100x magnification with a subsampling method. The area of the field of view was calculated and in at least five such areas in a straight transect across the middle of the slide the number of pollen grains of each species was counted. The pollen count within the area sampled was then multiplied in proportion to the area of the coverslip, to give the absolute host pollen load of the insect as well as the pollen load of neighbouring species of flowers. The latter was used to calculate the relative host pollen load. Both absolute and relative host pollen loads are defined in the next section.

4. Data analysis

For each species of plant in each of the three regions a list of visitors was generated. For each species on this list the visitation frequency (V_f) was calculated. This is proportion of the total number of insects caught on the host that the species in question represents, expressed as a percentage. The relative host pollen load (H_P) was also calculated for each species. This is the average relative abundance of host pollen grains in the pollen load, expressed as a percentage. The absolute host pollen load (H_L), described above, was also averaged for each species, and was ranked as follows:

Rank	Absolute host pollen abundance
1	< 50 grains
2	50-499 grains
3	500-999 grains
4	100-4999 grains
5	5000-9999 grains
6	> 10000 grains

The effectiveness of each insect visitor as a pollinator was assessed with a Pollinator Efficiency Index (PEI) (Goldberg 1998) where:

$$PEI=V_f*H_P*H_L$$

When the absolute pollen count was too high to count effectively, it was given a rank of 6 and two fields of view were sampled to get the relative host pollen load.

The average number of flower species represented in each insect species' pollen load was also calculated.

For each species of flower in each region all of the above measures of pollinator efficiency were tabulated and are presented below. For the purposes of comparison between regions a table was constructed, showing the major pollinators of each species in each area, making use of the PEI to assess major pollinators.

Results

1. Pollination syndromes

The tables presented below (Tables 2-14) show visitation frequency, sample size of visitors, Absolute host pollen load, Relative host pollen load, PEI and the average number of pollen type per species of pollinator. The pollinators are presented in descending order of pollinator efficiency. Not all insects caught were used in the pollen analysis procedure. Those that were not were used to increase the sample number for calculating visitation frequency (n_1). Hence the occasional discrepancy between n_1 and n_2. Where there is no discrepancy, and where n_2 is not shown, the average number of pollen types was calculated from the number of insects of that species that were caught. n_2 is also not shown when n_1 is equal to one. All Scarabaeidae visitors are monkey beetles, of the tribe Hopliini.

1.1 *Gazania krebsiana*

Table 2: Measures of pollinator efficiency for *Gazania krebsiana*, Niewoudtville.

Species	Family	Visitation frequency (%)	n_1	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave no. pollen types (n_2)
Phalacridae sp1	Phalacridae	37.80	31	480.38 ± 492.76	94.2 ± 16.9	0.712	1.38 ± 0.65 (13)
Lepisia macgregorii	Scarabaeidae	20.73	17	1674.81 ± 1643.09	56.6 ± 35.2	0.469	2.44 ± 0.88 (9)
Melyridae sp1	Melyridae	17.07	14	340.84 ± 422.41	92.7 ± 10.1	0.316	1.60 ± 0.89 (5)
Lepithrix sp2	Scarabaeidae	4.88	4	9653.41 ± 9845.11	85.9 ± 18.6	0.210	1.75 ± 0.50 (4)
Bombyliidae sp9	Bombyliidae	7.32	6	1700.66 ± 3146.69	64.0 ± 30.5	0.187	3 (4)
Doliogethes sp1	Bombyliidae	1.22	1	3842.40	87.9	0.043	3
Dasytes sp1	Melyridae	1.22	1	1721.28	51.9	0.025	2
Parisus fucatus	Bombyliidae	1.22	1	697.05	52.1	0.019	2
Chrysomelidae sp1	Chrysomelidae	1.22	1	170.70	38.7	0.009	3
Bombyliidae sp4	Bombyliidae	2.43	2	136.56 ± 144.85	11.7 ± 13.5	0.005	2.50 ± 0.71 (2)
Anthicidae sp2	Anthicidae	4.88	4	0	0	0	0

Table 3: Measures of pollinator efficiency for *Gazania krebsiana*, Cederberg.

Species	Family	Visitation frequency (%)	n_1	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave no. pollen types (n_2)
Heterochelus detritus	Scarabaeidae	17.19	11	1493.79 ± 1944.30	59.3 ± 26.6	0.407	2.82 ± 0.60 (11)
Bombyliidae sp3	Bombyliidae	56.25	36	391.20 ± 390.86	23.2 ± 27.9	0.261	2.83 ± 0.94 (12)
Lepithrix sp1	Scarabaeidae	10.94	7	2523.53 ± 3349.20	32.0 ± 21.8	0.140	3 ± 0 (7)
Heterochelus sp1	Scarabaeidae	3.12	2	768.17 ± 168.99	72.3 ± 14.6	0.068	2.5 ± 0.71 (2)
Monochelus niewoudtvillensis	Scarabaeidae	6.25	4	725.49 ± 686.44	65.1 ± 14.5	0.060	2.75 ± 0.5 (4)
Heterochelus dissidens	Scarabaeidae	3.12	2	699.89 ± 844.95	88.8 ± 15.9	0.055	2 ± 1.41 (2)
Platychelus sp1	Scarabaeidae	1.56	1	751.11	13.8	0.006	3
Colletidae sp1	Colletidae	1.56	1	341.41	14.3	0.005	3

Table 4: Measures of pollinator efficiency for *Gazania krebsiana*, Darling.

Species	Family	Visitation frequency (%)	n_1	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave no. pollen types (n_2)
Heterochelus nudus	Scarabaeidae	62.5	20	2232.83 ± 1755.37	38.3 ± 19.1	0.958	4.85 ± 0.87 (20)
Lepisia rupicola	Scarabaeidae	12.5	4	2133.82 ± 700.10	29.2 ± 37.0	0.146	4.00 ± 1.41 (2)
Bombyliidae sp5	Bombyliidae	15.63	5	735.17 ± 789.38	21.8 ± 18.4	0.102	3.40 ± 0.55 (5)
Chrysomelidae sp1	Chrysomelidae	6.25	2	257.48 ± 263.54	62.0 ± 9.1	0.078	3.00 ± 0.00 (2)
Bombyliidae sp8	Bombyliidae	3.12	1	68.3	18.2	0.011	3

1.2 *Dimorphotheca pluvialis*

Table 5: Measures of pollinator efficiency for *Dimorphotheca pluvialis*, Niewoudtville.

Species	Family	Visitation frequency (%)	n_1	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave no. pollen types (n_2)
Bombyliidae sp8	Bombyliidae	44.26	27	5779.17 ± 4589.20	99.4 ± 1.5	2.200	1.27 ± 0.46 (22)
Dasytes sp1	Melyridae	24.59	15	949.41 ± 1395.81	99.5 ± 1.0	0.734	1.20 ± 0.42 (10)
Bombyliidae sp5	Bombyliidae	9.83	6	8711.69 ± 5729.84	98.0 ± 3.5	0.482	1.5 ± 0.84 (6)
Nitidulidae sp1	Nitidulidae	6.56	4	2594.73 ± 1477.96	99.8 ± 0.4	0.262	1.25 ± 0.50 (4)
Bombyliidae sp12	Bombyliidae	8.20	5	648.7	100	0.246	1
Parisus fucatus	Bombyliidae	3.28	2	699.89 ± 72.42	85.5 ± 12.4	0.084	2.50 ± 0.71 (2)
Bombyliidae sp9	Bombyliidae	1.64	1	5257.70	100	0.082	1
Miridae sp1	Miridae	1.64	1	34.1	100	0.016	1

Table 6: Pollinator efficiency for *Dimorphotheca pluvialis*, Cederberg.

Species	Family	Visitation frequency (%)	n_1	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave no. pollen types (n_2)
Pachycnema crassipes	Scarabaeidae	47.73	21	3192.74 ± 3412.51	88.5 ± 14.8	1.690	2 ± 0.84 (21)
Meloidae sp1	Meloidae	20.45	9	3448.26 ± 3510.90	98.9 ± 2.0	0.809	1.57 ± 0.79 (9)
Iselma sp1	Meloidae	13.64	6	522.07 ± 230.07	88.8 ± 11.0	0.363	1.67 ± 0.52 (6)
Bombyliidae sp8	Bombyliidae	9.09	4	2372.81 ± 976.26	98.8 ± 2.5	0.359	1.25 ± 0.5 (4)
Miridae sp1	Miridae	4.55	1	853.5	96.2	0.131	2
Bombyliidae sp2	Bombyliidae	4.55	2	3140.98 ± 2076.16	61.5 ± 54.4	0.112	1.5 ± 0.71 (2)
Bombyliidae sp10	Bombyliidae	2.27	1	28.5	66.7	0.015	2
Parisus fucatus	Bombyliidae	2.27	1	28.5	0.5	0.011	2

Table 7: Measures of pollinator efficiency for *Dimorphotheca pluvialis*, Darling.

Species	Family	Visitation frequency (%)	n_1	Abs. Host pollen load	Rel. host pollen load (%)	PEI	Ave no. pollen types (n_2)
Bombyliidae sp2	Bombyliidae	30.00	3	7804.71 ± 3802.36	89.5 ± 18.2	1.343	1.50 ± 0.71 (3)
Bombyliidae sp5	Bombyliidae	30.00	3	4949.35 ± 4374.53	80.6 ± 31.3	0.967	1.67 ± 0.57 (3)
Chrysomelidae sp3	Chrysomelidae	20.00	2	3533.61 ± 4466.17	99.5 ± 0.7	0.796	2.00 ± 1.41 (2)
Bombyliidae sp8	Bombyliidae	10.00	1	3994.52	76	0.304	2
Doliogethes sp1	Bombyliidae	10.00	1	42.7	100	0.1	1

1.3 *Ursinia anthemoides*

Table 8: Measures of pollinator efficiency for *Ursinia anthemoides*, Niewoudtville.

Species	Family	Visitation frequency (%)	n_1	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave no. pollen types (n_2)
Monochelus sp1	Scarabaeidae	40.38	21	2038.02 ± 1799.07	97.3 ± 4.2	1.572	1.63 ± 0.72 (16)
Dasytes sp1	Melyridae	28.85	15	334.52 ± 368.73	82.0 ± 28.8	0.473	1.43 ± 0.53 (7)
Scrapter sp1	Colletidae	11.54	6	2610.00 ± 2088.32	94.0 ± 6.8	0.434	1.83 ± 0.98 (6)
Bibionidae sp1	Bibionidae	7.69	4	3270.00 ± 3168.58	96.4 ± 7.3	0.297	1.25 ± 0.50 (4)
Colletidae sp2	Colletidae	7.69	4	2318.33 ± 2135.23	96.6 ± 6.0	0.297	1.50 ± 0.58 (4)
Colletidae sp3	Colletidae	1.92	1	8566.67	88.6	0.085	3
Iselma sp1	Meloidae	1.92	1	150	100	0.038	1

Table 9: Measures of pollinator efficiency for *Ursinia anthemoides*, Cederberg.

Species	Family	Visitation frequency (%)	n_1	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave no. pollen types (n_2)
Dermestidae sp1	Dermestidae	42.19	27	1763.58 ± 1746.71	69.5 ± 35.0	1.173	2.07 ± 0.62 (14)
Pachycnema crassipes	Scarabaeidae	9.38	6	5895.65 ± 4188.72	97.8 ± 2.3	0.458	1.67 ± 0.52 (6)
Heterochelus septumlineatus	Scarabaeidae	10.94	7	4043.31 ± 1654.93	98.2 ± 2.8	0.430	1.71 ± 0.76 (7)
Miridae sp1	Miridae	3.13	2	644.42 ± 488.87	92.7 ± 10.4	0.087	2 ± 1.41 (2)
Acmeodera sp1	Buprestidae	1.56	1	227.60	100	0.031	1
Bombyliidae sp2	Bombyliidae	1.56	1	327.2	95.8	0.030	2
Phalacridae sp1	Phalacridae	3.13	2	334.30 ± 472.77	48.0 ± 67.8	0.030	1 ± 1.41 (2)
Dasytes sp1	Melyridae	4.69	3	87.12 ± 75.50	46.2 ± 50.4	0.022	1.67 ± 0.57 (3)
Acmeodera sp2	Buprestidae	1.56	1	0.00	0.0	0	1

Table 10: Meaures of pollinator efficiency for *Ursinia anthemoides*, Darling.

Species	Family	Visitation frequency (%)	n_1	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave no. pollen types (n_2)
Heterochelus sp2	Scarabaeidae	41.67	20	10409.78 ± 6096.24	100.0 ± 0.0	2.5	1.30 ± 0.57 (20)
Heterochelus nudus	Scarabaeidae	10.42	5	14960.66 ± 5254.16	95.0 ± 11.0	0.594	2.20 ± 0.84 (5)
Bombyliidae sp6	Bombyliidae	10.42	5	1686.57 ± 1535.52	99.8 ± 0.5	0.416	1.17 ± 0.41 (5)
Chrysomelidae sp1	Chrysomelidae	6.25	3	6134.03 ± 8187.50	100.0 ± 0.0	0.313	1.00 ± 0.00 (3)
Lagriidae sp1	Lagriidae	6.25	3	7396.13 ± 5207.93	100.0 ± 0.0	0.313	1.00 ± 0.00 (3)
Bombyliidae sp2	Bombyliidae	4.17	2	> 10 000	98.8 ± 1.7	0.247	2.00 ± 1.41 (2)
Rhigioglossa edentula	Tabanidae	4.17	2	23915.88 ± 7025.16	93.0 ± 0.3	0.233	2.50 ± 0.71 (2)
Iselma sp1	Meloidae	4.17	2	2577.66 ± 1520.91	100.0 ± 0.0	0.167	1.00 ± 0.00 (2)
Chrysomelidae sp2	Chrysomelidae	4.17	2	1524.97 ± 1995.69	94.8 ± 7.4	0.158	1.50 ± 0.71 (2)
Philoliche atricornis	Tabanidae	2.08	1	5121.17	99.3	0.103	2
Sciomyzidae sp1	Sciomyzidae	2.08	1	580.40	94.4	0.059	2
Lepithrix modesta	Scarabaeidae	2.08	1	10925.17	98.5	0.038	3
Pachycnema crassipes	Scarabaeidae	2.08	1	398.31	73.7	0.031	2

1.4 *Senecio arenarius*

Table 11: Meaures of pollinator efficiency for *Senecio arenarius*, Niewoudtville.

Species	Family	Visitation frequency (%)	n_1	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave no. pollen types (n_2)
Dasytes sp1	Melyridae	56.09	23	727.36 ± 966.56	71.0 ± 31.9	1.195	2.22 ± 1.00 (23)
Monochelus sp1	Scarabaeidae	12.20	5	705.58 ± 491.59	96.1 ± 3.6	0.352	2.40 ± 1.52 (5)
Dermestidae sp2	Dermestidae	7.32	3	3797.26 ± 4192.70	83.8 ± 28.1	0.245	1.33 ± 0.58 (3)
Lepithrix sp2	Scarabaeidae	7.32	3	642.99 ± 744.11	54.7 ± 38.5	0.120	3.00 ± 1.73 (3)
Anthicidae sp1	Anthicidae	4.88	2	142.25 ± 120.71	100.0 ± 0.0	0.098	1 (2)
Apis mellifera	Apidae	2.44	1	1223.39	85.1	0.083	2
Platychelus sp1	Scarabaeidae	2.44	1	298.74	100	0.049	1
Austroloechus sp1	Bombyliidae	2.44	1	455.22	91.4	0.045	2
Unknown sp1	Unkown	4.88	2	92.45 ± 130.74	46.5 ± 65.7	0.045	1.00 ± 1.41 (2)

Table 12: Measures of pollinator efficiency for *Senecio arenarius*, Cederberg.

Species	Family	Visitation frequency (%)	n_1	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave no. pollen types (n_2)
Tetraloniella sp1	Anthophoridae	18.75	3	7408.95 ± 1862.57	87.0 ± 12.4	0.816	2.67 ± 0.57 (3)
Calliphoridae sp1	Calliphoridae	12.50	2	337.15 ± 54.32	79.0 ± 29.8	0.198	2 ± 1.41 (2)
Austroloechus hypoleuchus	Bombyliidae	68.75	11	257.20 ± 179.02	13.2 ± 29.0	0.182	2.18 ± 0.60 (11)

Table 13: Measures of pollinator efficiency for *Senecio arenarius*, Darling.

Species	Family	Visitation frequency (%)	n_1	Abs. Host pollen load	Rel. host pollen load (%)	PEI	Ave no. pollen types (n_2)
Calliphoridae sp1	Calliphoridae	25.00	1	>10000	100	1.5	2
Unknown sp2	Unknown	25.00	1	4643.19	96.5	0.965	2
Apis mellifera	Apidae	25.00	1	1028.21	70.9	0.709	3
Heterochelus nudus	Scarabaeidae	25.00	1	4745.62	65.6	0.656	4

These tables are summarised below. For the purpose of the summary of pollinator information those pollinators that have visitation frequency less than 5% and also those that are only represented by one insect have been excluded. This is because these are unlikely to be effective pollinators as visitation is likely to be a chance occurrence or because pollen will have fallen of the insect by the time of the next visit (Goldberg

1998). Also, the sample size is not large enough to calculate the PEI confidently. The summary also serves as the regional comparison of pollinators for each species of flower (see Table 14 at the end of the section).

Gazania krebsiana flowers were pollinated by monkey beetles and Bombyliids across the entire range sampled, with the former always more efficient (i.e. they had a higher PEI). The species of Bombyliidae visiting *G. krebsiana* displayed complete turnover between all three sites. The species of monkey beetles did so too, but a number of genera did not turnover: *Heterochelus, Lepisia* and *Lepithrix*, although none of these were found in all the regions. *G. krebsiana* was only pollinated by insects outside of these two families in Niewoudtville, and thus had very little turnover at the family level. *Phalacridae* and *Melyridae* played important roles in the pollination of *G. krebsiana* in Niewoudtville, having PEIs of 0.712 and 0.316 respectively. *Chrysomelidae* visited the flowers in Darling but did not appear to be efficient pollinators (PEI=0.078)

Dimorphotheca pluvialis displayed more variation in pollination families, being pollinated by six different ones. The Bombyliidae were efficient pollinators in all three regions while the other five families displayed complete turnover. *Bombylidae sp8* was found in all three regions, *Bombylidae sp2* was found at both Darling and in the Cederberg, Bombylidae sp5 was found at Niewoudtville and Darling and *Parisus fucatus* was found at Niewoudtville and in the Cederberg. *Doliogethes sp1*was found only at Darling. Melyrid (*Dasytes* sp) and Nitidulid beetles were caught on the flowers in Niewoudtville with PEIs of 0.734 and 0.262 respectively. Two species of Meloid beetles *Iselma sp1* and Meloidae sp1 were caught only in the Cederberg and had PEIs of 0.363 and 0.809 respectively. One species of Chrysomelid was caught in Darling with a PEI of 0.796.

Ursinia anthemoides also had high variation in its families of pollinators: monkey beetles pollinated it efficiently across the entire range, with the other seven families displaying 100% turnover. Bombyliids were only found to be effective pollinators at Darling. Of the monkey beetles found on this flower the only species present in more than one region was *Pachycnema crassipes*, in the Cederberg and at Darling. *Heterochelus* was also present in these two regions, but had different species at each site. In Niewoudtville two species of Colletid bee were caught, Colletidae sp2 and *Scrapter sp1*, with PEIs of 0.297 and 0.434 respectively. Melyrid beetles, *Dasytes sp1*, were caught here too, with a PEI of 0.473. Bibionid flies were found to have a PEI of 0.297 in Niewoudtville. In the Cederberg *Dermestidae sp1*was the most efficient pollinator (PEI =1.173). *Chrysomelidae sp1*and *Lagriidae sp1*, both with PEI = 0.313 were found only in Darling.

Senecio arenarius had no pollinators in common between Niewoudtville and the Cederberg, although they did share *Austroloechus* of Bombyliidae. The representative of this genus in Niewoudtville, however, was caught only once. *Dasytes sp1*was the most efficient pollinator in Niewoudtville (PEI = 1.195) followed by *Dermestidae sp2* with PEI = 0.245. Two species of monkey beetle were caught here: *Lepithrix sp2* and *Monochelus sp1* with PEIs of 0.120 and 0.352 respectively. In the Cederberg the most common pollinator was *Austroloechus hypoleuchus* with a PEI of 0.182. *Tetraloniella sp1* (Anthophoridae) was the most important pollinator with a PEI of 0.816, followed by *Calliphoridae sp1*. with a PEI of 0.198. Only four insects were caught at Darling on this species because of inclement weather (see Tables 13 and 14).

Table 14: Pollinator presence/absence and PEI for each study species in each region showing only those pollinators with V_f >5% and n_1 >1

Scarab = Scarabaeidae; Niewoudt. = Niewoudtville; The PEI of the most important pollinator at each site is highlighted in **bold**

	Gazania krebsiana			*Dimorphotheca pluvialis*			*Ursinia anthemoides*			*Senecio arenarius*		
Pollinator	Niewoudt.	Cederberg	Darling	Niewoudt.	Cederberg	Darling	Niewoudt.	Cederberg	Darling	Niewoudt.	Cederberg	Darling
Anthophoridae; *Tetraloniella sp1*											**0.816**	
Bombyliidae; *Austroloechus hypoleu②chus*											0.182	
Bombyliidae sp2						**1.343**						
Bombyliidae sp3		0.261										
Bombyliidae sp5			0.102	0.482		0.967						
Bombyliidae sp6									0.416			
Bombyliidae sp8				**2.200**	0.359							
Bombyliidae sp9	0.187											
Bombyliidae sp12				0.246								
Bibionidae sp1							0.297					
Chrysomelidae sp1			0.078						0.313			
Chrysomelidae sp3						0.796						
Calliphoridae sp1											0.198	
Colletidae sp2							0.297					
Colletidae; *Scrapter sp1*							0.434					
Dermestidae sp1								**1.173**				
Dermestidae sp2										0.245		
Lagriidae sp1									0.313			
Meloidae sp1					0.809							
Meloidae; *Islema sp1*					0.363							
Melyridae sp1	0.316											
Melyridae; *Dasytes sp1*				0.734			**0.473**			**1.195**		
Nitidulidae sp1				0.262								
Phalacridae sp1	**0.712**											
Scarab; *Heterochelus sp2*									**2.500**			
Scarab; *Heterochelus detritus*		**0.407**										
Scarab; *Heterochelus nudus*			**0.958**						0.594			
Scarab; *H. septumlineatus*								0.430				
Scarab; *Lepisia macgregorii*	0.469											
Scarab; *Lepisia rupicola*			0.146									
Scarab; *Lepithrix sp1*		0.140										
Scarab; *Lepithrix sp2*										0.120		
Scarab; *Monochelus sp1*										0.352		
Scarab; *Monochelus niewoudtvillensis*		0.060										
Scarab; *Pachycnema crassipes*					**1.690**			0.458				

Discussion

Pollination syndromes and regional comparisons

The pollination syndromes of all four plant species studied have been described and compared between three geographical regions, with the exception of *S. arenarius* in the region of Darling. It is clear that there is a great deal of variation in the pollinator sets at the species level. There is a tendency for each plant species to have one or two families of major pollinators, with monkey beetles and bee flies being the most frequently occurring. This is logical, as theoretically a particular shape and colour of flower is likely to attract a particular guild of insects. Thus, across the geographical range this guild of insects would be expected to remain constant if flower morphology stays constant. Species within the guild may change; both of these predictions are met by the results of this project. Indeed, plant species populations in the three study regions share very few species of pollinator.

It is interesting to note that Robertson and Wyatt (1990) state that certain criteria must be met to support the hypothesis that pollinators vary across a geographical range: 1) both plant and pollinators must have evolved under the conditions where they are studied, 2) the main pollinators must differ across this range, and 3) it is necessary to demonstrate a genetically based variation in plant morphology across this range. The second criterion is met in this study and the first is assumed to have been met as plants were studied in their natural ranges. The third criterion is the most interesting as it appears to be irrelevant to this study. We have clearly shown a geographical variation in pollinators of four species of Asteraceae with probably no variation in plant, specifically flower, morphology. The species studied here are superficially very similar across their ranges. However, differences in ultraviolet reflectivity that could have an impact on visitation by insects (Proctor et al 1996) were not tested for the plant species in this study.

Nearly all the species in all the regions had bombyliid visitors. The only exceptions to this were *U. anthemoides* in Niewoudtville and S. arenarius in Darling. However, there was insufficient data from the site of the latter, so its pollination syndrome is not truly known. Monkey beetles were also found frequently on most of the species, and were often the most efficient pollinators. Both of these groups of insects are highy speciose, emphasising their importance as pollinators. In Southern Africa the Bombyliidae have 939 described species (Hesse 1938) and the monkey beetles have in excess of 700 described species (Peringuey 1902, Dalla Torre 1913, Kulzer 1960) and are under revision.

Bees played a very small role as pollinators among the plant species and the geographical range. Honey bees, *Apis mellifera*, were very infrequent visitors while other families such as Colletidae and Anthophoridae were only significant pollinators at Niewoudtville on *U. anthemoides* and in the Cederberg on *S. arenarius* respectively. There were a number of unexpected beetle families that appear to be very efficient pollinators. Melyrid and meloid beetles were fairly common across the range and often were one of the top three most efficient pollinators on a species, having high PEI values. Phalacrid beetles were found to be the most efficient pollinator on *G. krebsiana* at Niewoudtville and were not found anywhere else. Chrysomelid beetles served as pollinators only in Darling, on *D. pluvialis* and *U. anthemoides*. This family is known to be phytophagous (Scholtz and Holme 1996) so these visitors were probably eating petals, and not carrying out much pollination. Calliphorid flies were also found to be efficient pollinators on *S. arenarius* alone, in the Cederberg. (See Table 14 for the regional comparison of pollination guilds)

Dermestid beetles were found on two occasions to be important pollinators: in the Cederberg on *U. anthemoides* and at Niewoudtwille on *S. arenarius*. The importance of this family as pollinators is unknown. It apparently has numerous species, making it a potentially important group of pollinators, but only a fraction of their entire fauna is described (ca 30 species) for Southern Africa. Also little is known about their diet and presence on flowers. (Scholtz and Holm 1996). Other families that are potentially good pollinators are the Phalacridae (found on *G. krebsiana* in Niewoudtville) and the Meloidae which are found in all of the regions on most of the study species. The Phalacridae are poorly known in South Africa, with only 32 described species. They are known to congregate in flowers (Scholtz and Holm 1996). The Meloidae, which have 346 described species in Southern Africa are better known and often are found on flowers, being phytophagous.

The method used to describe the pollinator sets here assumes that all insects caught are representative of the entire pollinator set. Seasonal variation of pollinator sets is not taken into account. There could conceivably be very important pollinators that have been missed because they emerged earlier or later than the time of the study. To obtain this information the plants' visitors would have to be sampled on a weekly basis throughout the flowering season. However, this is probably not relevant here as the flowering season was very short and it is unlikely that there was a significant sequential emergence of pollinators.

Annuals and Perennials

Annuals are seasonal plants that are highly dependent on rainfall coming at the right time of year. Because of this dependence on rainfall their flowering seasons tend to change year to year. Insect emergence time also varies from year to year. The generalist strategy of annuals is therefore highly suited to their life histories. They emerge, flower and are opportunistic in terms of what pollinates them. Some species employ facultative autogamy to escape the problem of a poor insect year. Perennials, on the other hand, are more consistent in their floral displays. The timing thereof is also dependent on rainfall, but the plants are to a lesser degree as they survive from season to season. For this reason it was hypothesised that perennials would be have more consistent pollinator sets across geographical ranges.

There is a suggestion of this in the results of this study. The three annual species all had greater turnover of both species and families of pollinators than *Gazania krebsiana*. With sample sizes this low, however it can only be suggested that the pollination biology of more species of both annual and perennial Asteraceae be studied in detail.

Conservation implications

Simply put, to conserve species such as the Asteraceae flowers studied here habitats of both flowers and insects will have to be conserved. The flowers are highly vulnerable to plowing and grazing. Areas under the effects of these have lost numerous species of flowers (Smuts 1994) and quite probably insects. It is suggested, in the least case, that in order to conserve some of the range of plant-insect relationships, small reserves like the Waylands farm in Darling should be established at regular intervals across the entire range of the Western Cape. The insects that pollinate the flowers have to be identified as well as the plant species and soil types they depend on for reproduction. Insects are thus also vulnerable to plowing and trampling by livestock. It may be that the pollinators and flowers they pollinate have ranges that overlap during flowering season, but they may depend on different criteria for successful reproduction. Rebelo (1987) summarises the situation well when he writes:

"The effect of flower removal from natural plant populations on pollinator population, the resulting changes in pollinator dynamics, and its effect on seed set and seed quality in the remaining inflorescences are not known."

The results of this study indicate the importance of a few predictable groups of insects as pollinators of Asteraceae in the Western Cape: bombyliid flies and monkey beetles are by far the dominant pollinators. An unusual pollination syndrome is indicated for a wide variety of species in the arid parts of South Africa.

Acknowledgements

I thank Mike Picker for supervising this project and reassuring me when things seemed impossible. Special thanks go to Henry Jacobs and Joseph Booysen for providing so rapidly the materials neccesary for the pollen analysis. John Duckitt deserves special mention for allowing me to work on his farm Waylands in Darling. My parents deserve thanks too for providing transport unselfishly when plans had to change rapidly. Finally, I thank Vickie Maguire for her help, support and patience during the course of this project.

References

Coetzee JH and Giliomee JH 1987 Insects in association with the inflourescence of *Protea repens* (L.)(Proteaceae) and their role in pollination.

Cruden RW 1976 Pollination biology of *Nemophila menziesii* with comments on the evolution of oligolectic bees. *Evolution* **26** pp 373-389

Dalla Torre KW VON 1913 Coleoptororum Catalogus *Pars* **50** pp339-385

Faegri K 1978 Research in pollination ecology. In: The pollination of flowers by insects AJ Richards (ed.) *Academic Press*

Goldberg K 1998 Neglected pollinator syndromes in seasonally inundated Renosterveld *Unpublished Botany Honours Project* UCT

Hammer S, van Jaarsveld E, Chesselet P, Smith G, Hartmann H, van Wyk B, Klak C, Kurzweil H 1998 Mesembs of the world *Briza Publications*

Hesse AJ 1938 A revision of the Bombyliidae Part 1 *Annals of the South African Museum* **34**

Heywood VH 1985 Flowering plants of the world *Croom Helm*

Johnson 1992 Plant animal relationships. In: The ecology of Fynbos Richard Cowling (ed.) *Oxford University Press*

Johnson SD 1994 Pollination and the evolution of floral traits: selected studies in the Cape flora *Phd Botany Thesis* UCT

Johnson SD, Midgley JJ 1997 Fly pollination of *Gorteria diffusa* (Asteraceae), and a possible mimetic function for dark spots on the capitulum *American Journal of Botany* **84(4)** pp 429-436

Kulzer H 1960 Revision der Dichelus Untergattungen, Heterochelus Burm. Und Ischnochelus Burm. *Entomologische Arbeiten des Musuems G.Frey* **11(2)** pp 433-580

MacGillivray 1987 A centrifuging method for removal of insect pollen loads *Journal of the entomological society of South Africa* **50(2)** pp522-523

Manning and Goldblatt 1996 West Coast - South African Wildflower Guide 7 *Botanical Society of South Africa*

Picker, M.D. and Midgley, J.J. 1996. Pollination by monkey beetles (Coleoptera: Scarabaeidae: Hopliini): flower and colour preferences. *African Entomology* 4(1) pp7 – 14.

Peringuey L 1902 Descriptive catalogue of the Coleoptera of South Africa (Lucanidae and Scarabaeidae) *Transactions of the South African Philosophical Society* **12** pp1-920

Powell JA 1992 Interelationships of yuccas and yucca moths *Trends in Ecology and Evolution* **7** pp10-15

Proctor M, Yeo P,Lack A 1996 The natural history of pollination *HarperCollins Publishers*

Ramirez BW 1969 Fig wasps: mechanism of pollen transfer *Science* **163** pp 580-581

Rebelo AG 1987 Management implications In: A preliminary synthesis of pollination biology in the Cape Flora AG Rebelo (ed.)*South African National Scientific Programmes Report* **141**

Robertson C 1928 Flowers and Insects. Lists of visitors of four hundred and fifty three flowers. *Charles Robertson, Carlinville, Illinois, USA*

Robertson HG 1980 Pollination of selected *Erica* species in the Cape Fynbos. *Unpublished Zoology Honours Project* UCT

Robertson JL, Wyatt R 1990 Evidence for pollination ecotypes in the yellow fringed orchid, *Plantanthera ciliaris Evolution* **44(1)** pp 121-133

Scholtz CH, Holm E 1996 Insects of Southern Africa *University of Pretoria*

Smuts R 1994 Is local plant extinction a product of mutualism breakdown? *Unpublished Botany Honours Project* UCT

Valentine DH 1975 The taxonomic treatment of polymorphic variation *Watsonia* **10** pp 385-390

long ? Vogel S 1984 The *Diascia* flower and its bee – and oil-based symbiosis in Southern Africa *Acta Botanica Neerlandica* **33** pp509-518

Whitehead VB, Giliomee JH, Rebelo AG 1987 Insect pollination in the Cape Flora. In: A preliminary synthesis of pollination biology in the Cape Flora AG Rebelo (ed.) *South African National Scientific Programmes Report* **141**

Whitehead VB, Schelpe EACLE, Anthony NC 1984 The bee *Redivia longimanus* (Apoidea: Mellitidae) collecting pollen and oil from *Diascia longicornis* (Thunb.) Pruce (Scrophulariaceae). *South African Journal of Science* **80** p 286