

## Pollination of certain *Leucadendron* species (Proteaceae)

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Female plants of several species of the dioecious genus *Leucadendron* (Proteaceae) were regularly observed for possible insect pollinators. *Leucadendron* was found to be beetle pollinated with *Pria cinerascens* Er. (Coleoptera: Nitidulidae) the principal pollinator of *L. salignum* and *L. laureolum*, and a *Rhizophagus* sp. (Coleoptera: Rhizophagidae) the principal pollinator of *L. tinctum*. *L. daphnoides* was pollinated by a guild of small Coleoptera, Diptera and by the honey bee *Apis mellifera*. *L. sessile* was primarily pollinated by members of the Alticinae (Coleoptera: Alticidae) and Ceutorhynchinae (Coleoptera: Curculionidae), and *L. microcephalum* by *P. cinerascens* and a ceutorhynchinid. Experiments showed that *L. coniferum* was wind pollinated but *L. salignum*, *L. sessile*, *L. gandogeri* and *L. tinctum* were not. The pollination of the inconspicuous, yellowish flowers of *Leucadendron* by small non-specialized beetles is in accordance with the pollination syndrome for dioecious tropical trees.

Vroulike plante van verskeie tweehuisige *Leucadendron* (Proteaceae) spesies is gereeld ondersoek vir moontlike bestuiwers. *Leucadendron* is deur kewers bestuif met *Pria cinerascens* Er. (Coleoptera: Nitidulidae) die hoofbestuier van *L. salignum* en *L. laureolum*, en 'n *Rhizophagus* sp. (Coleoptera: Rhizophagidae) die hoofbestuier van *L. tinctum*. *L. daphnoides* is deur verskeie klein Coleoptera, Diptera en deur *Apis mellifera* bestuif. *L. sessile* is hoofsaaklik deur lede van die Alticinae (Coleoptera: Alticidae) en Ceutorhynchinae (Coleoptera: Curculionidae) bestuif, en *L. microcephalum* deur *P. cinerascens* en 'n Ceutorhynchinid. Experimente het getoon dat *L. coniferum* windbestuif was maar *L. salignum*, *L. sessile*, *L. gandogeri* en *L. tinctum* nie. Die bestuiwing van die redelik onopvallende, gelerige blomme van *Leucadendron* deur klein, nie-gespesialiseerde kewertjies is in ooreenstemming met die bestuiwingsindroom vir tweehuisige tropiese bome.

**Keywords:** Dioecy, *Leucadendron*, pollination

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### Introduction

In general very little is known about the insect pollination of the Cape flora. This is clear from a recent synthesis by Whitehead *et al.* (1987) in which the need for detailed studies rather than more anecdotal information on pollinators is stressed.

The pollinators of the Proteaceae, one of the dominant families in the Cape flora, have received little attention, the only comprehensive study being that of Coetzee & Giliomee (1987), who showed beetles to be the main pollinators. Pollination of the genus *Leucadendron* is of particular interest because all the species are dioecious. Williams (1972) estimated that of the 91 *Leucadendron* spp., 89% are insect pollinated, 6.6% wind pollinated, 3.3% probably extinct, and that one species *L. salicifolium* (Salisb.) Williams, is probably in transit from insect to wind pollination. Williams also noted that the beetle *Pria cinerascens* Er. is often associated with the flowers of this genus. This is of interest since the role of Coleoptera as pollinators has largely been ignored in pollination studies (Faegri & van der Pijl 1979). Also, beetles are only rarely the pollinators of dioecious plants: in a dry forest in Costa Rica 3% of the dioecious plants were pollinated by beetles compared to 80% by small bees (Bawa 1980).

This study was undertaken during the blooming periods of 1985 to 1987, to evaluate experimentally the

role of insects in the pollination of a number of *Leucadendron* spp., to identify the pollinators, and to determine the role of wind in the pollination of these species.

### Materials and Methods

*Leucadendron salignum* Berg was studied at the following sites: approximately 5 km south of Shaw's Pass in the Caledon district; throughout Bain's Kloof Pass; between Rooi Els and Pringle Bay; and in the Jonkershoek Forest Reserve. Exclusion experiments were conducted on *L. salignum* in Jonkershoek. *L. salicifolium* (Salisb.) and *L. microcephalum* (Gandoger) Gandoger and Schinz were studied in stands adjacent to the Nuweberg Forestry Station; *L. daphnoides* (Thunb.) Meisn. was studied in the Du Toit's Kloof Pass, *L. sessile* R. Br. in the Sir Lowry's Pass; *L. tinctum* Williams in the Houw Hoek Pass; *L. laureolum* (Lam.) Fourcade in the vicinity of the Palmiet River Mouth; *L. gandogeri* Schinz ex Gandoger in the vicinity of Pringle Bay; and *L. coniferum* (L.) Meisn. near Pearly Beach.

Exclusion experiments were conducted on *L. salignum*, *L. gandogeri*, *L. sessile*, *L. tinctum*, *L. microcephalum*, *L. coniferum* and *L. salicifolium*. Insects were excluded from the female flowers by placing closed sleeves of fine gauze mesh over the flowering shoots, ¼ mm × ¼ mm square aperture for *L. coniferum*, and 1 mm × ½ mm rectangular aperture for the other species. It was assumed that the gauze sleeves would allow wind

pollination to take place if wind pollination were operating in that species. Birds but not insects were excluded from *L. gandogerii* female flowers using similar sleeves of wire chicken mesh with an 18 mm × 18 mm aperture. The cones from the covered flowers were retrieved 7 to 12 months later and the seed set compared with that of uncovered cones. Covered and uncovered cones used for comparison were taken from the same plants, were formed in the same blooming season and were collected for analysis simultaneously.

A comparison was made between the number of cones developing from the capitula of *L. salignum* in excluded and control floral shoots. A cone was considered not to have developed when it had shown no increase in size after blooming and had dried up. This contrasted with developing cones which increased in size after blooming and did not dry up or fall off.

In evaluation of the seed set, the number of florets per capitulum was determined by counting the number of bracts per cone. The cones were then dissected to remove the seeds which had set and had developed since blooming. Seeds with a moist fleshy endosperm were taken as positive indications of pollination having occurred. The exclusion of insects was expected to cause either a decrease in the level of seed set and number of cones developing (insect or bird pollinated species) or to cause no such change (wind pollinated species). The seed set data were analysed using the method of Cox (1970) for comparing pairs of binary data. A left one-sided test was used assuming that more seeds set in the non-excluded control.

Potential insect pollinators were collected individually on female flowers if they displayed activity which could have led to pollination provided that they were carrying pollen, i.e. coming into contact with the stigmata. The numbers found therefore reflect the relative abundance of the species at the time of sampling. Collecting was undertaken on days with little or no wind and without rain. Flowers were inspected for pollinators from early morning to late afternoon for at least one day during the blooming period.

The insects collected were inspected for pollen by using the method of MacGillivray (1987). The insects' pollen load was washed off with xylene and the tubes in which they were collected were washed out for pollen. The pollen was embedded in a glycerine jelly pellet by centrifuging and then mounted on a microscope slide. These slides were examined microscopically for pollen from male plants of the particular species, and the pollen grains counted.

## Results

In all the insect-pollinated species studied, many more insects were observed on the more abundant male than female capitula. Insect species were often found on the male capitula which did not occur on the female but not vice versa. Some of these insects were physically unable to reach the female florets which were enclosed by the involucre leaves. This was the case with *L. laureolum*, where the honey bee *Apis mellifera* L. visited male but

**Table 1** Number of *L. salignum* cones developing on insect-excluded floral shoots compared with non-excluded control shoots, the level of seed set in insect-excluded cones compared with non-excluded control cones and the left one-sided significance levels (*P*), (Jonkershoek Forest Reserve, 1986)

Experiment no.	Cones developing			Seed set		
	Excluded <sup>a</sup>	Control <sup>b</sup>	<i>P</i>	Excluded <sup>c</sup>	Control <sup>d</sup>	<i>P</i>
1	0/5	1/8	0.29	0/24 <sup>e</sup>	11/30	<0.05
2	2/8	4/11	0.32	1/45	39/103	<0.05
3	1/9	3/17	0.38	0/33	23/82	<0.05
4	0/4	2/8	0.19	0/24 <sup>e</sup>	9/37	<0.05
5	1/1	2/2	0.41	4/21	18/55	0.13 <sup>f</sup>
6	3/4	3/6	0.25	0/76	40/76	<0.05
7	0/5	5/8	0.02	0/24 <sup>e</sup>	27/95	<0.05

<sup>a</sup>The number of developing cones/the number of cones that were excluded

<sup>b</sup>The number of developing cones/sample size

<sup>c</sup>The number of developing seeds/the number of florets (sum from the developing cones in a)

<sup>d</sup>The number of developing seeds/the number of florets (sum from the developing cones in b)

<sup>e</sup>The number of developing seeds/the average number of florets from all the developing cones

<sup>f</sup>The type I error in experiment 5 can be attributed to the sample size being too small

not female capitula. This difference between the insects encountered on male and female plants began when the male plants came into bloom long before the female plants, sometimes by several weeks. The higher incidence of insects on male plants continued through the blooming period of the female and into the period where the male plants continued to flower for a short period after the female plants had finished blooming.

The pollen load of almost all insects only contained pollen from the plant species on which they were caught. On specimens which carried other pollen, this foreign pollen never made up more than 50% of the total pollen load.

**Table 2** Pollen loads carried by pollinators of *L. salignum* at Jonkershoek (collected 27-06-1986), Bain's Kloof (collected 08-06-1986) and Pringle Bay (collected 22-08-1987)

Pollinator	No. collected	Av. no. of pollen grains	Std. E.
<b>Coleoptera</b>			
Cleridae			
<i>Prosymnus uytenbogaarti</i> Corp.	1	19	n/a
Coccinellidae			
<i>Rhizobius burmeisteri</i> Muls.	9	0.5	0.4
Nitidulidae			
<i>Pria cinerascens</i> Er.	37	191	101

*L. salignum*

The exclusion experiments showed that the exclusion of insects did not cause a significant decrease in the number of developing cones in spite of a significant reduction in the level of seed set (Table 1). Wind clearly does not play a significant role in the pollination of *L. salignum* since the seed set in insect-excluded cones was extremely low.

The principle pollinator appeared to be a minute nitidulid beetle (<2 mm), *Pria cinerascens* Er., which was collected at three of the four study sites (Table 2). In the Shaw's Pass region *P. cinerascens* was absent and apparently replaced by the coccinellid *Hippodamia variegata* (Goeze), (Table 3).

*L. daphnoides*

This species was pollinated by a guild of insects, mostly small Coleoptera (Table 4). The pollen load on *A. mellifera* was relatively low for this insect, indicating that they were visiting the flowers for nectar and not collecting pollen. In this species nectar is also produced in the male flowers (Williams 1972).

*L. salicifolium*

No insects were encountered on the male or female flowers. Clouds of pollen were released when the male plant was shaken and the pollen was not sticky indicating that this may be a wind-pollinated species. Exclusion

experiments were destroyed by fire before the results could be obtained.

*L. sessile*

A member of the coleopterous family Alticidae was the most abundant pollinator but carried a very low pollen load. Small, winged curculionids were not as abundant, but in view of their relatively heavy pollen loads were probably also important pollinators (Table 5). The results of exclusion experiments at two sites demonstrate that *L. sessile* is not wind pollinated (Tables 6 & 7).

Extensive bee activity was observed on the male flowers but the female flowers were not visited. The two specimens caught on female flowers (Table 5) alighted for no more than one second and it seems that the visits were made by mistake as these female flowers were in close proximity to the male flowers being visited. Therefore *A. mellifera* cannot be considered to be an important pollinator, although it should be noted that some dioecious plants like *Carica papaya* L. rely totally on 'mistake' pollination for fertilization (Baker 1976).

**Table 3** Pollen loads carried by pollinators of *L. salignum* in the vicinity of Shaw's Pass (collected 26-04-1986, 18-05-1086)

Pollinator	No. collected	Av. no. of pollen grains	Std. E.
<b>Coleoptera</b>			
<b>Anthicidae</b>			
<i>Formicomus caeruleus</i> (Thb.)	1	187	n/a
<b>Buprestidae</b>			
<i>Sphenopterinae</i> gen. sp. 1	1	40	n/a
<b>Coccinellidae</b>			
<i>Exochomus</i> sp.	1	1	n/a
<i>Hippodamia variegata</i> (Goeze)	35	441	354
<b>Diptera</b>			
<b>Calliphoridae, Rhiniinae</b>			
<i>Fainia</i> sp.	1	6	n/a
Rhiniini sp. 1	1	11	n/a
<i>Stomorphina ? cibrata</i> Bigot	1	71	n/a
<b>Muscidae</b>			
<i>Orthellio peronii</i> Desvoidy	1	7	n/a
<b>Platystematidae</b>			
<i>Neoardelio longiala</i> Steyskal	1	39	n/a
<b>Hymenoptera</b>			
<b>Masaridae</b>			
gen. sp. 1	1	65	n/a
<b>Proctotrupidae</b>			
<i>Exallomyx ?</i> sp.	1	3	n/a

**Table 4** Pollen loads carried by pollinators of *L. daphnoides* in Du Toit's Kloof Pass (collected 04-09-1987)

Pollinator	No. collected	Av. no. of pollen grains	Std. E.
<b>Coleoptera</b>			
<b>Alticidae</b>			
Alticinae gen. sp. 1	26	20	5
Alticinae gen. sp. 2	7	26	8
Alticinae gen. sp. 3	2	26	6
<b>Cleridae</b>			
<i>Dolichopsis cyanella</i> Gorham	8	78	19
<b>Coccinellidae</b>			
<i>Nephus quadrivittatus</i> Muls.	4	0.7	0.3
<b>Curculionidae</b>			
Ceutorhynchinae	1	37	n/a
<b>Mordellidae</b>			
<i>Anaspis</i> sp.	3	1.3	0.7
<b>Nitidulidae</b>			
<i>Pria cinerascens</i> Er.	26	4	2.3
<b>Rhizophagidae</b>			
<i>Rhizophagus</i> sp.	6	11	6
<b>Tenebrionidae</b>			
<i>Eutrapela</i> sp.	2	616	511
<b>Diptera</b>			
<b>Bibionidae</b>			
<i>Bibio turneri</i> Edwards	1	144	n/a
<b>Scathophagidae</b>			
<i>Scathophaga stercoraria</i> Wied	1	76	n/a
<b>Syrphidae</b>			
<i>Melanostoma</i> sp.	1	1460	n/a
<b>Hymenoptera</b>			
<i>Apis mellifera</i> L.	4	449	175

**Table 5** Pollen loads carried by pollinators of *L. sessile* in Sir Lowry's Pass (collected 05-08-1987)

Pollinator	No. collected	Av. no. of pollen grains	Std. E.
<b>Coleoptera</b>			
Alticidae			
Alticinae gen. sp. 1	37	1.5	0.3
Curculionidae			
Ceutorhynchinae	4	55.8	18.8
Nitidulidae			
<i>Pria cinerascens</i> Er.	6	2.8	1.4
<b>Hymenoptera</b>			
<i>Apis mellifera</i> L.	2	>1000	n/a

**Table 6** Number of *L. sessile* seeds set in insect-excluded cones compared with non-excluded controls (Sir Lowry's Pass, 1987), and the left one-sided significance levels (*P*)

Experiment no.	Seed set <sup>a</sup>		<i>P</i>
	Excluded	Control	
1	4/52	21/51	<0.001
2	2/46	11/46	<0.01
3	2/41	21/58	<0.001
4	2/47	16/45	<0.001
5	0/41	11/46	<0.01
6	4/38	11/37	0.022
7	0/40	10/44	<0.01
8	3/39	20/57	<0.01

<sup>a</sup>The number of developing seeds/the number of florets (per experiment: 1 cone excluded and 1 cone taken as a control)

**Table 7** Number of *L. sessile* seeds set in insect-excluded cones compared with non-excluded controls (Kogelberg, 1986)

Experiment no.	Seed set <sup>a</sup>	
	Excluded	Control
1	0	13
2	0	13
3	0	8
4	0	10
5	0	8
6	0	12
Average	0	10.7

<sup>a</sup>The number of seeds set per cone (per experiment: 1 cone excluded and 1 cone taken as a control)

**Table 8** Number of *L. tinctorum* seeds set in insect-excluded cones compared with non-excluded controls (Houw Hoek Pass, 1987) and the left one-sided significance levels (*P*)

Experiment no.	Seed set <sup>a</sup>		<i>P</i>
	Excluded	Control	
1	0/54	18/54	<0.001
2	4/67	28/76	<0.001
3	0/61	17/81	<0.001
4	3/82	21/84	<0.001

<sup>a</sup>The number of developing seeds/the number of florets (per experiment: 1 cone excluded and 1 cone taken as a control)

### *L. tinctorum*

Exclusion experiments showed that *L. tinctorum* was primarily insect pollinated (Table 8), and that a small beetle *Rhizophagus* sp. (Coleoptera: Rhizophagidae) is the principle pollinator (Table 9). Curculionids were less abundant, carried less pollen and there was greater variation in their pollen load but were probably still of some importance as pollinators.

### *L. microcephalum*

*Pria cinerascens* and a Ceutorhynchinae (Coleoptera: Curculionidae) appeared to be the primary pollinators (Table 10). Exclusion experiments were destroyed by fire.

### *L. laureolum*

*P. cinerascens* was the primary pollinator (Table 11). Exclusion experiments were not undertaken to evaluate the role of wind in the pollination of this species as wind was not expected to be of importance. This assumption was based on observations during a previous blooming season, i.e. there was a large number of insects in association with the female flowers, sticky pollen, no cloud

**Table 9** Pollen loads carried by pollinators of *L. tinctorum* in Houw Hoek Pass (collected 29-07-1987)

Pollinator	No. collected	Av. no. of pollen grains	Std. E.
<b>Coleoptera</b>			
Cryptophagidae			
<i>Micrambe</i> sp.	1	1	n/a
Curculionidae			
Ceutorhynchinae	5	249	165
Nitidulidae			
<i>Pria cinerascens</i> Er.	2	67	64
Rhizophagidae			
<i>Rhizophagus</i> sp.	32	352	54

**Table 10** Pollen loads carried by pollinators of *L. microcephalum* adjacent to Nuweberg Forestry Station (collected 23-07-1987)

Pollinator	No. collected	Av. no. of pollen grains	Std. E.
<b>Coleoptera</b>			
Curculionidae			
Ceutorhynchinae	6	58	29
Nitidulidae			
<i>Pria cinerascens</i> Er.	25	10	7
<b>Hemiptera</b>			
Scutelleridae	1	3	n/a

**Table 11** Pollen loads carried by pollinators of *L. laureolum* near the Palmiet River mouth (collected 12-06-1987)

Pollinator	No. collected	Av. no. of pollen grains	Std. E.
<b>Coleoptera</b>			
Curculionidae			
Ceutorhynchinae	2	25.5	12.5
Nitidulidae			
<i>Meligethes viridulus</i> Reitt.	1	164	n/a
<i>Pria cinerascens</i> Er.	50	8.2	3.5
<b>Hemiptera</b>			
Pentatomidae gen sp. 1	1	2	n/a

**Table 12** Number of *L. gandogerii* seeds set in insect- and bird-excluded cones compared with non-excluded controls (Pringle Bay, 1987), and the left one-sided significance levels (*P*)

Experiment no.	Seed set <sup>a</sup>		<i>P</i>
	Excluded	Control	
1	0/62	28/47	<0.001
2	1/48	4/49	0.095 <sup>b</sup>
3	3/50	10/50	<0.05
4	0/79	33/76	<0.01
5	1/88	10/87	<0.01

<sup>a</sup>The number of developing seeds/the number of florets (per experiment: 1 cone excluded and 1 cone taken as a control)

<sup>b</sup>The type 1 error in exp. 2 can be disregarded since the seed set of the control is exceptionally low compared with the seed set in the other controls

**Table 13** Number of *L. gandogerii* seeds set in bird-excluded cones compared with non-excluded controls (Pringle Bay, 1987), and the left one-sided significance levels (*P*)

Experiment no.	Seed set <sup>a</sup>		<i>P</i>
	Excluded	Control	
1	3/46	12/44	<0.01
2	17/52	24/56	0.142
3	8/52	22/45	<0.001
4	10/54	33/56	<0.001
5	32/63	28/55	0.495

<sup>a</sup>The number of developing seeds/the number of florets (per experiment: 1 cone excluded and 1 cone taken as a control)

**Table 14** Number of *L. coniferum* seeds set in insect-excluded cones compared with non-excluded controls (Pearly Beach, 1987), and the left one-sided significance levels (*P*)

Experiment no.	Seed set <sup>a</sup>		<i>P</i>
	Excluded	Control	
1	32/65	18/77	0.501
2	29/73	60/83	<0.001
3	27/59	34/61	0.144
4	18/58	24/65	0.249
5	19/67	13/62	0.669
6	17/66	31/73	0.021
7	36/72	45/69	0.035
8	33/63	33/65	0.928
9	37/67	48/77	0.195
10	44/77	28/55	0.740
11	42/67	39/64	0.919

<sup>a</sup>The number of developing seeds/the number of florets (per experiment: 1 cone excluded and 1 cone taken as a control)

### *L. gandogerii*

No insect pollinators could be found on the female capitula of this species. Since orange breasted sunbirds, *Nectarinia violacea* (L.) were seen visiting the flowers, an experiment was conducted to exclude birds but not insects. The results indicated that this species was not primarily wind pollinated and that it was probably insect pollinated (Table 12). The sunbirds seem to have contributed towards pollination as in three out of five cases there was a significant reduction in seed set when they were excluded (Table 13). It must be noted that the experiment to exclude birds but to allow insects access to the flowers also excluded the larger Lepidoptera.

of pollen released when the male plant was shaken and the female florets were enclosed by the involucre leaves.

### *L. coniferum*

Exclusion of insects from the female flowers of this species showed that it was wind pollinated (Table 14). This experiment also proved that the gauze exclusions allow wind-borne pollen to reach the florets. The plants were not inspected for pollinating fauna during bloom.

### Discussion

Previous workers have speculated that the pollination of *Leucadendron* is effected by bees (melittophily) (Vogel 1954) and by beetles (cantharophily) (Faegri 1965). Faegri mentioned that he found *Genuchus hottentottus* (F.) on *Leucadendron*. While this relatively large scarabaeid beetle is known to feed on nectar and pollen in *Protea* inflorescences (Coetzee & Giliomee 1987) it was not noticed on any of the *Leucadendron* species during this study. From the work undertaken here it appears that *Leucadendron* is indeed beetle pollinated, but that the pollen vectors are small beetles of the families Nitidulidae, Curculionidae and Alticidae. These beetles are also important pollinators of *Protea repens* (L.) (Coetzee & Giliomee 1985).

The observations on *Leucadendron* are in agreement with the general conclusion of Bawa (1980) that the great majority of dioecious species are pollinated by relatively small insects that forage constantly at a particular plant for a long time. Where the same or similar beetles are pollinators of self-compatible species such as *Protea* species, this may result in inbreeding depression, expressed in lower seed set, as is typical for many *Protea* species (Horn 1962), or in lower-quality seeds. In contrast, the seed set in the *Leucadendron* species studied was relatively high, lending support for the traditional argument that dioecy had evolved as an outbreeding mechanism (see for example Baker 1984). Other mechanisms promoting outbreeding in the Proteaceae are the strong protandrous habit, the separation of the inflorescences for rodents in some *Protea* species and for birds in genera like *Protea*, *Mimetus* and *Leucospermum* and wind pollination (anemophily). The latter may have evolved more than once in *Leucadendron* from entomophilous ancestors (Steiner 1988), probably as a result of further specialization of the sexes in producing and receiving pollen once their segregation was established.

While there are disadvantages for plants in being pollinated by relatively inactive, generalized feeders like small beetles it has the advantage that the pollinators' energetic demands can be satisfied by small rewards of nectar and pollen. This may be of particular significance for fynbos plants which generally grow on nutrient-poor soils.

The small, unspecialized pollinators of *Leucadendron* and the pale, inconspicuous, often small flowers of the genus are in agreement with the dioecious pollinator and flower syndrome of Bawa & Opler (1975). They found that most insect-pollinated dioecious species had small, white, yellow or pale green flowers. The similarities in the pollination biology of *Leucadendron* and the tropical species studied by Bawa & Opler led Steiner (1987) to

speculate that *Leucadendron* had a tropical rather than temperate origin.

Where *Pria cinerascens* was the chief pollinator, protection provided by the plants for the beetles appeared to be important. *P. cinerascens* was easily disturbed and searched for concealed clefts in the foliage to hide. They were seldom seen on exposed surfaces. On the male capitula they were mostly found concealed between the florets. The female capitula of *L. salignum* and *L. laureolum* are enclosed by the involucre leaves. *P. cinerascens* was also the principle pollinator of *L. microcephalum* where they were mostly encountered beneath the involucre bracts which enclose the lower portion of the female capitulum.

The natural pollinator fauna in the Shaw's Pass region appears to have been disturbed by the extensive presence of *Hippodamia variegata* (Table 3). *H. variegata* was first observed in South Africa in the late 1960's by Dr V.B. Whitehead, and is probably of European origin (V.B. Whitehead, pers. comm.). *Hippodamia* spp. often switch from an aphid diet to a non-insect diet such as pollen, honeydew, nectar or extra-floral nectary secretions when aphids are not available (Hagen 1962). Volkov (1937) reported that *Adonia variegata* Gze. (= *H. variegata*) switched from aphids on cotton to nectary secretions on cotton once the aphids had been eliminated. The attraction of pollen and nectar could account for the presence of *H. variegata* on *L. salignum* flowers in the winter which appeared to have resulted in the exclusion of *P. cinerascens* as the primary pollinator in this region. Not only had *H. variegata* replaced *P. cinerascens* as the main pollinator in Shaw's Pass, a number of other pollinators also appeared in this region which may be a result of the disturbance caused by the alien *H. variegata*. Although *H. variegata* appears to be a better pollinator of *L. salignum* than *P. cinerascens* the full extent of the impact of *H. variegata* on the plant and insects in association with the plant should be studied in detail. This is especially important in view of the many importations of similar insect predators for biological control of pest insects in agriculture.

*Apis mellifera* occurred abundantly on the male flowers of *L. sessile* but did not appear to be attracted to the female flowers, even though nectar was secreted by the female flowers and the involucre leaves did not enclose the flowers. The protein-rich pollen available in the male flower in addition to the production of nectar by the male florets of some *Leucadendron* species (Williams 1972), could account for the insects' preference for the male flowers. The early flowering of male plants, the more abundant and often more conspicuous male than female floral shoots and the abundant floral rewards of male flowers all help to ensure that potential pollinators move from male to female flowers, the direction they must move to effect pollination.

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