

Pollination biology in the Snowy Mountains of Australia: Comparisons with montane Colorado, USA

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Abstract

Various aspects of the pollination biology of the alpine flora of Kosciusko National Park, NSW, were examined from late December 1983 until the end of March 1984, including flowering phenology, corolla tube lengths, flower colour, ultraviolet reflectance patterns, visitation rates to the flowers and proboscis lengths of the flower-visiting insects. An average of 5.3 species flowered in each of 13, 2 m × 2 m montane plots and 5.6 species in the 13 alpine plots. The maximum number in flower simultaneously averaged 4.1 species in the montane and 3.3 in the alpine plots; flowering peaked in mid-January. Corolla tube lengths of the flora averaged 1.73 mm.

The most common floral colour was white or predominantly white (40 species), followed by yellow (14 species). Only six of the 38 species (16%) examined had some type of reflectance pattern; the remaining species all absorbed ultraviolet.

Flies appeared to be the major pollinators. The insects collected in the study area comprised 60 species of Diptera, 33 species of Hymenoptera, and several species each of Lepidoptera and Coleoptera. On average, 14.4% of flowers watched during 379 observation periods (10 min each) were visited. On average, each plant species was visited by 6.4 species of flies, 2.4 species of bees, wasps or sawflies, one species of butterfly or moth and 0.3 species of beetles. Visitation rates increased over the growing season, and were significantly affected by ambient tem-

perature (positively), light levels (positively) and wind speed (negatively).

The maximum proboscis length for the 25 most common species of bees was 2.76 mm, but 18 of 51 species of flies had proboscis lengths longer than this. The mean proboscis length for all 25 species of bees was 1.68 mm, and for 51 species of flies was 2.31 mm. Proboscis lengths for flies were positively correlated with the average corolla length for the plant species they visited. For bees, however, the range in proboscis lengths was relatively small and did not show this pattern.

There appear to be significant differences between the plant-pollinator community of alpine Australia and other alpine areas where bumblebees are common pollinators. These differences include shorter proboscis and corolla tube lengths, and perhaps an increased diversity and significance of flies as pollinators.

Introduction

There has recently been considerable interest in the pollination ecology of Australian plants, especially those pollinated by birds (e.g. Paton & Ford 1977; Ford *et al.* 1979; Keighery 1980; Whelan & Burbidge 1980; Pyke 1981, 1982; Pyke & Paton 1982) or mammals (e.g. Turner 1982; Wooller *et al.* 1983). Relatively little is known about the pollination of insect-pollinated species (see review of biotic pollination in Australia by Armstrong 1979), and no studies have dealt with alpine Australia or considered community-level aspects of flowering phenology. The aim of the present study was to carry out such a community-level study of the pollination biology of alpine plants in part of Kosciusko National Park in the Snowy Mountains of south-eastern New South Wales.

In studying the pollination biology of a number of co-occurring plant species there are many aspects that could be considered. We focused on the flowering phenology of each plant spe-

cies, the abundance and diversity of flowering throughout the growing season, the identities, proboscis lengths and visitation rates of flower-visiting insects, and corolla lengths and flower colours. Similar data have been collected for subalpine plant communities in the Colorado Rocky Mountains, USA, and alpine Chile, and we draw some comparisons between results of these studies and ours.

Study site and methods

The study was conducted between 21 December 1983 and 30 March 1984 in the Snowy Mountains, Kosciusko National Park, New South Wales ($36^{\circ}25'$; $148^{\circ}20'$), in the vicinity of Charlotte's Pass. Two sets of $2\text{ m} \times 2\text{ m}$ phenology plots, each marked with wooden stakes at the corners and delineated with string placed around nails in the wood stakes, were established on 22 and 23 December 1983. The plots were chosen before most flowering had begun, and were selected to represent most of the habitats available in the area. One set of 13 plots (1–13) was in the alpine zone, on the plateau north of Mt Stilwell and moving westwards down towards the Snowy River valley, at elevations ranging from 1940 to 2040 m. The other set of 11 plots (14–24), along Kangaroo Ridge, was in a montane habitat amongst snow gums (*Eucalyptus pauciflora niphophila*), ranging in elevation from 1860 to 1920 m. Two additional plots (25–26) were established in the same area in early January (2 and 4 January). Plots 1–13 are referred to as the alpine plots, and the remainder as the montane plots. A written and photographic description of the location of each plot is available from the authors.

Approximately every second day, flowers were counted in each of the phenology plots from 22 December to 12 March. The plots were checked again on 29 March, just after the first snowfall of the year.

Flowering phenologies for the montane and alpine plots were described and compared using the following indices: (i) total number of flowering species per plot; (ii) maximum number of simultaneously flowering species per plot; (iii) maximum number of flowers per plot; (iv) maximum flowering diversity, calculated using the formula: $H' = -\sum p_i \log p_i$ where H' is diversity and p_i is the proportion of total

flowers made up by plant species i ; (v) dates of maximum number of simultaneously flowering species, number of flowers, and flowering diversity per plot; and (vi) length of flowering period per plant species, calculated as the average for all plots in which a species occurred. In addition, the averages of number of flowers, number of flowering species and flowering diversity were compared for montane and alpine plots.

The Colorado phenology data presented below were obtained between 27 May and 12 September 1984, using 23 plots ($2\text{ m} \times 2\text{ m}$) in subalpine meadows (2800 m elevation) near the Rocky Mountain Biological Laboratory, Crested Butte, Colorado.

Flowers were collected, usually from seven different plants of each species, and the length of the corolla tube was measured using a vernier caliper to the nearest 0.01 mm. In most cases it was obvious where to measure the distance which must be reached in order to extract nectar; in only a few cases was it necessary to make more subjective measurements. A few flowers large enough for insects to crawl into, such as *Gentianella diemensis*, *Euphrasia collina*, *Prostanthera cuneata* and *Wahlenbergia ceracea*, were not measured because of the difficulty in deciding what was the critical distance. Open, flat flowers that presented a platform for pollinators and did not conceal nectar were also not measured (e.g. *Drosera arcturi*, *Epilobium* spp., *Kunzea mulleri*, *Neopaxia australasica*).

Most of the flower species that occurred in the phenology plots, and some others, were photographed in both visible and ultraviolet (UV) light to determine the frequency of UV reflectance patterns that might serve as nectar guides or other contrasting patterns to attract pollinators. Photographs were taken with a Pentax Spotmatic F or ME Super camera with an Asahi Pentax 85 mm ultra-achromatic fluorite-quartz lens, corrected for chromatic aberration from 220–1000 μm , using Kodak Tri-X or Plus-X black and white film. Flowers were picked, placed on the ground with a calibrated reflectance scale, and photographed with a series of filters that match the visual pigments of honeybees and bumblebees. Prints of the pictures taken with a UV filter that passes only UV light at 365 μm were used to look for evidence of reflectance patterns.

Data on insect visitation were collected in two ways. Incidental observations were made during phenological censuses of the flowers, and whenever the opportunity arose. Regular observations were made by a method developed by Arroyo *et al.* (1982) to facilitate comparisons among studies, which involves choosing a patch of flowers and watching it for 10 min, recording the number and species of flower visitors, and counting the total number of flowers being watched and the number visited by each insect. Between the 10 min intervals weather data were collected. Ambient temperature and relative humidity (Bacharach sling psychrometer; Bacharach Instruments, Pittsburgh, PA), wind speed (Simms hand-held anemometer; Simerl Instruments, Annapolis, MD), and light level (Sekonic light meter, model L-248) were recorded at, or close to, the level where insects were foraging. The effects of environmental variables on visitation rates were tested by calculating means for different categories (e.g. rates measured at low [$<10^{\circ}\text{C}$], medium [$10\text{--}15^{\circ}\text{C}$] and high [$>15^{\circ}\text{C}$] temperatures), and then comparing categories with a Kruskal-Wallis ANOVA or, for variables with only two categories, a Mann-Whitney U test.

Representative samples of each insect species were collected for identification. Voucher specimens were deposited in the collections at the Australian Museum. Proboscis lengths were measured on fresh specimens of most of the insects collected. The mouthparts were straightened out with a pair of forceps, and the length from the head to the distal end of the mouthparts was measured with vernier calipers to the nearest 0.01 mm.

Results

Flowering phenology

Flowering of several species (*Hovea purpurea*, *Epacris microphylla*, *Grevillea australis*, *Phebalium ovatifolium*, *Pimelea alpina* and *Ranunculus graniticola*) began before the phenology plots were established, but most flowering during the summer was recorded. Data from two plots are presented in Figs 1 and 2 (figures for other plots are available from the authors), and data for all 26 plots are summarized in Table 1.

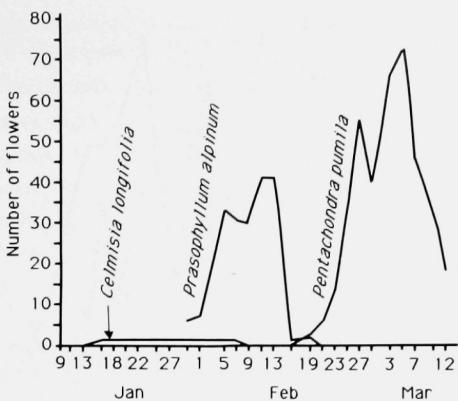


FIG. 1. Plot 1 (alpine) flowering phenology from 22 December 1983 to 12 March 1984. Dates on which flowers in the plot were counted are indicated.

There were no significant differences between means of montane and alpine plots for the total number of flowering species per plot or maximum number of simultaneously flowering species per plot, but the maximum number of flowers per plot did differ significantly (Table 2). The minimum number of species flowering per plot was the same for both areas (2), but the maximum of 9 for the montane plots was lower than that of 15 for the alpine plots. The range in number of flowers in a plot was higher in the montane plots (19–8501) than the alpine (68–5880); these differences appear to be due in large part to differences in the numbers of plots with *Epacris* species in them (plots covered almost entirely with these species produced thousands of flowers).

For each plot, the date with the maximum number of flowers is shown in Table 1. A disproportionate number of the dates occurred in the beginning of the flowering season; 11 of the 26 within the first three census dates (at the end of December), and 17 of them within the first seven dates (through 9 January). Graphs of the number of species in flower throughout the summer are similar for both areas (Fig. 3), indicating that the number of species in flower peaked about the middle of January, although the numbers were slightly higher for the alpine plots (Table 2). In individual plots, however, the number of species in flower sometimes peaked early, sometimes late, and was sometimes bimodal. Except for the fact that the two plots with the latest dates of peak flowering were both in the alpine set of plots, there was no

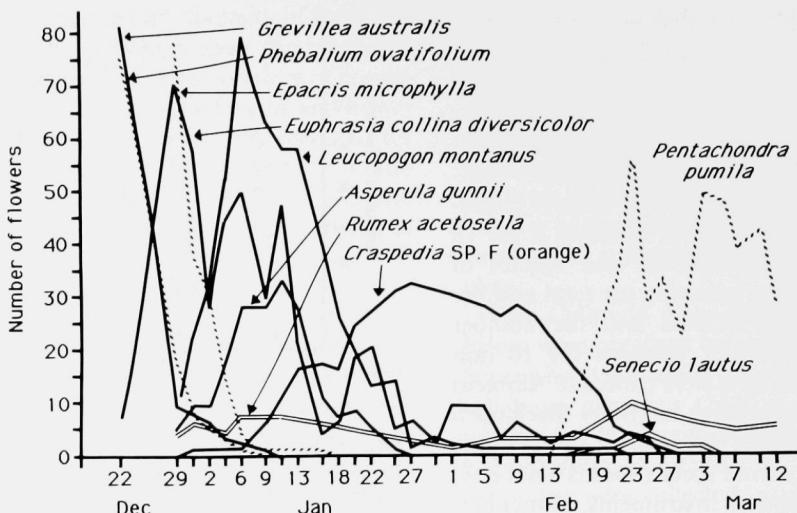


FIG. 2. Plot 12 (alpine) flowering phenology from 22 December 1983 to 12 March 1984. Dates on which flowers in the plot were counted are indicated.

particular trend for date of flowering with respect to habitat. Only two plots had their peak flowering after 9 February, both because of *Pentachondra pumila*. Peak flowering in the early part of the season can also be attributed to a few species, particularly *Phebalium ovatifolium* and *Epacris microphylla*. *Kunzea muelleri* was responsible for the peak flowering in three of the four mid-season peaks.

Data on the length of the flowering period were available for 41 species (Appendix 1); data were not available for species that started flowering substantially before the first census date. The length of the flowering period for individual species ranged from 4 (*Erigeron pappochromus*) to 63 days (*Leptorhynchus squamatus*), with a mean of 30 days (s.d. = 13, n = 41). The mean for native herbaceous plants (27 days, s.d. = 13, n = 26) was shorter than that for shrubs and sub-shrubs (34 days, s.d. = 9, n = 13), and the mean for the two weedy herbaceous species that occurred in the plots (*Hypochoeris radicata* and *Rumex acetosella*) was the longest (56 days, s.d. = 6).

To facilitate comparisons among the plots in our study, and with data from other studies, we calculated the diversity index H' for each date for each plot. The range of values of H' and the date of the maximum H' for each plot are shown in Table 1. Two plots never had more than one species in flower at a time so no diversity value could be calculated, and in two

plots overlap only occurred on a single date so only a single value could be calculated. The temporal distribution of maximum H' values was more even than that of peak flowering. Only three of the plots had maximum diversity values in the first three census dates, and eight during the first seven. Only three of the plots had their maximum values after 9 February, however.

Corolla lengths

Data on corolla tube lengths or shapes are shown in Appendix 1. Twelve species of flowers had no tube and are listed as 'open' flowers; they included a variety of taxa. No measurements were taken for six additional species that are entered by crawling into a large corolla tube ('crawl-in' flowers in Appendix 1). The mean

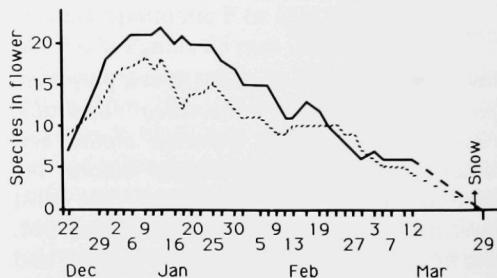


FIG. 3. The number of species in flower on each census date in 1983-84. Data for the alpine (—) and montane (---) plots are shown separately.

TABLE 1. Summary of flowering data from the phenology plots

Plot no.	Number of flowering species	Maximum number in flower simultaneously	Maximum number of flowers	Date of maximum flowers	Range of diversity indices	Date of maximum diversity
1	3	2	1448	5 Mar	0.06–0.18	30 Jan
2	3	3	131	29 Dec	0.14–0.43	9 Jan
3	2	1	5880*	29 Dec	0	
4	4	2	74	25 Feb	0.15–0.30	25 Jan
5	6	3	74	18 Jan	0.04–0.46	13 Jan
6†	4	2	2134	31 Dec	0.01–0.30	16 Jan
7	3	3	1034	11 Jan	0.01–0.34	11 Jan
8	3	2	68	30 Jan	0.03–0.24	29 Dec
9	11	5	84	16 Jan	0.26–0.62	29 Dec
10†	5	4	3607‡	29 Dec	0.13–0.33	25–27 Jan
11	6	4	1741†	22 Dec	0.06–0.50	31 Dec
12	15	11	2001‡	22 Dec	0.13–0.66	16 Feb
13	7	3	4978	4 Jan	0.02–0.32	18 Jan
14	7	4	325	6 Jan	0.05–0.43	2 Jan
15†	2	2	43	25 Jan	0.28	29 Dec
16	2	1	19	9 Feb	0	
17†	5	4	8501*	9 Jan	0.01–0.26	7 Feb
18	4	3	201	23 Dec	0.12–0.44	22 Jan
19	8	7	129	6 Jan	0.07–0.62	31 Dec
20	4	3	742	9 Jan	0.05–0.33	1 Feb
21	5	3	209	5 Feb	0.04–0.38	23–25 Feb
22†	6	2	100	23 Dec	0.09	23 Dec
23	5	3	387	13 Jan	0.05–0.31	2 Jan
24†	6	4	1819	29 Feb	0.07–0.40	4 Jan
25	6	3	1624*	29 Dec	0.03–0.34	9 Feb
26	9	4	63‡	4 Jan	0.09–0.56	13 Jan

*This was the first date that flowers were counted in this plot, and higher numbers may have occurred earlier.

†The number of flowers for one species was subsampled on one or more dates, and a total number for that species was estimated. This was done for two species of *Epacris* in plots where those species covered much of the plot.

‡*Celmisia longifolia* vegetation was in these plots, but no plants were flowering. Vegetation for *Ewartia nubigena* was seen in plots 6 and 7, *Richea continentis* vegetation was found in plots 8 and 9, and non-flowering *Craspedia* occurred in plot 8. These species were not included in the number of flowering species.

'Number of flowering species' includes species that were inferred to have flowered because fruits were found at some time during the summer. Plots 1–13 were located in alpine areas, and plots 14–26 were at slightly lower elevations amongst trees just below timberline. For counts of the number of flowers in a plot, capitulae (Asteraceae) and umbels (Apiaceae) were counted, rather than individual florets or flowers; in all other cases individual flowers were counted.

TABLE 2. Summary of comparisons of flowering in montane and alpine plots

	Australia				Colorado	
	Montane		Alpine		Montane	s.d.
	\bar{x}	s.d.	\bar{x}	s.d.	\bar{x}	s.d.
Total flowering species per plot	5.3	2.1	5.5	3.7	17.9	4.5
Maximum number of species flowering simultaneously	3.3	1.4	3.5	2.5	7.6	1.4
Maximum number of flowers per plot	1089.4	2304.1	1788.8	1948.6	363.9	340.4
Minimum number of species in a plot	2		2		8	
Maximum number of species in a plot	9		15		28	
Maximum number of flowers in a plot	8501		5880		1575	
Minimum number of flowers in a plot	19		68		88	

$n = 13$ for both areas in Australia and $n = 23$ for Colorado. The only significant difference (*t*-test) between the means for the two Australian sites was noted in the maximum number of flowers ($P < 0.001$), but all differences between the Colorado and Australian plots were highly significant ($P < 0.001$).

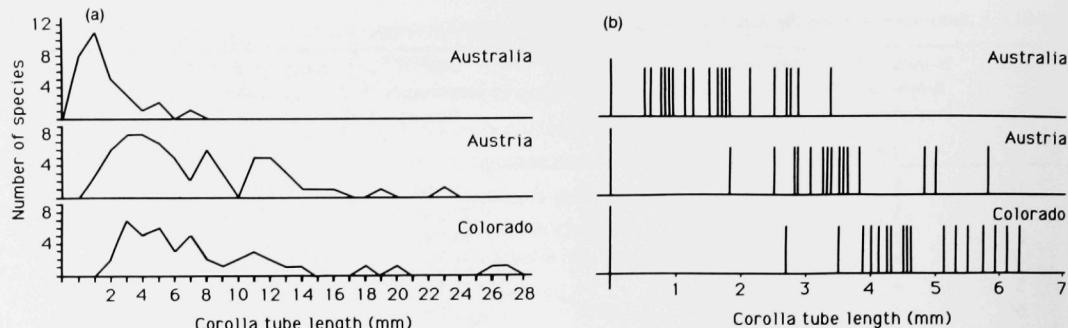


FIG. 4. (a) The frequency distribution of corolla tube lengths for all the flower species studied from the Snowy Mountains, Austria and Colorado. (b) The distribution of corolla tube lengths for Australian Asteraceae, compared with distributions from Austria and Colorado; each line represents a single species.

corolla length for those species that could be measured was 2.57 mm (s.d. = 1.85, n = 31); a frequency distribution of the corolla lengths of these species is shown in Fig. 4a. When 'open' flowers or those with no discernible tube are included as measurements of 0 length, the mean changes to 1.73 mm (s.d. = 1.94, n = 46). Statistics for flowers of just one family, Asteraceae, were also calculated; the mean was 1.70 mm (s.d. = 0.84, n = 18; Fig. 4b).

Flower colour

The most common flower colour was white, including all white (20 species), white petals with a yellow disk (10 species; e.g. *Brachycome* spp.) or conspicuous green ovary (two species; e.g. *Drosera arcturi*) or white petals with veins or spots of another colour (four species; e.g. *Euphrasia alsa*) (Appendix 1). Three additional species were primarily white, although with some other colour (e.g. *Geranium potentilloides*). The second most common pattern was yellow, including 12 all yellow species, and one with conspicuous green ovaries (*Astelia alpina*). Colours represented by a single species each were orange, orange and yellow, red, blue, pink-purple, and reddish-brown/green.

There was no significant difference between the corolla tube lengths of predominantly white and predominantly yellow flowers (mean = 1.89 and 1.54 mm, n = 20 and 12, respectively; 'open' and 'crawl-in' flowers were excluded from these calculations).

UV reflectance patterns

Most of the flowers appear to be strongly absorbing, or dark, in UV light, often in striking

contrast to their appearance in visible light (Appendix 1). Only six of the 38 species (16%) examined had any reflective parts on their flowers; four (three Asteraceae, one Ranunculaceae) of these had conspicuous patterns, and two (*Pimelea ligustrina* and *Oxylobium ellipticum*) had very small contrasting spots that might be considered nectar guides (Fig. 5). The reflectance pattern in one additional species (*Pentachondra pumila*) appears to change with flower age; older flowers are lighter in UV light than fresh flowers.

Flower visitors

Appendix 2 lists the variety of insect species that were collected from flowers in the study area; the small proportion that could be identified to species level reflects the lack of knowledge about these alpine insects. Thirty-two species of Hymenoptera were collected, including eight families (27 species) of bees, two species of wasps, and three species of sawflies (Pergidae). One bee species and the wasp species were collected flying around holes in the ground (presumably nest sites), but were never observed on flowers. The most commonly represented bee families were the Colletidae and Halictidae; the other five families were each represented by only a single species. One of these families, the Apidae, was only represented by the introduced honeybee, *Apis mellifera*. Neither wasp species was common, but one of the three species of sawfly was quite common. Sixty species of Diptera were collected, representing 23 families; an additional six species (approximately) were not identified. One of these 23 families (Rhagionidae), how-

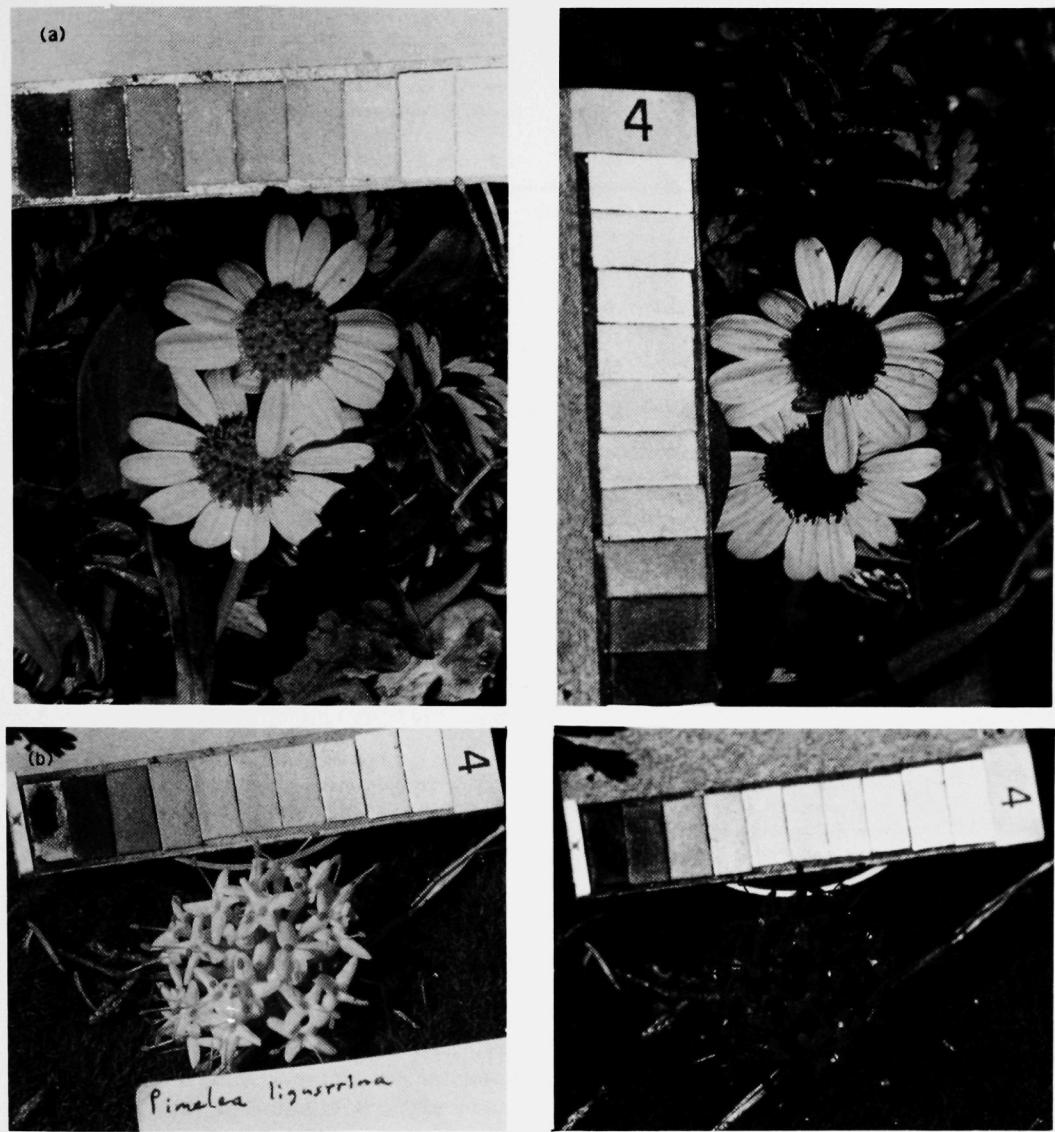


FIG. 5. Comparisons of two species in visible and UV light. The same reflectance scale is shown in each picture: (a) *Senecio lautus*; (b) *Pimelea ligustrina*.

ever, was represented only by a blood-feeding species that was not observed on flowers. Fifteen of these families were represented by a single species, and only four families (Calliphoridae, Muscidae, Empidae, Tachinidae) were represented by more than five species.

Only three species of Lepidoptera were identified (Appendix 2). Although one additional very small species of moth was relatively common, it was not identified. Several species of beetles were also observed on flowers, but they

were also not identified and are not included in most of the following results.

Data on the flower visitation of these insects are presented in Table 3. Although two species of bees visited 11 and 13 species of flowers, 11 species of bees were only recorded from a single flower species. One of the three sawfly species was recorded from 12 species of flowers, while the other two were only seen on one or two species of flowers. Of the 56 species of flies for which visitation data were recorded, one

TABLE 3. Summary of the plant species observed, visitation rates and flower visitors

Species	Observation periods	Flowers visited (%)		Percentage of flowers visited	Flowers visited	Fly species observed % of n flowers	Bee/wasp species % of n flowers	Lepidopteran species % of n flowers	Beetle species % of n flowers
		n	\bar{x}	s.d.	Range	n			
1 <i>Aciphylla glacialis</i>	10	15.1	22.2		0-57	264	7 26	2 74	3
2 <i>Asperula gunnii</i>	4	4.4	4.0		0-9	57	5 100		
3 <i>Baeckia gunniana</i>	15	13.0	13.8		0-46	238	15 92	1 8	
4 <i>Brachycome scapigera</i>	6	9.7	8.2		5-26	26	6 96	1	2 4
5 <i>Brachycome stolonifera</i>	9	6.4	8.6		0-26	14	7 93		1 7
6 <i>Celmisia longifolia</i>	9	56.6	35.9		11-121	71	13 77	6 10	5 7 2 6
7 <i>Craspedia</i> (orange sp. and yellow sp.)*	13	39.8	22.0		8-79	157	10 59	6 22	2 15 2 5
8 <i>Drosera arcturi</i>	5	0							
9 <i>Epacris glacialis</i>	2	2.2	0.3		0-1	1	1 100		
10 <i>Epacris microphylla</i>	6	4.2	5.3		0-13	105	6 93	2 7	
11 <i>Epacris paludosa</i>	6	0.2	0.4		0-1	2		1 100	†
12 <i>Epacris petrophila</i>	21	9.8	15.9		0-75	391	19 93	3 2	2 5
13 <i>Eplibium gunnianum</i>	6	11.6	9.5		0-22	27	3 67	2 38	
14 <i>Euphrasia alsa</i>	8	2.0	4.1			19		1 79	1 21
15 <i>Euphrasia collina diversicolor</i>	12	7.0	13.9		0-46	22	2 32	2 68	1
16 <i>Euphrasia collina glacialis</i>	5	0.7	1.5		0-3	1	1 100		
17 <i>Gentianella diemensis</i>	10	22.9	20.7		2-55	95	11 86	3 13	1 1
18 <i>Helichrysum alpinum</i>	7	15.5	9.6		0-26	271	8 54	1 6	2 39
19 <i>Helichrysum scorpioides</i>	7	31.0	33.5		4-94	113	5 46		4 54
20 <i>Helipterum albicans</i>	7	29.9	32.5		0-87	50	11 96	1 2	1 2
21 <i>Helipterum anthemoides</i>	1	14.3			14.3	4	4		1 100
22 <i>Hypochoeris radicata</i>	9	22.5	16.2		0-53	63	5 21	7 69	
23 <i>Kunzea muelleri</i>	11	20.4	16.5		0-41	201	1 1	5 99	
24 <i>Leptorhynchus squamatus</i>	12	11.9	16.2		0-46	79	4 91		3 9
25 <i>Leucopogon montanus</i>	8	6.5	5.7		0-15	103	10 77	3 23	
26 <i>Microseris lanceolata</i>	5	74.2	63.1		1-147	92	2 55	2 45	
27 <i>Neopaxia australasica</i>	4	23.1	28.1		0-61	24	7 100		
28 <i>Olearia phlogopappa subrepanda</i>	5	5.6	9.0		0-21	7	3 100		
29 <i>Orites lancifolia</i>	14	18.5	15.4		0-54	332	17 44	9 56	
30 <i>Oxylobium ellipticum</i>	16	6.1	10.6		0-33	80	1 15	5 85	

TABLE 3 continued.

31	<i>Pentachondra pumila</i>	12	3.2	7.2	0-25	61	7	97	1	3		
32	<i>Phebalium ovatifolium</i>	8	3.9	5.4	0-14	53	5	87	1	2		1
33	<i>Pimelea ligustrina</i>	6	3.2	4.4		98	3	19	1	81‡		
34	<i>Prasophyllum alpinum</i>	2	0									
35	<i>Prostanthera cuneata</i>	25	12.3	12.1	0-33	228	16	43	8	53	1	2
36	<i>Richea continentis</i>	12	5.7	8.3	0-20	162	6	20	1	80		
37	<i>Senecio gunnii</i>	10	18.3	18.4	0-50	117	6	96				1
38	<i>Senecio lautus</i>	20	20.8	11.9	0-40	191	14	63	2	6	10	31
39	<i>Senecio pectinatus</i>	6	29.1	34.6	0-80	17	4	47	1	24	1	29
40	<i>Stackhousia pulvinaris</i>	5	0.7	1.6	0-4	8	2	100				
41	<i>Stylidium graminifolium</i>	8	1.6	2.2	0-5	9			5	78	1	22§
42	<i>Viola betonicifolia</i>	1	0									
43	<i>Wahlenbergia ceracea</i>	11	35.7	33.91	0-127	116	9	43	7	57		

*Data for both colours were lumped.

†Flowers were commonly visited by *Agrostis infusa* at night.

‡*Apis mellifera*. One individual of *Zosterops lateralis* (grey-breasted white-eye) was also observed visiting flowers on one occasion.

§The butterfly was not triggering the flowers.

Visitation rates are calculated as the percentage of flowers that were visited during a 10 min observation period. The total number of flowers visited during all observation periods is shown, as are the number of fly, bee or wasp, lepidopteran, and beetle species observed visiting flowers, and the proportion of flowers visited by each of these groups. The number of flower-visiting species includes 42 sightings in addition to those made during regular observations, so some of the numbers of species observed do not have an associated value for percentage of flowers.

visited 22 species of flowers, but 23 were only recorded from a single species of flower, and 14 were only seen on two species of flowers. One species of butterfly (*Oreixenica orichora*) visited 10 species of flowers, but two species of moths were only recorded on a single flower species each.

Visitation rates

Visitation rates were quantified by 379 observation periods of 10 min duration made on a total of 43 flower species (Table 3). The average rate of visitation was 14.4 (s.e.m. = 15.6) (i.e. 14.4% of the flowers being observed were visited during a 10 min period; these values can be converted to the units of visits per flower per min used in some other studies (e.g. Arroyo *et al.* 1985), by dividing by 1000, with a range of 0-74.2. Only seven flower species were visited during every observation period, and only three

species were never observed to be visited (two of these were only observed for one or two 10 min periods). Nineteen species had rates less than 10, and only two species had rates higher than 50. When these flower visits are broken down by visitor type, 62.3% were found to have been visited by flies, 30.8% by Hymenoptera, 11.2% by (diurnal) Lepidoptera and 1.9% by beetles (Table 4). On average, each species of flower was visited by 6.4 species of flies, 2.4 species of Hymenoptera, 1.0 lepidopteran species and 0.3 species of beetle (Table 4).

There was no significant correlation between mean corolla tube length and mean visitation rate ($n = 37$, $r = -0.284$, $P > 0.05$). There was a significant difference in visitation rate between species that began flowering (in any plot) before 7 January ($n = 20$, $\bar{x} = 12.04$, s.d. = 14.95) and those that began after 7 February ($n = 5$, $\bar{x} = 18.18$, s.d. = 10.54; t -test, $P < 0.01$). A phenological difference in visitation rate was also indicated by comparisons of all visitation rates

TABLE 4. Summary of flower visitation by different taxa

	Mean	s.d.	n
Number of Diptera species per flower species	6.4	5.0	40
Number of Hymenoptera species per flower species	2.4	2.5	40
Number of lepidopteran species per flower species	1.0	1.9	40
Number of coleopteran species per flower species	0.3	0.7	40
Percentage of flower visits made by Diptera	62.3	34.9	39
Percentage of flower visits made by Hymenoptera	30.8	35.0	39
Percentage of flower visits made by Lepidoptera	11.2	24.8	36
Percentage of flower visits made by Coleoptera	1.9	6.5	39

In a few cases flower species were not observed for percentage-visitation, but notes were made about what taxa of visitors were on the flowers, so sample sizes for the two indices differ.

measured in December or January ($\bar{x} = 12.11$) with those measured in February or March ($\bar{x} = 20.25$) (Table 5).

The effects of environmental variables on visitation rates were also significant (Table 5).

TABLE 5. Summary of the effects of environmental variables on visitation rates

Temperature	<10°C	10–15°C	>15°C
mean	5.28	13.6	16.68
s.d.	8.07	16.79	24.07
n	19	103	255
Wind speed	<2.5 m/s	2.5–3.0 m/s	>3.0 m/s
mean	18.02	16.44	11.09
s.d.	22.29	27.69	17.16
n	177	65	135
Light level	0–15.25	>15.25	
mean	11.41	18.13	
s.d.	17.43	24.31	
n	161	216	
Date	Dec-Jan	Feb-Mar	
mean	12.11	20.25	
s.d.	19.11	24.90	
n	231	146	

Differences among temperature classes are significant (Kruskal-Wallis statistic = 6.32, $P = 0.042$), as are those among classes of wind speed (Kruskal-Wallis statistic = 16.71, $P < 0.001$). Differences between classes of light level (Mann-Whitney U, $P = 0.001$) and date (Mann-Whitney U, $P < 0.001$) were also significant. Light levels are given as Sekonic light meter units; 15.25 units is equivalent to approximately 40 225 lux (3738 foot-candles).

When visitation rates were split among three classes of ambient temperature, rates increased with increasing temperature: <10°C (5.28), 10°–15°C (13.6) and >15°C (16.68). Visitation rates declined with three categories of increasing wind speed: <2.5 knots (18.02), 2.5–3.0 knots (16.44), and >3.0 knots (11.09). Visitation rates increased with two categories of light level: 0–40,190 lux (11.41) and >40,190 lux (18.13).

Proboscis lengths

Proboscis lengths for 28 species of Hymenoptera are reported in Appendix 2; for five species for which sufficient data were available separate means are shown for each sex. Data for 51 species of Diptera are also reported in the same table. The mean proboscis length for 25 bee species (not including the introduced honeybee [*Apis*] or the one individual of *Megachile*) was 1.68 mm, and for 51 fly species, 2.31 mm. When the additional five species of Hymenoptera (sawflies and wasps) were included with the bees, the mean changed only slightly, to 1.59 mm. Only two species of Hymenoptera, the introduced honeybee and the only individual of *Megachile* sp. observed during the study, had proboscis lengths over 5 mm. All the other species of bees had proboscis lengths under 3 mm (the longest was 2.76 mm, *Lasioglossum* sp., sp. 3). In contrast, two species of flies had proboscis lengths over 5 mm, and 18 species had means longer than 2.76 mm.

Correlations between proboscis lengths of flower visitors and the corolla tube lengths of the flowers they visited were also calculated. The correlation between proboscis length of 35 species of Diptera (species for which there were at least two measurements) and the mean corolla length of flowers they visited were calculated in two ways, with and without measurements of 0 mm (for 'open' corollas or 'crawl-in' flowers) included. In both cases the correlation coefficient was significant ($P < 0.01$); when only flowers with measurable corolla tubes were included, the equation was $y = 0.875 + 0.616x$, $n = 26$, $r = 0.669$, and when flowers of 0 length were included, the equation became $y = -0.003 + 0.534x$, $n = 35$, $r = 0.592$. Similar correlations were calculated for the Hymenoptera (excluding *Apis mellifera*), but neither correlation was significant ($P > 0.05$).

Discussion

Flowering phenology

The density of flowers of different species is unlikely to vary synchronously among years, since each species is likely to respond to different environmental parameters or to respond to the same parameters differently. For example, if some species preform flower buds, while others do not, favourable growing conditions might be reflected in the same year by increased flowering of some species, and in future years by other species. Similarly, a late frost or low snowpack the previous winter can also affect flower production differentially (Inouye 1987 unpubl. obs.). The 1983–84 season in the Snowy Mountains was particularly poor for flowering by *Celmisia longifolia*, which is 'one of the most important and abundant plants in the alpine flora' (Costin *et al.* 1979). Although it was present vegetatively in many plots, it flowered (sparsely) in only three of them. However, it appeared to be a good year for flowering by most of the Epacridaceae. Despite the likelihood that flower production in the phenology plots will vary from year to year, the temporal sequence of flowering is probably much more constant. In an analogous study of phenology in the Colorado Rocky Mountains, flowering order was found to be quite constant, despite substantial differences in the actual date of flowering and flower abundance (Inouye unpubl. obs.).

The species abundance and diversity (H') of flowering in the alpine and montane plots in Australia were significantly lower than those for a similar series of montane plots in the Colorado Rocky Mountains. In the 21 Colorado plots, in 1984, the range in total number of flowering species was 10–28, with a mean of 17.9; in contrast, only two of the 26 Australian plots had more than 10 species (Table 1). The same relationship holds for the number of species simultaneously in flower. In Colorado, the maximum number of species in flower ranged from 5 to 11 ($\bar{x} = 7.6$); only two Australian plots had more than five species in flower simultaneously ($\bar{x} = 3.3$). Correspondingly, the maximum H' for the Colorado plots was 0.55, and only four of the Australian plots had maxima that exceeded 0.55. The maximum number of flowers, however, was

greater in nine of the Australian plots than in any of the Colorado plots; in seven of these the large numbers were from flowering by *Epacris* species.

Corolla lengths

The distribution of corolla tube lengths in a flora is likely to reflect the morphologies of the mouthparts of the pollinators. Thus, given the absence of any long-tongued bees or long-billed birds in the Australian alpine region, it was not surprising to find that the corolla tube lengths are shorter than those of other areas of the world where such long-tongued pollinators occur (e.g. Inouye 1979). The mean for Australia (2.57 mm) is significantly shorter than those for Colorado (7.7 mm, s.d. = 3.7 mm; $n = 41$; $P < 0.001$, Mann-Whitney U) or Austria (8.6 and 9.5 mm in two different sites, s.d. = 4.5 and 4.9, $n = 36$ and 30; $P < 0.001$, Mann-Whitney U; Inouye 1979) (Fig. 4a). When data for just the Asteraceae are compared, the mean for Australia (1.70 mm, s.d. = 0.84, $n = 18$) is still significantly shorter than those for the other sites (Colorado = 4.77 mm, s.d. = 1.02, $n = 16$; Austria = 3.65 mm, s.d. = 1.22, $n = 13$; $P < 0.001$, Mann-Whitney U) (Fig. 4b). These differences in corolla length correspond to differences in insect proboscis length between the sites (see below). Flowers of the Australian Asteraceae also appear to be somewhat more variable within a species than are those from Austria or Colorado; the average coefficient of variations are 10.86 ($n = 20$), 8.75 ($n = 15$), and 6.45 ($n = 15$), respectively.

Flower colour

White flowers are typically associated with visitation by nocturnal pollinators such as moths (Scogin 1983) or perhaps with fly visitation (Kevan 1983). Most Diptera that visit flowers are considered to be unspecialized anthophiles, and are thought to be attracted to yellow flowers, although there may be a special relationship between blue flowers in Europe and bombyliid flies (Kevan 1983). Thus the predominant flower colours found in alpine Australia, white and yellow, are perhaps what one would have expected for a flower-visiting

fauna that is comprised largely of flies. There does not appear to be much evidence for a seasonal progression of colour in the flowering plants, which has been suggested for some communities (Kevan 1983); although there is a bias towards late flowering for yellow species, white-flowered species are distributed across the flowering season.

UV reflectance patterns

As Kevan (1983) pointed out, there is a tendency to collect data on UV reflection patterns *in vacuo*, although there is a variety of interesting questions that can be asked about the biogeographical distribution, taxonomic distribution and function of such patterns. The first step towards answering such questions is necessarily documentation of the patterns in a community. Only a few studies have quantified the proportion of a flora that has UV reflectance patterns. Kevan (1972) determined the spectral reflection curves for 73 species from the Canadian Arctic, and found that 13.7% reflected UV. He found that white flowers reflected little or no UV. One of the white flowers in our study, *Pimelea ligustrina*, appeared to have a tiny reflective spot at the entrance to the corolla tube, that might represent a nectar guide. Kevan also found that yellow flowers never reflected UV over their entire surface. This was also true for the Kosciusko flora. The five species besides *P. ligustrina* that reflected UV were all yellow or yellow-orange, and none reflected UV from all parts of their flowers.

Guldberg and Atsatt (1975) found that 33% of 300 species of flowers representing 61 families showed some reflection pattern. Of the 183 species that were California natives, 27% reflected some UV. These figures were in agreement with those reported from earlier studies in Europe, America and Russia (cited in Guldberg & Atsatt 1975). In contrast, Utech and Kawano (1975) found that 32 of 52 species (62%) showed reflection patterns in the perianth and/or stamens. Most of their species were native Japanese plants, while the remainder were weeds, cultivated species or introduced from North America. Thus the proportion of the Kosciusko flora with UV reflectance patterns appears to be low, as does that from the Canadian Arctic (Kevan 1972). As Kevan (1983) noted, 'more data are needed from entire

regional floras' in order to explore the significance of these figures. Additional data on the visual pigments of flower-visiting flies would also aid interpretation of these patterns.

Flower visitors

Armstrong (1979), in a review of biotic pollination mechanisms in the Australian flora, listed 44 families of Diptera as flower-visitors. We observed 18 of these families in our study sites, and in addition saw five others, adding two new superfamilies to his list. We observed species from four of the five families of Australian bees (all but the Apidae). Although most of the Colletidae are oligolectic on Myrtaceae (Armstrong 1979), only one of the species we observed (*Leioproctus* sp., plot 1 females) was found predominantly on Myrtaceae (*Kunzea muelleri*); however only two species of Myrtaceae occurred in our study area. None of the common bee species appeared to be oligolectic.

Relatively few community-level studies have been made of alpine pollination, and apparently none has been conducted previously in Australia. Arroyo *et al.* (1982) studied 137 species of zoophilous plants in the alpine of the Chilean Andes. Over the range in elevation from 2200 to 3600 m (substantially higher than our study sites), they found that the most important pollinators were Hymenoptera (50% of the flora), Diptera (46%), and Lepidoptera (butterflies; 24%). However, within this range the significance of bees as pollinators decreased with increasing altitude, and the proportion of fly-pollinated species increased; almost 70% of the zoophilous flora was pollinated by flies at the highest elevation, although the abundance of the fly species also decreased with elevation. Moldenke and Lincoln (1979), in a study of alpine pollination in Colorado, found the largest proportion of the zoophilous flora (29 species, 31%) to be bumblebee-visited, with another 29 species (31%) visited by solitary bees. It is difficult to summarize their taxonomic data by pollinator order, since they have broken lists down to family and do not provide information on overlap among flower species, but flies were apparently the next most important group (28 species, 31%; only syrphid and muscoid flies included). McCall (1986) found that the visitation rates to flowers (measured the same way as our study) were highest

for flies in a study of alpine New Hampshire (Mt Washington).

Primack (1978, 1983) studied montane and alpine pollinator assemblages in New Zealand, which resembles alpine Australia in not having native social bees, and also in having some of the same plant genera as our study sites. He did not provide quantitative data on a community level, but found some of the same genera of halictid and colletid bees, and found a variety of syrphid, calliphorid, tachinid (the most common family), and other less common flies (e.g. Tabanidae, Asilidae, Bibionidae, Empidae, Stratiomyidae, Dolichopodidae and Cyrtidae). Dipterans were the most abundant flower visitors, comprising 50–80% of the total flower visitors in two sites (Primack 1983).

One point of interest in our study was the co-occurrence of several very similar species of bees. In fact, individuals listed as one species in our field observations were later determined to be a group of several similar species (e.g. *Lasioglossum*). Thus the rarity of some species indicated in Appendix 2 probably reflects in part a lack of collecting on our part, rather than a real rarity of those species. This complication prevented us from using some of the observational data in our analyses.

Visitation rates

The correlation of visitation rate and environmental variables observed was not unexpected; given that only one or two of the fly species can thermoregulate (*Scaptia maculiventris* and *Tabanus froggatti*, Tabanidae; Inouye unpubl. data), it is not surprising that visitation rates increase with temperature, as well as with light level (Table 5). It is also obvious that the activity of relatively small insects is likely to be restricted by high winds, and visitation rates were negatively correlated with wind speed (Table 5). There are only a few other studies which quantitatively relate visitation rates to environmental variables. Arroyo *et al.* (1982) and McCall (1986) studied sites in alpine Chile, mediterranean scrub in South Africa, alpine New Hampshire, and woodland-meadow in Massachusetts, using the same technique adopted in this study. In her study of alpine New Hampshire (Mt Washington), McCall (1986) also found significant differences in visitation rates, and patterns similar to those

we found, at different temperatures, at different times of the growing season, and light levels; however, there was lower insect activity during moderate winds than at higher or lower levels. The visitation rates McCall found on Mt Washington were about the same as those we observed at low temperatures (6.5 at temperatures <10°C), but were about twice as high as ours at the other ranges (26.1 at 10–15°C, 27.5 at 15–25°C; compare with data in Table 5).

Arroyo *et al.* (1985), in a study of the high Andes of central Chile, found that the average visitation rate decreased with increasing elevation (from 6.1 to 3.65 to 1.64 at their three levels of altitude). Mean visitation rate peaked in mid-late summer at all elevations, and was greatest at ambient temperatures which matched the most common temperatures at each elevation. In general, the rates they measured appear to be significantly lower than those we found.

Proboscis lengths

The proboscis lengths of the flower visitors in alpine Australia were significantly shorter than those of flower visitors in most other alpine areas in the world (although they are probably quite similar to those in New Zealand, judging by the list of insects in Primack [1983]). For example, European bumblebees have proboscis lengths up to 18 mm long, and those of North American bumblebees are up to 13 mm (Inouye 1977). Although we did not measure the proboscis lengths of the few common species of Lepidoptera in our study site, which may be as long as those of Lepidoptera in other alpine areas, the overall mean for Australian alpine flower visitors would certainly be shorter than that for Europe or North America.

Studies in other floral communities have found a general correspondence between the proboscis length of flower-visiting insects and the corolla tube lengths of the flowers that they visit (e.g. Inouye 1978, 1980). Inspection of our data reveals that such a correlation exists for the Diptera, but not for the Hymenoptera. This may reflect in part the relatively small range of proboscis lengths of the Hymenoptera (0.9–2.45 mm) compared with the Diptera (0.55–5.37 mm), and the fact that some Hymenoptera may visit flowers for pollen, and not nectar (although data for *Richea continentis*, which

did not appear to be visited for nectar by any species, were not included in the correlation). There did not appear to be any incidents of nectar-robbing (Inouye 1983), a behaviour by which flower-visitors might circumvent morphological constraints on nectar collection by a mismatch between corolla tube length and proboscis length. There was, however, one species of fly (*Comptosia sylvana*?) that appeared to be feeding from flowers of *Aciphylla glacialis* and *Leucopogon montanus* by placing its legs into them and then cleaning nectar from its legs with its mouthparts; a similar feeding method was recently described for a tropical bee species (Vogel & Michener 1985).

In conclusion, our study indicates that there are probably major differences in the plant-pollinator community of alpine Australia, compared with other parts of the world, where (with the exception of New Zealand) bumblebees are very common pollinators. These differences are reflected in the shorter proboscis and corolla tube lengths, and perhaps in the diversity and significance of flies as pollinators. The alpine flora appears to be significantly less diverse in Australia than in Colorado, although it is not possible to make detailed comparisons with other areas yet. This type of community-level analysis should provide additional insight into plant-pollinator communities as additional comparative data become available.

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APPENDIX 1. Summary of the plant species in the phenology plots

For flower colour, if flowers had two contrasting colours, such as a sunflower with ray petals of one colour and a disk of another, or a contrasting conspicuous ovary, then the second (central) colour is shown in parentheses. A blank entry indicates that data were not recorded for that species. NA = not applicable (e.g. no standard deviation could be calculated because sample size was 1). Taxonomy follows Costin *et al.* (1979).

Species	Corolla length (mm)		Flower colour	UV reflection	Length of flowering period		
	s.d.	n			\bar{x}	s.d.	n
1 <i>Aciphylla glacialis</i> (F. Muell.) Benth.			Open	White	36	3	2
2 <i>Asperula gunnii</i> Hook. f.	1.36	0.31	21	White	25	5	2
3 <i>Astelia alpina</i> R. Br.				Yellow (green)	27	17	2
4 <i>Baeckia gunniana</i> Schau.			Open	White (green)	37	10	2
5 <i>Brachycome nivalis</i> F. Muell.	2.2	0.1	5	White (yellow)			
6 <i>Brachycome obovata</i> G.L. Davis	1.80	0.14	20	White (yellow)	31	NA	1
7 <i>Brachycome scapiformis</i> (<i>Brachycome</i> sp. of Costin <i>et al.</i>)					23	12	2
8 <i>Brachycome scapigera</i> (Sieb. ex Spreng.) DC.	2.14	0.24	35	White (yellow)			
9 <i>Brachycome stolonifera</i> G.L. Davis	1.61	0.13	35	White (yellow)	Dark	24	5
10 <i>Caladenia lyallii</i> Hook. f.			Crawl-in?	White	Dark	15	NA
11 <i>Caltha introloba</i> F. Muell.			Open	White (yellow)	Dark		
12 <i>Celmisia longifolia</i> Cass.	2.75	0.27	35	White (yellow)	Dark	34	16
13 <i>Craspedia</i> *							
Orange sp.	0.80	0.09	35	Orange	Dark	40	14
Yellow sp.	0.90	0.15	35	Yellow	Dark		
14 <i>Drosera arcturi</i> Hook.			Open	White (green)	Dark	13	1
15 <i>Epacris glacialis</i> (F. Muell.)	3.97	0.36	35	White	Dark	29	4
16 <i>Epacris microphylla</i> R. Br.	1.90	0.20	25	White		34	6
17 <i>Epacris paludosa</i> R. Br.	6.35	0.70	35	White		31	NA
18 <i>Epacris petrophila</i> Hook. f.	2.30	0.45	35	White	Dark	44	2

APPENDIX 1. continued

19 <i>Epilobium gunnianum</i> Hausskn.		Open	White	Dark				
20 <i>Epilobium tasmanicum</i> Hausskn.		Open	White	Dark				
21 <i>Erigeron pappocromus</i> Labill.	1.72	0.36	41	White (yellow)		4	1	
22 <i>Euphrasia alsa</i> F. Muell.		Crawl-in(?)	White (violet veins)	Dark			2	
23 <i>Euphrasia collina</i> R. Br. <i>diversicolor</i> Barker (ined.)		Crawl-in	White and violet		25	5	4	
24 <i>Euphrasia collina</i> R. Br. <i>glacialis</i> (Wettst.) Barker (ined.)		Crawl-in	White		42	NA	1	
25 <i>Ewartia nubigena</i> (F. Muell.) Beauverd	0.84	0.07	13	White		12	NA	1
26 <i>Gentianella diemensis</i> (Griseb.) J. H. Willis		Open	White (purple veins)		24	18	3	
27 <i>Geranium potentilloides</i> L'Her. ex DC.			White/pink	Dark				
28 <i>Helichrysum alpinum</i> N. Wakef.	0.46	0.10	35	White	Dark			
29 <i>Helichrysum scorpioides</i> Labill.	1.84	0.27	35	Yellow	Dark	16	1	2
30 <i>Helipterum albicans</i> (A. Cunn.) DC.	1.52	0.14	70	White (yellow)	Dark	42	NA	1
31 <i>Helipterum anthemoides</i> (Sieb. ex Spreng) DC.	1.73	0.12	26	White (yellow)	Dark			
32 <i>Hypochoeris radicata</i> L.		No tube	Yellow	Dark disk, lighter rays	52	NA	1	
33 <i>Kunzea muelleri</i> Benth.		Open	Yellow	Dark	26	11	9	
34 <i>Leptorhynchos squamatus</i> (Labill.) Less.	1.2	0.15	35	Yellow	Dark	63	NA	1
35 <i>Leucopogon montanus</i> (R. Br.) J. H. Willis	1.85	0.19	35	White		45	14	3
36 <i>Microseris lanceolata</i> (Walp.) Sch.-Bip.		No tube	Yellow					
37 <i>Neopaxia australasica</i> (Hook. f.) O. Nilss.		Open	White	Dark				
38 <i>Olearia phlogopappa</i> (Labill.) DC.	2.48	0.17	21	White (yellow)	Dark			
39 <i>Orites lancifolia</i> F. Muell.		No tube(?)	Yellow		29	1	2	
40 <i>Oxylobium ellipticum</i> (Labill.) R. Br.	3.70	0.29	13	Orange and yellow	Light, dark guide	22	10	5
41 <i>Parantennaria uniceps</i> (F. Muell.) Beauverd	0.77	0.08	15	White		27	NA	1
42 <i>Pentachondra pumila</i> (J. R. et G. Forst.) R. Br.	5.32	0.43	35	White	Dark; old flowers lighter	41	14	5
43 <i>Phebalium ovatifolium</i> F. Muell.		Open	White					
44 <i>Pimelea alpina</i> F. Muell. ex Meissn.	4.17	0.56	32	White	Dark	17	4	2
45 <i>Pimelea ligustrina</i> Labill.	8.49	0.99	34	White	Dark, possibly a light nectar guide	45	NA	1
46 <i>Prasophyllum alpinum</i> R. Br.			Reddish-brown and green		22	1	2	
47 <i>Prasophyllum suttonii</i> Rogers et Rees			White (mauve lip)	Dark				
48 <i>Prostanthera cuneata</i> Benth.		Crawl-in	White (orange and violet spots)	Dark	39	12	6	
49 <i>Ranunculus anemoneus</i> F. Muell.		Open	White (yellow)	Dark				
50 <i>Ranunculus graniticola</i> Melville		Open	Yellow	Dark centre, light petals				
51 <i>Richea continentis</i> B. L. Burtt		No nectar(?)	White		16	NA	1	
52 <i>Rumex acetosa</i> L.			Red		60	33	4	
53 <i>Senecio gunni</i> (Hook. f.) Belcher	0.56	0.08	35	Yellow	Dark	53	NA	1
54 <i>Senecio lautus</i> Forst. f. ex Willd.	2.85	0.42	35	Yellow	Dark disk, light rays	16	4	3
55 <i>Senecio pectinatus</i> DC.	3.38	0.27	35	Yellow	Dark disk, light rays	21	NA	1
56 <i>Stackhousia pulvinaris</i> F. Muell.	5.58	0.38	30	Yellow	Dark	25	0	2
57 <i>Stylium graminifolium</i> Swartz ex Willd.			Pink-purple	Dark				
58 <i>Viola betonicifolia</i> Sm.	3.00	0.40	6	White and violet	Dark			
59 <i>Wahlenbergia ceracea</i> Lothian		Crawl-in	Blue	Dark				

Data for the following species were not collected, but numbers are needed for use in Appendix 2.

60 *Achillea millefolium*

61 *Aciphylla simplicifolia* (F. Muell.)

62 *Brachycome* sp.

*Data for both colours (species) of *Craspedia* were lumped.

APPENDIX 2. Summary of data for the insect species collected or observed visiting flowers

Numbers of the flower species correspond to the species numbers in Table 3; if more than one individual visitor was collected from a flower species the number is shown in parentheses after the flower species code. Taxonomy for the Diptera (family level and above) follows the Catalog of Nearctic Diptera (Research Branch, Agriculture, Canada, 1981). Species names were provided by the taxonomists cited in the Acknowledgments.

Species	Number collected	Proboscis length (mm)		Date of first and last collection or observation	Flower species visited			
		\bar{x}	s.d.					
ORDER HYMENOPTERA								
Superfamily Apoidea								
Family Anthophoridae								
1 <i>Exoneura</i> (<i>Exoneura</i>) sp. (all females)	7	2.45	0.29	5 30 Dec–5 Mar	12(2), 19, 39(7), 40, 48(38), 54(2)			
2 <i>Exoneura</i> (<i>Exoneura</i>) sp. (male)	1	2.16		19 Jan	39			
Family Apidae								
3 <i>Apis mellifera</i>	3	5.50	0.57	2 18 Jan–20 Jan	45(3)			
Family Colletidae								
4 <i>Euryglossa</i> (<i>Euhesma</i>) sp. 1 (all females)	4	0.9	0.07	4 9 Jan–6 Feb	40(2), 48			
5 <i>Euryglossa</i> (<i>Euhesma</i>) sp. 2 (all females)	2	1.10	(n = 1)	5 Jan–9 Jan	39, 40			
6 <i>Euryglossa</i> (<i>Callohesma</i>) sp. (female)	1	0.70		5 Mar	60			
7 <i>Hylaeus</i> (<i>Prosopisteron</i>) <i>semipersonatus</i> (female)	1	1.36		13 Feb	36			
8 <i>Hylaeus</i> (<i>Prosopisteron</i>) species (female)	1	1.44		16 Feb	4			
9 <i>Hylaeus</i> (<i>Pseudohylaeus</i>) sp. 1	8	0.19	0.11	7 19 Jan–6 Feb	By holes in ground			
10 <i>Hyphesma</i> sp. (female)	1	?		5 Jan	39			
11 <i>Leioproctus</i> (<i>Leioproctus</i>) sp. 1 (all females)	22	2.05	0.16	19 5 Jan–6 Feb	13(3), 18, 32(12), 33(185), 36, 39(43), 40(3), 48(12), 51(12), 54, 59(28)			
12 <i>Leioproctus</i> (<i>Leioproctus</i>) (presumed male of above species)	24	1.87	0.11	24 9 Jan–5 Mar	13, 36, 48, 54, 59			
13 <i>Leioproctus</i> (<i>Leioproctus</i>) sp. 2 (male)	1	1.42		6 Feb	36			
14 <i>Leioproctus</i> (<i>Leioproctus</i>) sp. 3 (all females)	3	2.09	0.17	3 30 Dec–3 Jan	39(2), 43			
15 <i>Leioproctus</i> possibly male of sp. 3	1	1.62		19 Jan	39			
Family Halictidae								
16 <i>Lasioglossum</i> (<i>Austrevylaeus</i>) sp. (all females)	8	1.60	0.08	7 23 Dec–5 Mar	13, 23, 26, 32(2), 36, 54, 59			
17 <i>Lasioglossum</i> (<i>Chilalictus</i>) sp. 1 (all males)	6	1.21	0.11	6 5 Mar	60(6)			
18 <i>Lasioglossum</i> (<i>?Chilalictus</i>) sp. 2 (all females)	3	1.98	0.11	3 3 Jan–25 Mar	26, 40(2)			
19 <i>Lasioglossum</i> (<i>Chilalictus</i>) sp. 3 (all females)	2	2.02	0.20	2 30 Dec–4 Jan	39, 48			
20 <i>Lasioglossum</i> (<i>Chilalictus</i>) sp. 4 (all females)	3	2.35	0.06	3 5 Jan–14 Feb	13, 57, 59			
21 <i>Lasioglossum</i> (<i>Chilalictus</i>) sp. 5 (all females)	21	1.35	0.12	19 29 Dec–5 Mar	12(4), 13(6), 18(4), 23(6), 32(51), 33, 35, 36(2), 39(2), 40(12), 48(12), 59(8), 60(3)			
22 <i>Lasioglossum</i> (<i>Chilalictus</i>) sp. 6 (female)	1	1.86		9 Jan	40			
23 <i>Lasioglossum</i> (<i>Parasphecodes</i>) sp. 1 (all females)	6	2.15	0.10	5 29 Dec–25 Feb	12, 13, 32(2), 40, 48(2)			
24 <i>Lasioglossum</i> (<i>Parasphecodes</i>) sp. 1 (all males)	3	2.01	0.10	3 23 Feb–5 May	32(2), 54			
25 <i>Lasioglossum</i> (<i>Parasphecodes</i>) sp. 2 (all males)	5	1.76	0.06	5 5 Mar	26, 60(4)			
26 <i>Lasioglossum</i> (<i>Parasphecodes</i>) sp. 2 (female)	1	1.56		5 Mar	60			
27 <i>Lasioglossum</i> (<i>Parasphecodes</i>) sp. 3 (female)	1	2.76		12 Jan	51			
Family Megachilidae								
28 <i>Megachile</i> sp. (male)	1	5.14		23 Feb	57			

APPENDIX 2. continued

Superfamily Tenthredinoidea						
Family Pergidae						
29 Euryinae sp. 1	12	1.08	0.10	7	29 Dec–11 Feb	1(83), 12, 13, 18, 23(6), 32(49), 35(2), 39(6), 40(11), 43, 48(7), 59(7)
30 Euryinae sp. 2	3	1.33	0.07	2	29 Dec–9 Jan	23(3)
31 Euryinae sp. 3	3	1.58	0.11	2	29 Dec	1(2), 23
Superfamily Scolioidea						
Family Tiphiidae						
32 Anthoboscinae	1	0.90			14 Feb	30
Superfamily Sphecoidea						
Family Sphecidae (Larrinae)						
33 <i>Tachysphex</i> sp.	3	0.88	0.13	3	Near holes in ground	
ORDER DIPTERA						
Suborder Nematocera						
Infraorder Bibionomorpha						
Family Bibionidae (March flies)						
1 <i>Dilophus</i> sp.	10	0.57	0.04	2	14 Feb–29 Feb	4, 26(47), 32, 59(3)
Superfamily Bibionoidea						
Family Sciaridae (Dark-winged fungus gnats, root gnats)						
2 Unidentified	7	?			3 Jan–27 Feb	1(2), 4(2), 18, 39(2)
Suborder Brachycera						
Infraorder Tabanomorpha						
Superfamily Tabanoidea						
Family Pelecoprychidae (Pelecoprychid flies)						
3 <i>Pelecoprychus rubidus</i> (males and females)	8	4.44	0.27	6	5 Jan–20 Jan	18(2), 39(7), 40, 45, 51(3)
Family Tabanidae (Horse flies and deer flies)						
4 <i>Tabanus froggatti</i>	8	3.53	0.99	6	10 Jan–29 Feb	4, 18, 42
Family Rhagionidae (Snipe flies)						
5 <i>Spania clelandi</i> (<i>Sphaniopsis</i> sp.)	2	?			25 Feb–5 Mar	Biting PI
Superfamily Stratiomyoidea						
Family Stratiomyidae (Soldier flies)						
6 Unidentified	1	2.38			11 Jan	18
Infraorder Asilomorpha						
Superfamily Asiloidea						
Family Therevidae (Stiletto flies)						
7 Unidentified	1	?			3 Jan	1
Superfamily Bombylioidea						
Family Acroceridae (Small-headed flies)						
8 <i>Ogcodes</i> sp.	1	?			29 Dec	?
Family Bombyliidae (Bee flies)						
9 <i>Comptosia sylvana</i>	2	3.36 (n=1)			30 Dec–5 Jan	1(16), 39
10 <i>Villa</i> sp.	2	3.24	0.40	2	6 Jan–1 Feb	30(5), 42
Superfamily Empidoidea						
Family Empididae (Dance flies)						
11 <i>Empis</i> sp. A	2	1.39	0.04	2	30 Jan	?
12 <i>Empis</i> sp. B	1	1.24			23 Feb	13
13 <i>Empis</i> sp. C	3	2.48	0.23	2	9 Feb–25 Feb	4, 7, 26(3), 59
14 <i>Empis</i> sp. D	2	2.31	0.07	2	20 Jan–1 Feb	8, 30
15 <i>Empis</i> sp. E	4	2.70	0.53	4	11 Jan–25 Feb	18, 30, 48, 59

APPENDIX 2. continued

16 <i>Empis</i> sp. F	2	1.93	0.16	2	3 Jan	43
17 Unidentified	1	1.98			3 Jan	39
Family Dolichopodidae (Long-legged flies)						
18 (?) <i>Diostracus</i> sp. I	1	?			11 Feb	46
Infraorder Muscomorpha-Aschiza						
Family Syrphidae (Syrphid flies)				Superfamily Syrphoidea		
19 <i>Eristalis tenax</i>	3	5.37	0.96	3	9 Jan–18 Jan	13(2), 45(3)
20 <i>Melangyna</i> sp.	8	1.92	0.36	7	30 Dec–23 Feb	8(3), 30(8), 39, 43(2), 48, 54, 59
21 <i>Syrphus</i> sp.	1	1.36			30 Dec	39
Infraorder Muscomorpha-Acalyptratae						
Family Platystomatidae (Picture-winged flies)				Superfamily Tephritoidea		
22 <i>Rivellia</i> sp. F	3	0.55	0.10	3	11 Feb–27 Feb	4(2), 59
Family Tephritidae (Fruit flies)						
23 <i>Sphenella marginata</i>	1	0.66			13 Jan	61
24 <i>Tephritis</i> sp. A	10	0.63	0.06	3	29 Dec–23 Feb	1, 13(6), 30(2)
25 <i>Tephritis</i> sp. B	6	1.08	0.09	4	27 Jan–27 Feb	13(4), 29(3), 32, 34(4)
Family Agromyzidae (Leaf miner flies)				Superfamily Opomyzoidea		
26 <i>Phytoliriomyza</i> sp.	1				6 Feb	28
Family Lauxaniidae (Lauxaniid flies)				Superfamily Lauxanioidea		
27 <i>Incurviseta</i> sp. D	9	1.17	0.16	6	3 Jan–27 Feb	1(28), 4, 8(5), 9, 12(23), 13(41), 23(2), 26, 28, 29(39), 32(2), 34(2), 35, 36(39), 39(3), 43, 45, 46, 53(19), 54(17), 55(2), 59(2)
28 <i>Incurviseta</i> sp. K	1	0.56			11 Jan	18
29 <i>Poecilohetaerus</i> sp.	6	0.78	0.18	5	3 Jan–27 Feb	1(8), 2(6), 4(3), 23(6), 26, 28(2), 35, 37(3), 38(3), 39(2), 46, 53, 54, 56
30 <i>Sapromyza</i> sp.	4	1.50	0.35	4	21 Feb–25 Feb	13, 46, 48(2)
Family Heleomyzidae (Heleomyzid flies)				Superfamily Sphaeroceroidea		
31 <i>Tapeigaster nigricornis</i>	1	1.58			27 Feb	4
Family Drosophilidae (Pomace flies)				Superfamily Ephydrioidea		
32 <i>Scaptomyza australis</i>	3	?			5 Jan–19 Jan	1, 37(2)
Family Ephydriidae (Shore flies)						
33 <i>Hydrellia</i> sp.	2	?			5 Jan	1(2)
Family Chloropidae (Chloropid flies)						
34 <i>Chloromerus</i> sp.	1	?			6 Feb	53
Infraorder Schizophora-Calyptatae						
Family Muscidae (Muscid flies)				Superfamily Muscoidea		
35 <i>Coenosia</i> sp. A	2	0.81	0.07	2	18 Jan–19 Jan	2, 37
36 <i>Coenosia</i> sp. B	7	0.89	0.18	7	9 Feb–27 Feb	4(7)
37 <i>Helina</i> sp. A	2	1.10	0.08	2	18 Jan–19 Jan	18, 39
38 <i>Helina</i> sp. B	2	2.65	0.10	2	1 Feb–29 Feb	4, 42
39 <i>Limnophora</i> sp.	1	1.20			23 Feb	13
40 <i>Musca vetustissima</i> (Walker) (females)	7	1.12	0.18	7	30 Dec–11 Jan	1(3), 12(6), 18(4), 26, 28, 39(2)

APPENDIX 2. continued

41 <i>Musca vetustissima</i> (Walker) (males)	5	1.04	0.13	5 6 Jan–25 Feb	4(10), 18(2), 19(2), 26, 28(7), 30, 32, 35
42 <i>Prohardya carinata</i>	1	1.74		19 Jan	39
Superfamily Oestroidea					
Family Calliphoridae (Blow flies)					
43 <i>Calliphora fulvicoxa</i> (Hardy)	1	3.34		30 Dec	43
44 <i>Calliphora hilli</i> (Patton)	1	4.14		3 Jan	43
45 <i>Calliphora stygia</i> (Fabr.)	2	4.05	0.21	2 5 Jan–19 Jan	39(2)
46 <i>Calliphora</i> sp. (<i>tibialis</i> group)	1	3.64		19 Jan	39
47 <i>Calliphora</i> sp. A (robusta group)	10	2.92	0.35	10 30 Dec–14 Feb	4(5), 8, 9, 18(17), 26, 30, 35(8), 39(4), 43(2), 46(2), 51(3), 54
48 <i>Calliphora</i> sp. B (robusta group)	4	3.55	1.01	4 30 Dec–18 Jan	39(2), 43(2), 48
Family Tachinidae (Tachinid flies)					
49 <i>Alophera</i> sp.	5	1.53	0.32	5 23 Feb–5 Mar	13, 60(4)
50 <i>Chaetopthalamus dorsalis</i>	1	3.92		13 Feb	48
51 <i>Prosena</i> sp. C	5	3.71	0.39	3 3 Jan–5 Mar	12, 13(3), 30, 38, 46, 48, 54, 60, 62
52 <i>Rutilia</i> sp. (inusta group)	1	5.20		29 Dec	39
53 <i>Scaptia alpina</i>	1	3.44		27 Jan	30
54 <i>Senostoma</i> sp. (<i>Prosena</i> species A)	2	2.92	0.31	2 6 Feb–23 Feb	13, 54
55 <i>Senostoma</i> sp. (<i>Prosena</i> species B)	5	4.48	1.36	5 27 Jan–29 Feb	13, 30, 42(4)
56 <i>Senostoma</i> sp. (<i>Prosena</i> species D)	2	3.51	0.41	2 3 Jan–20 Jan	16, 43, 46
57 Unidentified no. 1	5	2.71	0.31	5 27 Jan–14 Feb	4, 30, 42, 54(2)
58 Unidentified no. 2	2	1.74	0.68	2 19 Jan–31 Jan	4, 39
59 Unidentified no. 3	2	1.77	0.07	2 20 Jan–30 Jan	8, 13
60 Unidentified no. 4	3	1.87	0.30	3 11 Jan–14 Feb	4(2), 16
ORDER LEPIDOPTERA					
Noctuidae					
<i>Agrostis infusa</i>	0	(many observed)		31 Dec	17 (many)
Sphingidae					
<i>Hippotion scrofa</i>	0			3 Jan	17
Satyridae					
<i>Oreixenica orichora</i>	0			5 Jan–5 Mar	8(1), 12(2), 23(1), 29(5), 30, 34, 46, 54(19), 55(5), 57

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