Neglected pollinator syndromes in seasonally inundated Renosterveld.

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Supervisors:
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Submitted in partial fulfilment of the degree of B.Sc (Hons.) to the
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ABSTRACT

A range of fairly common plants were investigated in Darling in the Western Cape, to determine their pollinator syndromes, and to evaluate the relative importance of monkey beetles (Scarabaeidae: Rutelinae: Hopliini) and relatively short-tongued horseflies (Tabanidae) in their pollination. Detailed observations showed that all the plants investigated are visited by more than one insect species. Visitation rates and pollen loads of all insects found on the plants were used to assess their pollination efficiency. For all plants investigated, only a subset of the visitor-suite was found to contribute to the plant's reproductive success. *Geissorhiza radians* (Thunb.) Goldblatt and *Wachendorfia paniculata* L. seem to have specialized pollinator systems, both relying on tabanids for their pollination, while *Heliophila coronipifolia*, L. *Monsonia speciosa*, L.f. *Ornothogalum thyrsoides*, Jacq. *Romulea hirsuta* (Klatt) Baker and *Ursinia anthemoides* (L.) Poir. appear to have more generalized pollinator syndromes. Monkey beetles were the predominant and generally the most efficient pollinators for all these species. It is therefore concluded that these two insect groups are important pollinators of the plants investigated and probably play a part in the pollination of several other plants in the community.

An evaluation of the larval requirements of pollinators revealed that although some species show clear patterns in terms of what types of soil conditions they prefer, successful emergence of insect species is generally not limited by a shortage of suitable habitats. Environmental variability may therefore play the largest role in determining the emergence and abundance of pollinators. This has implications for plants reliant on insects for their pollination, especially for species with specialized pollinator syndromes. Fluctuations in the environment may be a partial explanation for the prevalence of the generalized pollination syndromes observed.

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INTRODUCTION

Southern Africa is endowed with an extremely rich flora, possessing more than 20 000 plant species (Arnold and de Wet, 1993), of which about 80% are endemic (Goldblatt, 1978). The flora of the western Cape, in particular is generally viewed as the "hot-spot" of plant diversity. Although covering less than 4% of the land surface of southern Africa, the Cape Floristic Region (*sensu* Goldblatt, 1978) boasts more than 8500 species, with more than 73% endemic to the region (Goldblatt, 1978).

While more than 80% of the plants in the western Cape are insect pollinated (Steiner, 1987), relatively few detailed pollination studies have been carried out. The work that has been done has mostly focused on the tight partnerships between highly specialized members of the Iridaceae and Orchidaceae and their pollinators, the long-tongued flies (Goldblatt *et al* 1995; Goldblatt and Manning, 1996; Manning and Goldblatt, 1997). However, numerous observations and studies have shown that plants are seldom visited and pollinated by only one insect species, and that an insect species is seldom restricted to one flower (Baker and Hurd, 1968; Waser, 1998). More often plants are visited by several insect species, many of which carry pollen, and most insects visit a variety of flowers (Herrera, 1996; Waser *et al.* 1996). Thus, globally, generalist pollination systems appear to prevail.

Although highly specialized flower mutualisms are evidenced in the western Cape, the Cape Flora has a large proportion of species which exhibit relatively unspecialized floral morphology. This is highlighted by the fact the Asteraceae and the Aizoaceae, the two largest families of flowering plants in the region (Goldblatt, 1978), are generally characterized by open dish- or bowl-shaped flowers. Furthermore, while the majority of plants in this region are insect pollinated (Steiner, 1987; Whitehead *et al*, 1987), there is evidence to suggest that these ecosystems may be pollinator limited (Marloth 1908;

Johnson and Bond, 1997). This being the case, generalist pollinators may be extremely important for the reproductive success of many flowering plants.

Since very little is known about the generalist pollination syndromes which seem to be a dominant feature in most ecosystems, the primary objective of this study was to investigate various aspects of such systems in a region of the southwestern Cape. This was achieved by selecting a range of fairly common insect-pollinated plants on a seasonally inundated Renosterveld fragment, near Darling, and addressing the following questions:

- Are the flowers investigated visited by a wide range of insects or do close plant-pollinator interactions predominate?
- Do all visitors contribute equally to the pollination of these plant species?
- How generalist are the insect visitors in terms of their floral foraging behaviour?

In particular, the relative importance of two common insect groups in pollinating these flowers was assessed. The first of these are the monkey beetles (Scarabaeidae: Rutelinae: Hopliini), a diverse insect tribe largely endemic to southern Africa (Steiner, 1996) and very common in the Western Cape (Scholtz and Holm, 1996). South Africa arguably boasts the highest diversity of flower-visiting beetles in the world (Steiner, 1996), and this, together with the fact that very few studies have evaluated this tribe's pollinator potential, makes this common and abundant group an ideal candidate for further investigation. Their ephemeral emergence generally coincides with the spring-flowering period in Namaqualand and the southwestern Cape (Picker and Midgley, 1996), and recent studies have shown that they visit predominantly open bowl-shaped flowers of the Asteraceae, Aizoaceae, Hyacinthaceae and Iridaceae (Struck, 1994; Picker and Midgley, 1996). These insects thus appear to represent the typical "generalist pollinator", possessing neither specialized morphology nor forming exclusive interactions with a single flower species.

Relatively short-tongued horseflies (Tabanidae) were the second group of insects investigated. Seventeen genera and 227 species have been recorded in South Africa (Usher, 1972), but only a few of the longer-tongued species have been evaluated for their role in pollination (Goldblatt *et al* 1995; Goldblatt and Manning 1996). More than 40 species are found in the western Cape (Usher, 1972), many of which do not display specialized elongated mouthparts. Several species such as *Rhagioglossa edentula* (Wiedemann) are found in great abundance in the Darling area, and are often coated in pollen (Usher, 1972, M. Picker, pers. comm.).

This study thus partly serves as a preliminary documentation of the role of these two groups of insects in pollination, about which almost nothing is known.

Finally, no investigations have attempted to determine the larval habitat preferences of insect pollinators in the southwestern Cape. In an agricultural landscape which is under constant threat of further fragmentation and habitat destruction, and is exposed to a high degree of habitat disturbance in the form of grazing and ploughing, such an understanding is imperative for the effective management of plant resources. In addition, the area of Darling is a popular tourist attraction in the western Cape, due to its seasonal displays of (Heydenrych and Littlewort 1995). Maintaining the integrity of plant-pollinator relations would therefore serve both the ecology and the ecotourism industry in the area. Thus the second aim of this project was to undertake a preliminary investigation of the larval habitat requirements of pollinators found in the study area.

STUDY AREA

The study was conducted near Darling (33°05'S; 18°23'E), in the Western Cape Province, South Africa (Figure 1), from July to September 1998. The topography of the area consists mainly of gentle undulating hills and valleys occasionally intercepted by granite outcrops. Being relatively close to the coast, elevations seldom exceed 460 m above sea level. The region is subject to a meditteranean climate, with hot dry summers and mild wet winters, receiving an average of 500mm per year.

The indigenous vegetation is classified as Renosterveld, which is affiliated to fynbos but is characterised by the presence of "Renosterbos" (*Elytropappus rhinocerotis*) and numerous members of the Asteraceae, Iridaceae Liliaceae and Oxalidaceae (Mc Dowell and Moll, 1992). Renosterveld is mainly restricted to granite and shale-derived soils (Boucher and Moll, 1980), which are highly valuable to agriculture. Therefore most of the area is presently under cultivation, and only isolated pockets of indigenous vegetation can be found on the steeper hills and on some of the farms.

The study was undertaken on a seasonally inundated Renosterveld fragment on "Waylands" a farm situated 3km outside the town of Darling. It possesses a large area which has never been ploughed and is only occasionally used for grazing livestock. This fragment is thus fairly representative of indigenous Renosterveld and is one of the private "reserves" that displays a large array of wildflowers during spring.

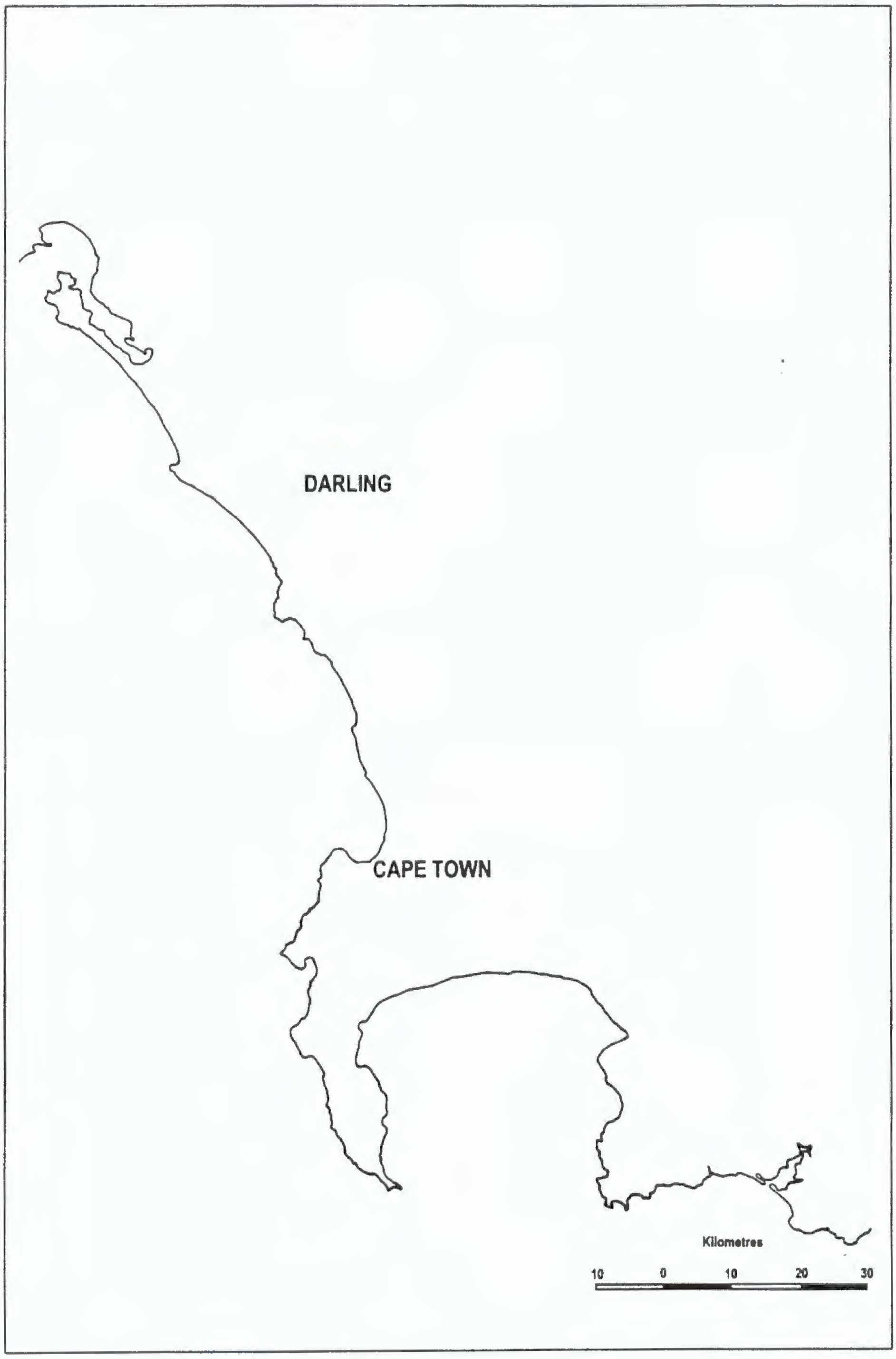

Figure 1: Map showing the position of Darling in the Western Cape Province, South Africa.

METHODS

1. Pollinator guilds

1.1 Selection of study plants

To determine which plant species to investigate, preliminary observations ? were made of flower were visitation by tabanids and/or monkey beetles. A total of nine fairly common plant species were identified, of which seven species from six different families were eventually chosen for closer investigation. These were identified in the Bolus Herbarium (Table 1).

Table 1: Flowering plants investigated for their pollinator syndromes.

Plant species	Family	Distribution	Floral morphology
Geissorhiza radians (Thunb.) Goldblatt	IRIDACEAE	Darling - Gordons Bay	• cup-shaped • red and purple
Heliophila coronopifolia L	BRASSICACEAE	Vanrhynsdorp - Caledon	• open • blue
Monsonia speciosa L.f.	GERANIACEAE	Clanwilliam - Caledon	• dish-shaped • pink with orange pollen
Ornothogalum thyrsoides Jacq	COLCHICACEAE	widespread throughout CFR	• cup-shaped • white with dark stamens
Romulea hisuta (Klatt) Baker	IRIDACEAE	Clanwilliam - Elim	• open, shallowly tubular • pink
Ursinia anthemoides (L.) Poir.	ASTERACEAE);	Namaqualand - PE	• dish-shaped • yellow ray florets, dark centre
Wachendorfia paniculata L.	HAEMODORACEAE	Clanwilliam - PE	• tubular, enantiostylous • pink

1.2 Pollinator observations

In order to identify the suite of insects that visited each species of flower, all insects found on the flowers were caught and subsequently identified as far as possible. A relative measure of visitation frequency by each insect species was then obtained, by observing and noting the first 30 individuals found on each plant species. A further 15 insects, belonging to the same species previously idebtifies, were then randomly caught, and their pollen loads analysed.

The approximate time each species spent on the flowers was estimated, and, where possible, its activities were recorded.

The tabanid, *Rhagioglossa edentula*. which is usually very abundant in spring (M. Picker, pers. comm.), was noted on several plant species but was not seen during any of the detailed observations on the select flower species. Since some individuals were carrying a significant pollen load, 10 individuals were caught for pollen analysis.

1.3 Procedure for pollen removal and analysis

Pollen was removed from the insects using a centrifuge method, as described by MacGillivray (1987). The technique entails shaking pollen off the insect into xylene, agitating it using a vortex mixer, and then centrifuging the suspended pollen into the glycerol gel at the bottom of eppendorf vials. The pollen was thus forced into the gel, which was then removed and melted onto a microscope slide for subsequent pollen analysis.

The pollen load from each insect was visually assessed for different types of pollen morphs, using a light transmission microscope, a 25 or 63 X magnification for counting pollen grains and a 160 X magnification for pollen identification. Where the pollen load was very small, absolute pollen abundance was obtained by counting individual grains. In the case of large pollen loads, pollen abundance was roughly estimated by scanning the entire area under the coverslip. Since some pollen would have been lost during the pollen removal procedure, and as only relative pollen loads were important for the study, precise counts were not carried out. Total pollen load was assessed in a similar manner.

A pollen library of all plants under investigation was created by collecting pollen directly from the flower, placing it in a xylene suspension and centrifuging it into glycerol gel. In so doing, any potential distortion of pollen by xylene would have been the same for the pollen library and the pollinator pollen load. The pollen library allowed for easy identification and assessment of the relative abundance of "host" pollen found on each insect. Relative abundances of the other pollen morphs were also determined.

1.4 Data analysis

For each plant under investigation, a comprehensive species list of all insect visitors was compiled. Visitation frequency of each insect species was further evaluated, by calculating the abundance of each insect species as a percentage of the 30 insects observed. Where more than one individual of a particular species was collected from the host plant, the "absolute host pollen load" was determined. This is the average amount of host pollen carried by each insect species, measured as number of pollen grains. The "relative host pollen load" was also calculated for each insect species separately. This is the abundance of host pollen relative to the total pollen load, expressed either as a proportion or a percentage. The average number of different pollen types was determined from all individuals of one species, irrespective of the plant on which they were found.

In order to try and assimilate the various measures of pollinator efficiency, different measures of pollinator efficiency were combined in an equation termed the "Pollinator efficiency index" (PEI). This index was calculated for each insect species found on a particular species of plant, as follows:

$$PEI = V_f * H_P * H_L$$

where V_f is the visitation frequency of that insect species, expressed as a proportion of all 30 observations; H_P is the relative host pollen load, expressed as a proportion; and H_L is the absolute pollen load, ranked from one to six, as follows:

RANK	**Absolute pollen abundance**
1	< 50 grains
2	50 - 499 grains
3	500 - 1000 grains
4	1000 - 5000 grains
5	5000 - 10000 grains
6	>10000 grains

Thus, theoretically, PEI values range from 0 to 6.

In the formulation of this equation and for subsequent interpretation of results, certain assumptions need clarification. Firstly, visitation frequency is assumed to be proportional to potential pollinator efficiency, providing the plant under investigation does not exhibit specialized flower phenology. In the case of more specialized floral structures, closer examination of both plant morphology and the insects concerned will be necessary, before visitation frequency can be assumed to be a relatively reliable measure of pollinator efficiency.

While the equation gives equal weight to visitation frequency and relative host pollen load (H_P), where visitation frequency is less than 5% the insect is considered an ineffectual pollinator. This assumption is based on the reasoning that very low visitation frequency immediately reduces the chance of pollen transfer between two flowers of the same species, either because visitation is merely a chance occurrence, or because the pollen will have fallen off by the time the insect revisits the plant species in question. The PEI is such situations was therefore not calculated.

Another assumption is that absolute host pollen abundance (H_L) is more important than relative host pollen load, since an insect carrying a very small amount of pollen from a particular plant will be less likely to pollinate that species effectively, irrespective of whether it is carrying a pure or mixed pollen load. However, where comparing insects with equivalent absolute host pollen loads, relative host pollen load will be important for determining pollinator efficiency.

Thus, the PEI is acknowledged as being a fairly crude estimate of pollinator efficiency. However, since this index has been developed to assess the relative contribution of each insect of a pollinator suite, the absolute values of the index are unimportant. It should also be pointed out that the indices are used as comparisons of pollinator efficiency among insects found on individual plant species. They cannot be used to assess relative importance of a pollinator species pollinating different plant species.

A measure of different pollen types found on various insects has not been incorporated into the equation of PEI, since it is considered of secondary importance. It is assumed that visitation rates and absolute host pollen abundance, followed by relative host pollen load are more important in determining pollinator efficiency than the number of different pollen types the insect is carrying. This measure is used simply to assess the plant fidelity of a particular insect, which gives some indication of the degree of foraging selectivity of an insect. It was only used to assess pollination efficiency, where the PEI and component values were found to be congruent.

2 Larval requirements of insect pollinators

2.1 Site selection

To obtain an idea of which pollinators use fairly open seasonally inundated ground for their larval development, and to assess their preference of particular soil conditions, thirty emergence traps were constructed. A detailed description and diagram of the traps is given in Appendix 1. The basic design consisted of a metal hoop, roughly 1m in diameter which formed the base of the trap. This was enclosed by a netting cone. An opening was left at the top and the netting glued to a 90° bend which in turn led into a sealed jar that was filled periodically with 70% alcohol. This general design was based on the principle that insects are negatively geotaxic. Thus after emerging from the soil, adults will move upwards and eventually be caught in the "killing-jar".

The traps were set up on the 22 July 1998, and laid out in five transects, consisting of six traps each, with the two most extreme traps placed 50 to 150 m apart. These were set up in different depressions, each of which was characterised by a substantial body of standing water at the time of selection. A moisture gradient from completely inundated to reasonably dry, was used as the primary criteria for site selection, as soil moisture content was one of the habitat variables under investigation. In each transect, one trap was placed completely submerged in the standing water, while a second was placed on the margin of the waterbody. A third was placed on soil which was substantially elevated and dry in order for it not to be considered a part of the wetland. The remaining three traps were placed at regular intervals in between. Since the aim of setting the traps was merely to try to obtain some idea of the likely habitats of larval stages of pollinator guilds, the transects attempted to cover some of the variation in the landscape and were not treated as replicates in any way. However, due to the size-constraints of the traps, areas covered by shrub vegetation could not be sampled, and thus only areas with relatively short vegetation were enclosed.

Jars emptied of all their contents periodically until 29 September. Any insects clearly not important as pollinators, such as midges and mosquitoes, were discarded. The remaining insects were collected and kept in 70% alcohol for later identification and analysis.

2.2 Soil collection and analysis

On 13 September, after a relatively dry period, single soil samples, weighing between 50 and 150g, were collected from each trap, using a small soil auger, and placed in sealed packets. These were taken back to the laboratory where soil moisture content, organic content and percentage sand were determined. The reason for assessing soil moisture content has already been elucidated. Organic content may be an important factor in that larvae may congregate in organically rich soils which possibly serve as a food source. Percentage sand is a rough measure of soil types, with the lower the percentage sand, the higher the clay fraction. It is hypothesized that larvae prefer more sandy soils, as this allows greater mobility. Clay soils also often become anoxic and water logged, conditions generally not favoured by larvae.

Since soil moisture content fluctuates greatly, soil samples should have been taken repeatedly during the study period. However, time constraints allowed only for one sample from each trap to be collected and analyzed. While the results obtained cannot be seen as absolute, they at least provided a relative measure of soil moisture, and allowed for a gradient of soil moisture to be obtained for all thirty traps. In this way, comparisons could be made between the emergence of insects in the various traps. It further gave some indication of which traps fell within the boundaries of the "wetland". Site descriptions incorporated in the interpretation of results, explain discrepancies observed between measured soil water content and the overall condition observed for the particular site.

Each of the wet samples were sieved through a 2mm sieve, in order to remove large organic material such as roots and twigs. In the case of the clay-type soils, this was not possible, since the sample would not have passed through the sieve without the aid of water. The samples were then weighed out into three replicates samples roughly weighing 25g each. Exact masses were recorded, whereafter the samples were dried in an oven at 60°C for 24hours. Weights were again obtained and soil moisture content was calculated, using the following equation:

$$\text{Soil Moisture content} = [W(i) - W(f)]/W(f)$$

where $W(i)$ represents the initial weight taken before the sample was dried, and $W(f)$ is the weight of the oven dried sample. Since the density of water is 1g/ml, soil moisture content is expressed in ml/g, although actual measurements of water content are taken in grams.

About 10g of the oven dried soils from each site were then transferred into porcelain crucibles and the precise weights recorded. These were furnaced for 4 hours, at 450°C in order to burn off the organics. The weights were again obtained and the percentage organics was calculated as follows:

$$\% \text{ Organics} = [W(f) - W(a)]/W(f)*100$$

where $W(a)$ is the weight of the ashed sample.

Separate soil analysis was conducted to determine percentage sand. The soils were initially dried as before at 60°C for 24 hours and then about 25g from each sample was weighed and precisely recorded. Each sample was then carefully washed through a 63 μm sieve to remove all the silt and clay components. The removal of these latter components was assumed to be complete when the water which had passed through the sieve, was no longer discoloured. The sample that remained in the sieve was collected and ashed in the same way as previously mentioned, since the coarse particulate organic matter had to be removed before the sand fraction of the soil samples could be obtained. Percentage sand content was determined in the following way:

$$\% \text{ Sand} = W(a)/W(fi)*100$$

where $W(fi)$ is the initial dry weight of the sample prior to sieving.

2.3 Data analysis

All species which emerged in the traps were identified as far as possible and their numbers recorded. Frequencies of species emergence were examined by determining whether the abundance of a particular insect was in any way related to soil conditions. For each species, the overall soil conditions in which they were found, was determined by averaging percentage sand, percentage organics and soil moisture content, from the soil corresponding to the traps from which they were collected. This information was assimilated in a summary table in order to obtain some indication of the possible habitat requirements of the larval stages of these insects. Since water content was not always found to be a reliable measure of how inundated the site had been, habitat descriptions taken at each of each of the traps were also used to define habitats. For the insects which emerged with sufficient frequency, a Spearman Rank correlation coefficient (Zar, 1984) was used to determine the relationship between insect emergence and all the habitat variables measured. This coefficient was calculated using all the traps, not simply the traps in which the insects were found. A one-way chi-squared test was further employed to test whether the abundance of insects differed significantly from expected, given the null hypothesis that a particular habitat variable had no effect on the emergence of insects. In order to do this, each habitat variable was divided into three categories, according to a subjective rating (See Appendix 2), and traps were assigned to these groups accordingly. The frequency of insects for each category was then determined by summing the numbers of individuals found in the relevant traps throughout the study period. It was expected that if the abundance of emerging insects was independent of a particular habitat variable that the frequency of insects in the different categories would not be different.

RESULTS

1. Pollination syndromes

For each plant investigated, the suite of insect visitors and their role in pollination was independently assessed. Particular emphasis is places on the importance of monkey beetles and tabanids in the pollination of these flower species.

1.1 Geissorhiza radians

While two insect species were observed on *Geissorhiza radians, Apis mellifera* was observed very infrequently (Table 2). Furthermore, its absolute and relative host pollen load was insignificant compared to that carried by *Tabanidae* sp1. Therefore the PEI for the latter species is more than 5 orders of magnitude greater than the PEI for *Apidae* sp1. This plant species apparently has no other pollinators.

Table 2: Measures of pollinator efficiency for the insects observed on the flowers *Geissorhiza radians*. Absolute and relative host pollen loads were obtained from individuals found on *G.radians*, while the average number of pollen types was calculated from all individuals of that species collected for pollen analysis, irrespective of the plant from which it was collected. Sample size is given in parentheses.

Species	Family	Visitation frequency (%)	n	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave. no. pollen types (n)
Apis mellifera	APIDAE	11.11	1	101	0.4	8.8*10	5.67 ± 2.08 (3)
Tabanidae sp1	TABANIDAE	88.89	9	1801.8 ± 2072.7	50.0 ± 32.5	1.33	3.62 ± 1.18 (9)

1.2 Heliophila coronopifolia

Heliophila coronopifolia was visited by a large suite of insect species, of which four were monkey beetles (Table 3). *Peritrichia cinerea* was observed most often on the flowers, followed by *Anisonyx ursus* and *A.mellifera* (Table 3). Of all the species observed more than once, *A.mellifera* was found to carry more than 15 times as much *Heliophila* pollen as any other species, with the relative host pollen load also much higher than any other visitor. These factors resulted in the highest PEI of all species observed. Comparing PEIs amongst the remaining insects, *P. cinerea* had the highest followed by *A.ursus*.

Table 3: Measures of pollinator efficiency for the insects observed on the flowers of *Heliophila coronipifolia*. Absolute and relative host pollen loads were obtained from individuals found on *H.coronipifolia*, while the average number of pollen types was calculated from all individuals of that species collected for pollen analysis, irrespective of the plant from which it was collected. Sample size is given in parentheses. Where visitation frequency was less than 5%, PEI was not calculated.

Species	Family	Visitation frequency (%)	n	Abs host pollen load	Rel. host pollen load (%)	PEI	Ave. no. pollen types (n)
Anisonyx ursu	SCARABAEIDAE: Hopliini	16.7	3	1081.7 ± 897.8	43.0 ± 19.8	0.287	4.3 ± 0.6 (3)
Apis mellifera	APIDAE	16.7	2	15750 ± 3889.1	95.9 ± 1.5	0.961	5.7 ± 2.1 (3)
Bombyliidae sp1	BOMBYLIIDAE	3.3	-	-	-	-	4.3 ± 1.0 (7)
Halictidae	HALICTIDAE	3.3	-	-	-	-	-
Hopliini sp1	SCARABAEIDAE: Hopliini	3.3	-	-	-	-	-
Lepithrix ornatella	SCARABAEIDAE: Hopliini	10.0	3	802.5 ± 604	81.3 ± 2.8	0.244	3.5 ± 0.7 (15)
Peritrichia cinerea	SCARABAEIDAE: Hopliini	43.0	7	525.7	28.8 ± 22.6	0.371	3.9 ±0.6 (13)
Syrphid sp1	SYRPHIDAE	3.3	-	-	-	-	-

1.3 Monsonia speciosa

Monsonia speciosa had a relatively small suite of insect visitors, dominated in by the monkey beetle, *Lepithrix ornatella* (Table 4). While both its absolute and relative host pollen load were fairly small, in contrast to *Bombyliidae* sp2 (the species with the second highest visitation rate), its PEI was four orders of magnitude greater. Note that while the standard deviations for absolute and relative host pollen loads are very great for *L.ornatella,* its visitation frequency was more than 12 times as great as for *Bombyliidae* sp2. The average number of pollen grains carried by each species did not differ markedly.

Table 3: Measures of pollinator efficiency for the insects observed on the flowers of *Monsonia speciosa*. . Absolute and relative host pollen loads were obtained from individuals found on *M.speciosa*, while the average number of pollen types was calculated from all individuals of that species collected for pollen analysis, irrespective of the plant from which it was collected. Sample size is given in parentheses.

Species	Family	Visitation frequency (%)	n	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave. no. pollen types (n)
Bombyliidae sp2	BOMBYLIIDAE	6.7	2	23.5 ± 23.3	1.7 ± 1.0	1.8 $*10^{-}$	3.3 ± 1.2 (3)
Heterochelus athriticus	SCARABAEIDAE: Hopliini	3.3	0	-	-	-	2.8 ± 0.9 (8)
Lepithrix ornatella	SCARABAEIDAE: Hopliini	90	13	61.1 ± 235.2	12.6 ± 19.0	0.227	3.5 ±0.7 (15)

1.4 Ornothogalum thyrsoides

Table 5 shows that three out of five species observed on *Ornothogalum thyrsoides*. were monkey beetles. *Heterochelus* sp, was not analyzed for pollen as it was observed only once on this plant species. Therefore its PEI was not calculated. Although *Rhagioglossa edentula* was not observed during detailed observations of the plant, all individuals were carrying sufficient quantities of *Ornothogalum* pollen to warrant determination of the PEI. A visitation frequency (V_f) of 0.05 was used in the calculation, which is probably an underestimation of this insect's potential pollinator efficiency, since, each individual caught carried *Ornothogalum* pollen, implying that this species is be a fairly regular visitor to this plant.

Two monkey beetle species showed the highest PEIs (Table 5). Note that while *Peritrichia cinerea* had a much higher relative host pollen load, the average absolute pollen load carried by *Pachycnema flavolineata* was almost three times greater. *Apis mellifera* carried both fairly high absolute host pollen loads as well as high relative pollen loads. *P. flavolineata* had, on average the lowest average number of pollen types, followed by *P.cinerea.* Due to the low observed visitation of *Rhagioglossa*, the PEI was found to be the lowest of the four species.

Table 5: Measures of pollinator efficiency for the insects observed on the flowers of *Ornothogalum thyrsoides*. Absolute and relative host pollen loads were obtained from individuals found on *O.thyrsoides*, while the average number of pollen types was calculated from all individuals of that species collected for pollen analysis, irrespective of the plant from which it was collected. Sample size is given in parentheses.

Species	Family	Visitation frequency (%)	n	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave. no. pollen types (n)
Pachycnema flavolineata	SCARABAEIDAE: Hopliini	40	6	6283.3 ± 7089.5	71.5 ± 34.3	1.42	3.7 ± 1.4 (7)
Peritrichia cinerea	SCARABAEIDAE: Hopliini	36.7	6	2733.3 ± 1522.717	93.3 ± 7.3	1.36	3.9 ± 0.6 (13)
***Heterochelus* sp.**	SCARABAEIDAE: Hopliini	-	-	-	-	-	3.3 ± 0.6 (3)
Rhagioglossa edentula	TABANIDAE	-	10	957.5 ± 996.3	11.6 ± 10.3	0.01	4.9 ± 1.0 (10)
Apis mellifera	APIDAE	23.3	2	5700.0 ± 989.9	95.7 ± 6.1	1.12	5.7 ± 2.1 (3)

1.5 Romulea hirsuta

While the suite of insect visitors was composed almost entirely of monkey beetles, the two predominant insects were *Lepisia rupicola* and a species of colletid bee (Table 6). *Heterochelus athriticus* was observed more than once, but its low absolute and relative host pollen load, as well as its low visitation frequency, resulted in a PEI which was markedly lower than the two more common species. Contrasting the results for the colletid and *L. rupicola,* it is clear that while the monkey beetle had a higher visitation frequency and PEI, the colletid generally carried both a higher absolute and relative host pollen load.

Table 6: Measures of pollinator efficiency for the insects observed on the flowers of *Romulea Hirsuta.* Absolute and relative host pollen loads were obtained from individuals found on *R.hirsuta*, while the average number of pollen types was calculated from all individuals of that species collected for pollen analysis, irrespective of the plant from which it was collected. Sample size is given in parentheses. Where visitation frequency was less than 5%, PEI was not calculated.

Species	Family	Visitation frequency (%)	n	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave. no. pollen types (n)
Apidae sp1	APIDAE	3.3	-	-	-	-	5 (1)
Colletidae	COLLETIDAE	33.3	4	867.5 ± 409	57.4	0.574	3.5 ± 0.6 (4)
Heterochelus athriticus	SCARABAEIBAE: Hopliini	6.7	1	101	9.6	0.013	2.8 ± 0.9 (8)
Lepisia rupico	SCARABAEIBAE: Hopliini	50	9	583.3 ± 400	44.4 ± 30.6	0.666	3.5 ± 1.0 (12)
Lepithrix ornatella	SCARABAEIBAE: Hopliini	3.3	-	-	-	-	3.5 ± 0.7 (15)
Pachycnema flavolineata	SCARABAEIBAE: Hopliini	3.3	-	-	-	-	3.7 ± 1.4 (7)

1.6 Ursinia anthemoides

Ursinia anthemoides was visited by a fairly large range of species, four of which were monkey beetles (Table 7) Of these, only *Heterochelus athriticus* was observed in relatively high numbers. *Bombyliidae* sp1 was however observed visiting the flowers most frequently (Table 7). *Heterochelus* sp. and *Lepisia rupicola* were noted visiting the plant on several occasions (Table 7).

Bombyliidae sp2 and *H. athriticus* were found to have very similar PEIs. There were also differences in visitation frequency, absolute host pollen load and average number of pollen types carried for these species. Note, also, the higher average absolute host pollen load carried by *Heterochelus* sp. and *Lepisia rupicola*.

Table 7: Measures of pollinator efficiency for the insects observed on the flowers of *Ursinia anthemoides*. Absolute and relative host pollen loads were obtained from individuals found on *U.anthemoides*, while the average number of pollen types was calculated from all individuals of that species collected for pollen analysis, irrespective of the plant from which it was collected. Sample size is given in parentheses.

Species	Family	Visitation frequency (%)	n	Abs. host pollen load	Rel. host pollen load (%)	PEI	Ave. no. pollen types (n)
Apidae sp2	APIDAE	4.65	1	1700.0	48.6	0.090	-
***Bombyliidae* sp1**	BOMBYLIIDAE	55.81	7	995.7 ± 815.4	93.0 ± 5.0	1.558	3.3 ± 1.2 (7)
Heterochelus athriticus	SCARABAEIDAE: Hopliini	39.53	7	1375.7 ± 1233.2	97.8 ± 3.8	1.546	2.8 ± 0.9 (8)
***Heterochelus* sp.**	SCARABAEIDAE: Hopliini	9.30	3	5333.3 ± 4163.3	79.0 ± 21.4	0.368	3.3 ± 0.6 (3)
Lepisia rupico	SCARABAEIDAE: Hopliini	9.30	3	4433.3 ± 378.6	90.9 ± 5.0	0.338	3.5 ± 1.0 (12)
Lepithrix ornatella	SCARABAEIDAE: Hopliini	2.32	1	3680	96.8	0.090	3.5 ± 0.8 (15)

1.7 *Wachendorfia paniculata*

Philoliche angulata a tabanid, was one of four insect species found to visit *Wachendorfia paniculata* (Table 8). The average absolute and relative host pollen loads were noticeably higher for this species, than for the rest (Table 8). The PEI therefore is markedly higher than for the remaining three species. Note the extremely low average absolute host pollen loads for *Apidae* sp3 and *Australeocus hypoleucas* and the absence of *W. paniculata* pollen on *Bombyliidae* sp1.

Table 8: Measures of pollinator efficiency for the insects observed on the flowers of *Wachendorfia paniculata.* Absolute and relative host pollen loads were obtained from individuals found on *W.paniculata*, while the average number of pollen types was calculated from all individuals of that species collected for pollen analysis, irrespective of the plant from which it was collected. Sample size is given in parentheses.

Species	Family	Visitation frequency (%)	n	Abs host pollen load	Rel. host pollen load (%)	PEI	Ave. no. pollen types (n)
Apidae sp3	APIDAE	33.3	5	4.0 ± 2.2	1.9 ± 1.2	6.4*10^{-}	5.8 ± 0.8 (5)
Australeocus hypoleucas	BOMBYLIIDAE	20	3	8.3 ± 10.4	12.8 ± 12.5	0.026	4.0 ± 1.0 (3)
Bombyliidae sp1	BOMBYLIIDAE	6.7	1	0	0	0	4.3 ± 1.0 (7)
Philoliche angulata	TABANIDAE	40	6	88.3 ± 165.	17.4 ± 25.2	0.139	4.7 ± 1.8 (6)

2. Larval requirements of insect pollinators

Of all potential insect pollinators caught during the sampling period (Appendix 3), two species of monkey beetles and two species of syrphid, emerged as the most common insects. Both species of monkey beetles were found in relatively sandy soils (79.7 ± 9.1% and 83.8 ± 11.3% for *Anysonyx* sp. and *Heterchelus* sp. respectively), in traps of intermediate water content. In contrast, both syrphid species were found in traps with lower percentage sand (67.0 ± 22.0% and 56.2 ± 24.6% for syrphid sp1 and syrphid sp2, respectively). They were generally found in traps closer to the standing waterbodies, and were generally associated with higher percentage organics (12.4 ± 13.8% and 8.2 ± 8.45 for the two syrphid species, when compared to 2.0 ± 0.2% and 4.6 ± 6.9% for the monkey beetles). The relatively high standard deviations for each of these species indicates a poor correlation between insect emergence and organic content in the soil.

Since *Anisonyx* sp. and Syrphid sp1 were only found in two traps no further statistical analysis could be carried out on these species. Only *Heterochelus* sp1 and syrphid sp2 were therefore analysed statistically.

Using the Spearman Rank Correlation coefficient, the frequency of *Heterochelus* emergence was found to be significantly positively correlated with percentage sand (r = 0.429, t(n-2) = 2.513, n = 30, p =0.018), while no significant relationship was observed between emergence frequency and percentage organic matter (r = -0.343, t(n-2) = -1.933, n=30, p = 0.063) or water content (r =0.130, t(n-2) = 0.695, n=30, p = 0.493). For syrphid sp2, no significant relationship was found between insect emergence and any of the habitat variables (Percentage sand: r =-0.261, t(n-2) = -1.432, n=30, p = 0.163; Percentage organics: r =0.177, t(n-2) = 0.950, n=30, p = 0.350; Water content: r =0.068, t(n-2) = 0.360, n=30, p = 0.722). Figures 1 and 2 illustrate the relationship between the frequency of insect emergence and the three habitat variables, for *Heterochelus* sp. and Syrphid sp2, respectively. Results of subsequent chi-squared tests carried out on the same data, are displayed on Figures 1 and 2, particularly for the relationship between monkey beetle emergence and water content (Fig 1C) and for the relationship between the abundance of syrphid 2 and all environmental variables, where a linear relationship is not observed.

In order to see how closely percentage organics was related to percentage sand, a Pearsons Product Moment (Zar, 1984) correlation was used for the traps in which *Heterochelus* emerged, revealing a highly significant relationship ($r^2 = 0.98$; $n=7$; $p<0.00001$). This result needs consideration for interpretation of the likely habitat preferences of this species.

Figure 4 displays the abundance and sequence of emerging insects over the study period. While there is a great deal of overlap of peak emergence of the insects differences can be observed.

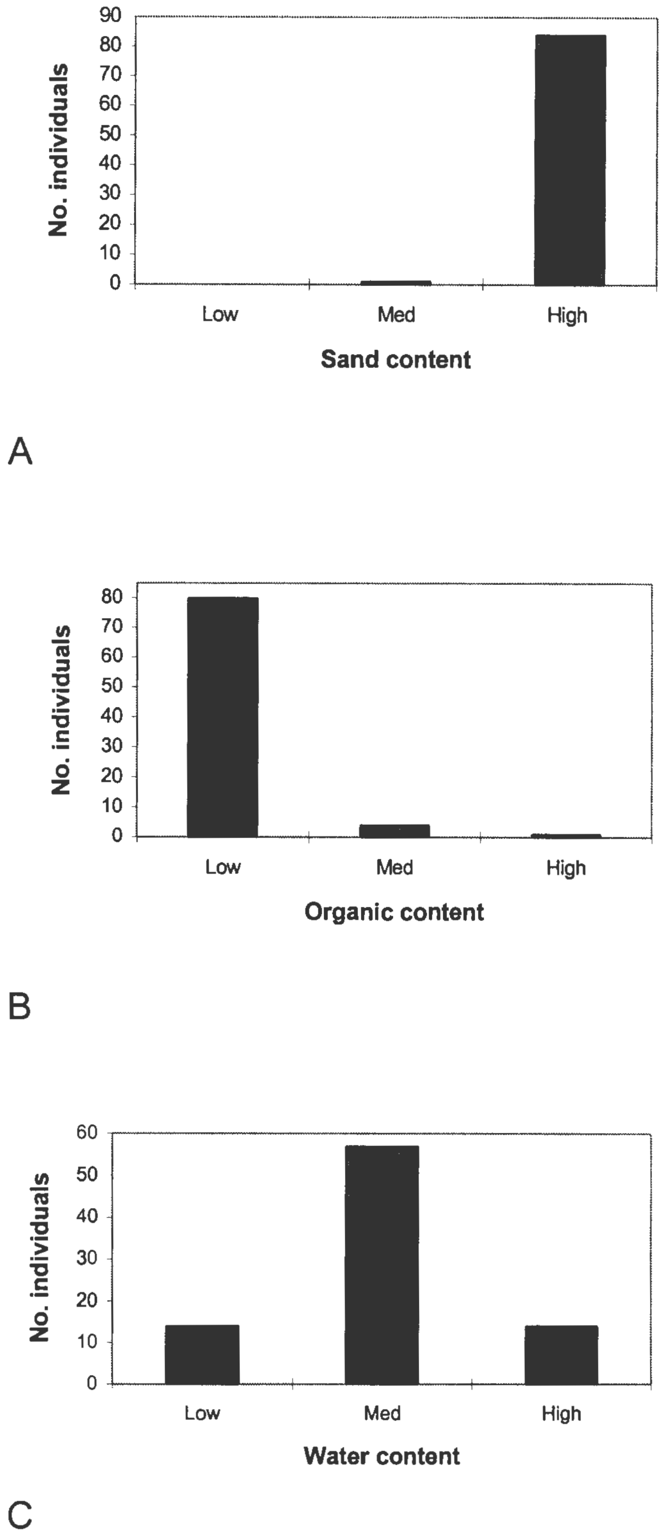

Figure 2: The relationship between emergence of *Heterchelus* sp adults and three habitat variables. The results of the chi-square tests are as follows: A: **Percentage sand**: $\chi^2 = 106.6$, df = 2, $p<0.0001$; B: **Percentage organics**: $\chi^2 = 121.0$, df = 2, $p<0.0001$; C: **Water content**: $\chi^2 = 44.9$, df = 2, $p<0.0001$.

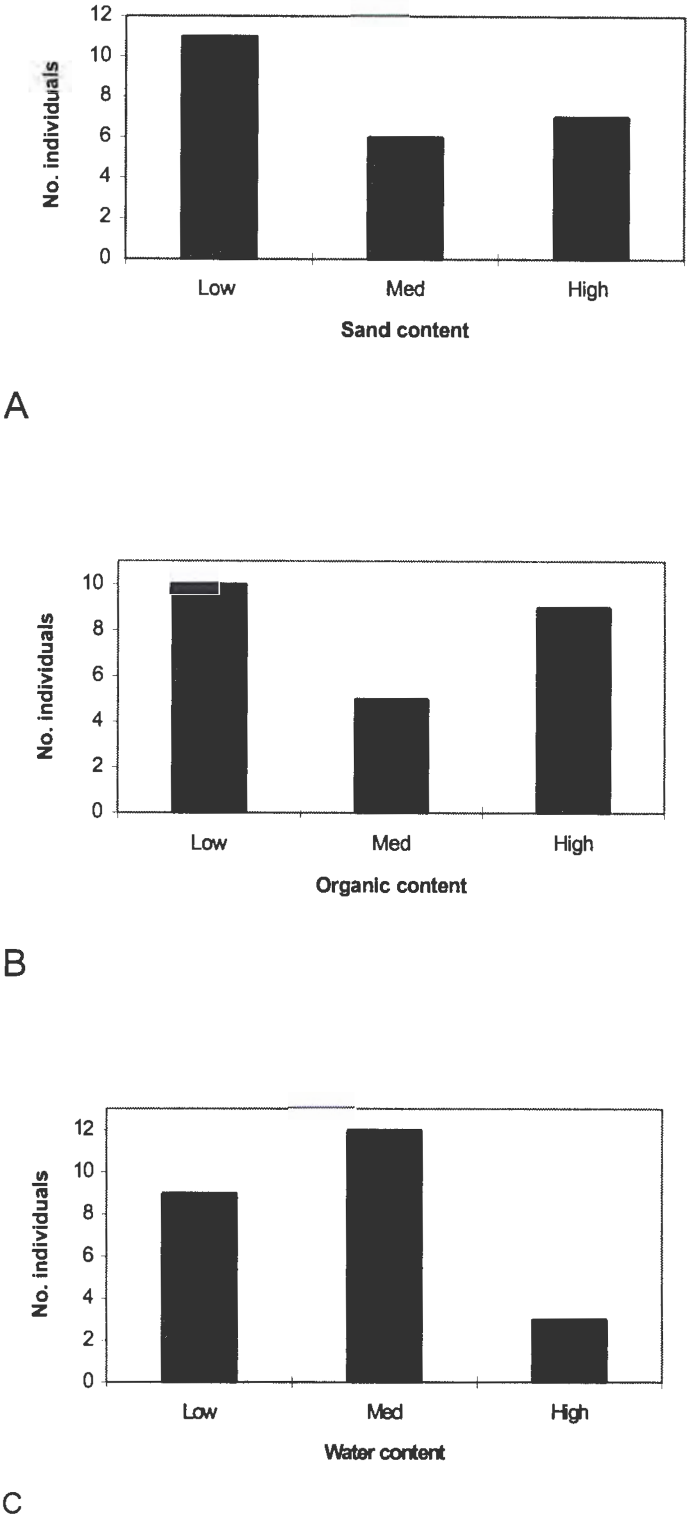

Figure 3: The relationship between emergence of Syrpid sp2 adults and three habitat variables. The results of the chi-square tests are as follows: A: **Percentage sand**: $\chi^2 = 2.26$, df = 2, p=0.32; B: **Percentage organics**: $\chi^2 = 1.74$, df = 2, p=0.42; C: **Water content**: $\chi^2 = 3.40$, df = 2, p<0.18

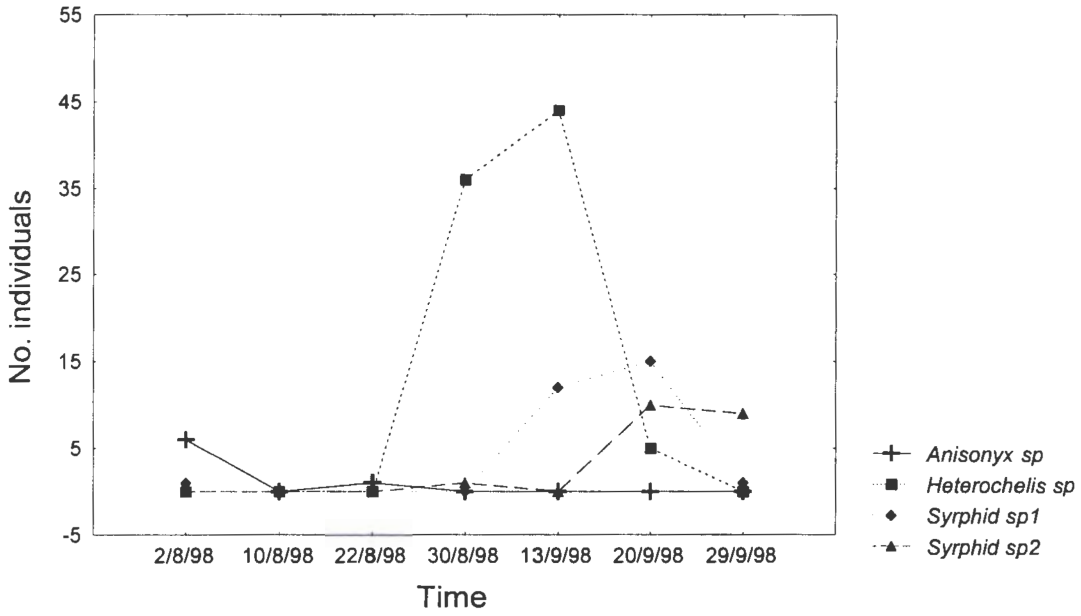

Figure 4: Changes in emergence of the four most common species over time.

DISCUSSION

Many studies have evaluated the number of insect taxa visiting flowers to assess the trend towards generalization in plant-pollinator interactions (Herrera 1996; Waser *et al* 1996). Recording all insects found on a particular plant species is imperative if the degree of generalization is to be correctly ascertained. While some of the smaller insects found on flowers were ignored in this study, the results clearly demonstrate that all plants investigated potentially have more generalized pollination syndromes than might be directly predicted from floral phenology, since all plants were visited by more than one species of insects. This is consistent with other studies that have observed that the number of insect taxa visiting plants does not seem to be associated with specialized flower morphology (McCall and Primack 1992); and Herrera 1996).

However, closer examination of frequency of occurrence, host pollen loads carried by these insects, as well as differences in behaviour, demonstrated that usually only a subset of the total suite of visitors had the potential to be effective pollinators. This pattern is clearly evidenced by the range in PEI values found on insects visiting the same plant. For example, although *U.anthemoides* was frequented by six insect species, pollination efficiency varied from 0.09 to well over 1.5 (Table 7). Only one species from each suite of insect visitors was considered capable of being an effective pollinator for *G.radians* and *W.paniculata* the plant in question. This finding is not surprising in light of the high degree of endemism of *Geissorhiza*, (which could be interpretted in terms of a dependent pollination partnership) and the specialized floral design of *Wachendorfia.* However, even the more common plants with open flowers that are assessible and visited by a large range of insects, demonstrate a measure of specificity in the sense that not all insect visitors were potential pollinators.

Of all insects observed on the flowers investigated seven species of monkey beetle, three tabanids, two bombylids and one colletid are implicated at important pollinators of the flowering plants investigated. *A.mellifera* is not included in this list, for, although it generally carries a large pollen load, and is a frequent visitor of several of the plants investigated, a fairly recent paper by Westerkamp (1991) has pointed out that honeybees are poor pollinators. This is because bees collect pollen systematically, storing it in their pollen sacs and groom themselves meticulously. Thus the pollen picked up by this species from one flower is seldom available for transfer to others.

Of the remaining pollinator groups identified, tabanids and monkey beetles seem to contribute most to the successful pollination of all the plants investigated. Of the three tabanids investigated, *Philoliche angulata* and Tabanidae sp1 are implicated as the sole pollinators of *W.paniculata* and *G.radians* respectively. In the case of former association, the very small host pollen load carried by the tabanid may bring its pollinator efficiency into question. However, after the insects had been collected from *Wachendorfia*, the anthers of the host plants were inspected, revealing very little pollen. This may serve as explanation for the negligible pollen load of all species observed on this plant. The fact that *P.angulata* carried more than ten times as much pollen as any other species, highlights its ability to pick up *Wachendorfia* pollen even when this pollen is scarce.

Rhaggioglossa endulata, the third tabanid, does not seem to be closely associated with any particular plant, although it was frequently observed on flowers of *Dimorphotheca pluvialis* and *O.thyrsoides*. Only its potential role in pollination of *O.thyrsoides* was assessed, with the results suggesting it probably plays only a relatively minor role in pollinating this plant. However, its potential as an effective pollinator should not be under-rated. These horseflies were almost always dusted with large quantities of pollen, which were later identified as asteraceous pollen. Its small size (in comparison to the other two horseflies), and its short proboscis is also clearly suited to the morphology of

Asteraceae and similar open flowers with shallow nectaries. It would therefore not be surprising if this species is a generalist pollinator of a range of relatively unspecialized flowers. From casual observation of the plants it was observed visiting, it is tentatively surmised that *Rhagioglossa* is likely to pollinate white flowers with dark centres, which is the overall colour pattern of both *D.pluvialis* and *O.thyrsoides*

Plants visited by monkey beetles all had relatively open flowers which are easily accessible to most insects. The suite of insect visitors was therefore generally fairly large. However, in all cases, monkey beetles were implicated as efficient pollinators, usually comprising the predominant insects as well as the most effective pollinators of the visitor suite.

While they may be fairly ubiquitous in their floral foraging range, monkey beetle behaviour is not as erratic as is sometimes assumed. Picker and Midgley (1996) clearly demonstrated that monkey beetles can be effectively be separated into three main guilds, according to colour preferences of different monkey beetle species. This implies that, although monkey beetles are not loyal to particular plant species, they are fairly closely associated with particular floral assemblages. The results of this study appear to substantiate this argument, in that, although all species visited several different plants (evidenced from casual observation and analysis of pollen loads), they generally appear to expend most of their energy and time visiting only one or two particular plant species. This degree of constancy on the part of these insects, together with observed high visitation frequencies of their "preferred" flowers, indicates that they are in fact reliable pollinators of these plants. In addition, most of the monkey beetles observed, were highly mobile and hirsute, factors which both contribute to effective pollen transfer. Finally, the large absolute host pollen loads carried by most species, leaves very little doubt that these insects are important pollinators of a variety of plants in the Darling area.

Although the study of the larval habitat some useful documentation of emergence of numerous insect pollinators from a seasonally inundated area, the data collected was insufficient to isolate the preferred habitats of most of these insects. Only syrphids and monkey beetles emerged in sufficient abundance to warrant further investigation. Some syrphids have aquatic larvae which generally live in polluted or organically rich waters (Scholtz and Holm, 1996). While syrphid sp1 may have aquatic larvae (since all individuls emerged from submerged traps or traps placed close to the margins of standing waterbodies), syrphid sp2 was found in habitats with large variation in soil moisture content. Furthermore, no relationship was observed between adult emergence and any of the three habitat variables measured. This indicates that the larvae of this species belongs to a group of syrphid larvae that are free-living on the surface of vegetation (Scholtz and Holm, 1996), and is therefore not directly affected by soil conditions. The monkey beetle *Heterochelus* sp. on the other hand demonstrates a strong relationship between adult abundance and all three habitat variables, with frequency of emergence being greatest at sites with high percentage sand, organics and medium moisture content (Figure 3). However, the strong negative correlation between organics and sand fraction suggests that low organics is not a condition chosen by this species, but rather an artefact of their preference for sandy soils. It seems likely that soil moisture is important as a cue for emergence, rather than a requirement for larval development. If this were not the case, larvae should be correlated more strongly to soils which can retain water for longer. The other monkey beetle was also found in a range of similar conditions and it is therefore speculated that monkey beetle larvae in generally may be associated with well drained sandy soils.

Tabanids are usually found in the study area in great profusion. Nothing is known about the larval stages of horseflies in South Africa, although work by Oldroyd (1964) indicates their close affiliation with aquatic ecosystems. It has therefore been speculated that their larval stages are dependent on wetlands or seasonally inundated areas. However, very few horseflies emerged in the traps. While this could merely be a result of a “poor horsefly season” (M.Picker, J.Duckitt, pers.comm.), Oldroyd (1964) points out that horsefly larvae are only semi-aquatic and that pupae will drown if submerged for any period of time. In a highly seasonal environment such as that of the southwestern Cape, winter rains can suddenly inundate vast areas of ground. Since tabanid pupae cannot survive complete submersion, it is more likely that the larval habitats of this groups are in well-drained soils, and not closely associated with wetlands.

This study indicates that the availability of suitable larval conditions is important for insect pollinators, but that for some groups at least, these requirements are not highly specific. Further, given the theory that the western Cape Flora is pollinator-limited, it can be predicted that an excess of suitable habitats exist for pollinator larvae. Thus, although it is important to document their habitats, it is probably of greater value to assess the relative impacts of human disturbance such as ploughing, on the larval survival of these species.

CONCLUSION

From the results obtained, it appears that the pollination success of many flowers in the Darling area is linked to the presence and abundance particularly of monkey beetles and tabanids. However, the emergence and abundance does not seem to be linked so much to the availability of suitable habitats, as to suitable environmental conditions. Synchronized insect emergence which coincides with the spring flowering season, suggests that environmental cues such as rainfall and changes in temperatures may be extremely important for successful emergence. However there is some indicationthat both insect abundance and composition varies from year to year. While no trends can be extracted from just one season's data, the difference in the timing of peak emergence of the four insect species examined (Figure 4) is consistent with the above suggestion, since it indicates that the environmental cues are highly specific for different insects. Since the Western Cape has a fairly variable climate, with rainfall and temperatures fluctuating quite considerably, it can be speculated that the abundance and composition of emergent pollinators is likely to vary from year to year. This has considerable implications for flowers reliant on insects for pollination. For while generalised plant-pollinator syndromes are generally perceived as less effective than specialized systems due to the high degree of pollen wastage, and problems associated with pollen contamination, such syndromes may be very efficient in variable environments, since such plants are not reliant on a single insect for reproductive success. A plant visited and pollinated by several insects is assured of some pollen transfer every year, since it is likely that at least a subset of its pollinator suite will emerge every year. In contrast, plants adapted to pollination by only one insect are highly susceptible to suffering complete reproductive failure in years where its pollinator does not emerge in sufficient abundance. In a highly variable environment it may therefore be beneficial to possess a generalized pollination system, and it may be that such systems are in fact a form of specialization in themselves. Furthermore, in a pollinator-limited environment, it may be as beneficial to a plant to attract as many potential pollinators as possible, as to develop a highly efficient pollination system with only one insect.

Adaptation to pollinators has certainly played an important role in the evolution and speciation of plants in the Western Cape Flora (Johnson, 1997), but until recently the consensus opinion has been that these plant-pollinator interactions have resulted primarily in the adaptive radiation of highly specialized flowers. However, it may be the case that trends towards the adaptation of specialized systems have been accompanied by selection for plants which are specifically adapted towards generalised pollination syndromes. Further research is necessary to establish the degree to which one may be able to view apparently-generalist pollination systems in terms of a form of specialization. Particular emphasis should be placed on assessing the extent to which environmental and climatic variability affects the reproductive success of "generalized" versus "specialized" flowering plants, since the ability to cope with fluctuations in the enviroment is imperative to the long-term survival of a species.

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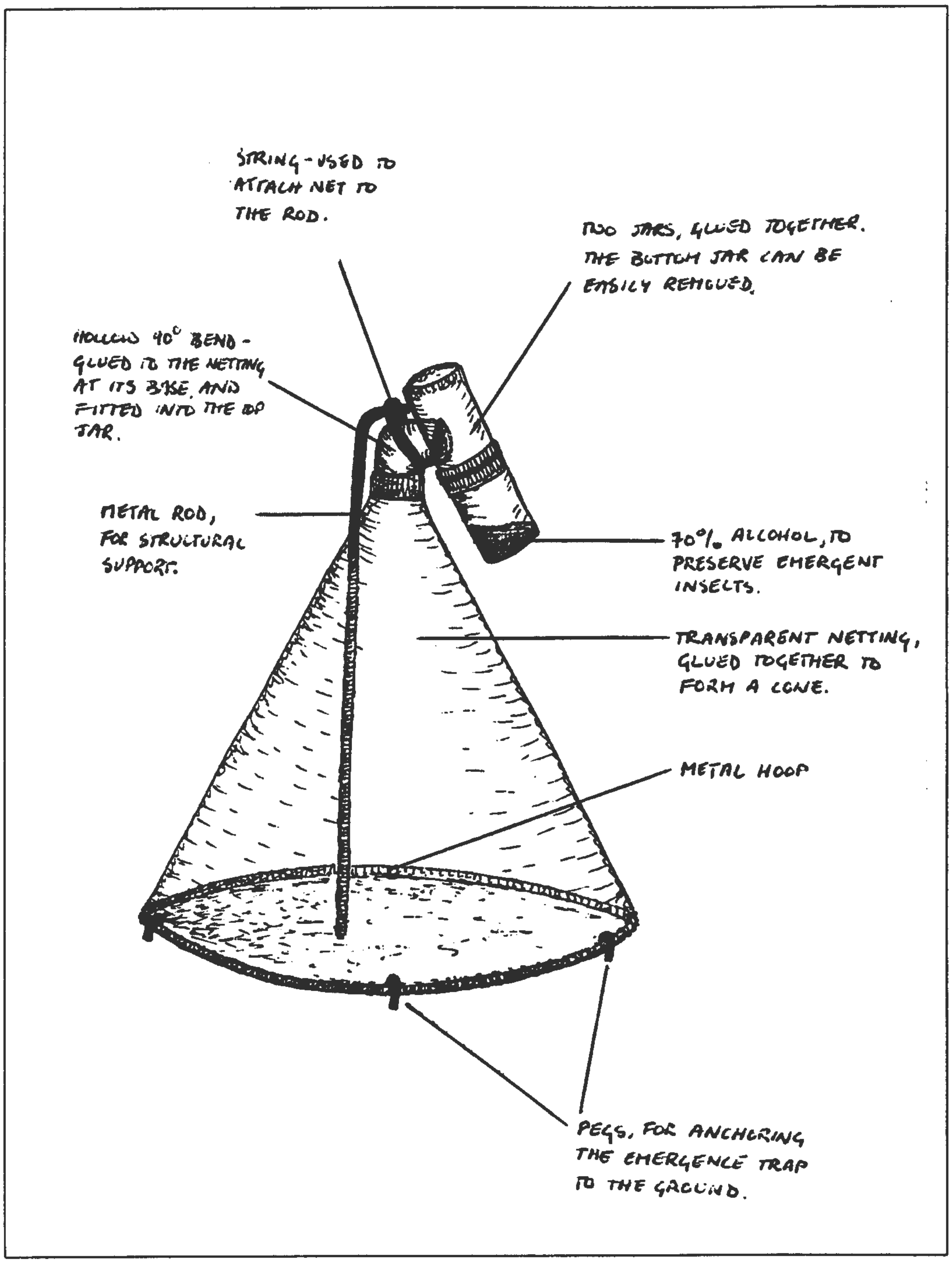
APPENDIX 1:

Emergence-trap design



APPENDIX 2:

Criteria for the categories assigned to the three habitat variables.

Percentage sand:

Low: <50% sand
Medium: 50 - 75% sand
High: >75% sand

Percentage organics:

Low: <3% organics
Medium: 3 - 8% organics
High: >8% organics

Water content:

Low: <0.35ml/g
Medium: 0.35 - 0.50ml/g
High: >0.50ml/g

APPENDIX 3

A comprehensive list of all insect pollinators caught in emergence traps.

Family	No of species caught
Calliphoridae	1
Masaridae	1
Noctuidea	1
Scarabaeidae	2
Sciomyzidae	1
Syrphidae	2