

## VARIABILITY IN NEW ZEALAND MONTANE AND ALPINE POLLINATOR ASSEMBLAGES

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**SUMMARY:** New Zealand does not possess native social bees and many of the advanced insects which pollinate plants in other areas of the world. The flowers of most New Zealand plants are visited by a wide range of unspecialised insect species. These assemblages of flower-visiting insects on New Zealand montane and alpine plants are highly variable. Six factors which affect the relative frequency of different flower visitors on a plant species at a particular time are examined: weather, habitat, diel variation, plant mating type, animal competition, and sexual behaviour of the pollinators. Knowledge of these factors allows the dynamic nature of New Zealand pollinator assemblages to be investigated. The unspecialised floral syndromes possessed by most New Zealand plants are viewed as an adaptation to highly variable pollinator assemblages: flowers are visited by whatever pollinators are immediately available.

### INTRODUCTION

Alpine and montane plants in most areas of the world are pollinated by specialised insects such as honey bees, bumble bees, other social bees, bee flies, hawkmoths, and butterflies, as well as nectar-feeding birds. In these areas, one species of animal may be the exclusive pollinator of a plant species. In striking contrast, the New Zealand montane and alpine zone lacks native social bees and other groups of advanced flower-visiting insects. Butterflies and nectar-feeding birds are not abundant. Honey bees and bumble bees have been introduced by man into New Zealand, but these insects are not common on native plants in the alpine and montane zones. As a result, New Zealand presents an unusual opportunity to study the pollination ecology of plants in the absence of these animals which are so important elsewhere in the world.

Pollination research on alpine and montane New Zealand plants has been limited. Heine (1938) and Thomson (1927) concluded as a result of preliminary surveys that New Zealand plants do not have specialised pollination systems and that insects in general, and bees in particular, are relatively scarce as pollinators. Since these surveys, the few studies of specific groups, such as *Pimelea* (Burrows, 1960), *Epilobium* (Raven and Raven, 1976), and *Discaria toumatou* (Primack, in press), and an additional survey of montane and alpine pollinators (Primack, unpublished), have confirmed that a large number of

insect species may visit the flowers of anyone plant species. These later studies have shown that pollinating insects, in particular native solitary bees, may at times be quite abundant on flowers. However, the pollination ecologies of the great majority of New Zealand montane and alpine plants are still known only superficially.

The lack of special relationships between pollinators and plants certainly deterred many research workers from working on these systems. Pollinator assemblages of most New Zealand montane and alpine plants are too variable in both time and space, and are frequently composed of too many species, to be studied easily. Hence, rather than surveying the foraging behaviour of pollinators and determining the abundance of different pollinators at one particular time, as described by Primack and Silander (1975), it is more informative in these areas of New Zealand to study the factors affecting the composition of pollinator assemblages. These factors may then be used to explain some of the dramatic changes in pollinator abundance and give a more dynamic picture of plant-animal interactions in New Zealand. The approaches suggested in this paper will hopefully lead to more detailed studies of specific groups of plants.

### STUDY AREAS AND METHODS

It has been postulated that individual pollinators will forage in the most efficient way on the plant species which provides the greatest nutritional rewards at a particular time (Heinrich and Raven, 1972). A species of pollinator need not visit only the

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flowers of a plant species for which pollination theory suggests it is adapted, nor need it provide that plant with reliable pollination service. In this paper, animals which visit flowers to feed on nectar and pollen, contacting the anthers and the stigma, are considered to be pollinators. In more detailed studies, the presence of pollen on the body of the animal, and the potential for the animal to transfer pollen to a receptive stigma, should be checked before an animal is recognised as a pollinator.

Observations were made in December 1976 and January and February 1977 on visitors to the flowers in the montane short tussock grasslands and scrub vegetation of Cass, Canterbury, at an altitude of approximately 600 m (see Burrows, 1977), and the subalpine and alpine grasslands of the Craigieburn Mountains and Arthur's Pass and Mt. Cook National Parks (see Mark and Adams, 1973; Hayward, 1967; Wilson, 1976). In all flower-visitor surveys, every insect individual was counted that was visiting the flowers of a plant species within a certain area. Plant nomenclature follows Allan (1961). Voucher specimens of all insects are deposited with the University of Canterbury Zoology Department. The names of native bees correspond to a forthcoming article by Dr Barry Donovan of the DSIR Entomology Division.

#### WEATHER AND POLLINATOR ACTIVITY

The influences of wind (Eisikowitch and Galil, 1971), rain (Hagerup, 1951), extreme heat (Hagerup, 1932), and temperature (Heinrich, 1975) on pollinator activity have been studied. The differences in foraging behaviour, flight capabilities, and physiology of birds and each order and species of insect, will presumably result in varying responses of these species to shifts in the weather.

The number of insects visiting the flowers of the shrub manuka, *Leptospermum scoparium* (Myrtaceae), were counted over 10 minute intervals in different weather conditions at two shrub-grassland populations at Cass; the Goldney Saddle area, a northeast-facing slope, on 31 December 1976, and the Cass Hill area, a southwest-facing slope, on 22 and 23 January 1977. In cold, cloudy conditions at both localities, whether or not there was any precipitation, the large orange tachinid flies in the genus *Protohystricia* were the most common insect visitors on the manuka flowers (Table 1). In these cold, cloudy conditions, solitary bees in the genera *Lasioglossum* (Halictidae) and *Leioproctus* (Colletidae) were seldom seen, while syrphid flies, calliphorid flies and other flies were present in moderate abundance. With the onset of warm, sunny weather, large numbers of solitary bees began arriving at the

TABLE 1. The percentage of different insect visitors to flowers of manuka, *Leptospermum scoparium*, under various weather conditions at two localities in the Cass District: Goldney Saddle (31 December 1976) and Cass Hill (22 and 23 January 1977). Temperatures are considered to be warm when above 20.C. and to be cold when below 15.C.

CONDITIONS	GOLDNEY SADDLE				CASS HILL	
	10:30	11:30	13:30	14:30	11:00	12:00
Time	10:30	11:30	13:30	14:30	11:00	12:00
Temperature	Cold	Warm	Cold	Cold	Warm	Warm
Cloud cover	Cloudy	Sunny	Cloudy	Cloudy	Sunny	Sunny
Wind	Calm	Calm	Windy	Calm	Windy	Calm
FLOWER VISITOR						
<i>Protohystricia</i> sp.	54	19	50	56	4	2
<i>Calliphora</i> sp.	2	2	23	12	2	2
Syrphidae	10	6	4	14	43	18
<i>Philia</i> sp.	5	10	8			1
Other Dipterans	3	5	12	16	22	10
Solitary Bees	26	59		2	24	65
Other Insects	1				5	2
Sample Size:	109	124	26	50	100	100

manuka flowers, soon forming the majority of the pollinators present. In such conditions, *Protohystricia* and the calliphorid flies also increased moderately in abundance and activity, while the solitary bees increased tremendously in both abundance and activity. In one situation at Cass Hill, where there was sunny, warm weather with a strong wind, syrphids in particular foraged actively while the bigger calliphorid and *Protohystricia* flies were not foraging. On a subsequent day on which the weather was sunny and warm but exceptionally windy, no insects of any type were observed visiting the manuka flowers.

As another example, in fine, late December weather an assemblage of butterflies (*Lycaena boldenarum*), small tachinid flies, small *Lasioglossum* bees, and an ant, *Chelaner antarcticus*, visited the small yellowish flowers of the prostrate, subdioecious shrub *Muehlenbeckia axillaris* (polygonaceae) along the gully at the base of Cass Hill. In sunny weather, the butterflies, bees, and flies, the most common visitors to the flowers of this species, were foraging actively and often flying several metres to another patch of flowers. In overcast weather, the butterflies and bees did not forage, leaving only the flies and the ants as flower visitors. In a series of late December days on which the day-time temperature became progressively colder, the flies, and then even the ants, ceased foraging. In this one small area, butterflies, flies, or ants could be at times the most abundant flower visitors on *Muehlenbeckia*, depending on the weather conditions.

Insects respond to changes in the weather in a surprisingly short time. For example, after a period of continuous rain for three days in early January at Cass, there came a brief period of sunshine, and within 15 seconds flies began visiting the manuka flowers. On cold, overcast days, solitary bees began arriving in great numbers on the flowering manuka bushes at Cass only minutes after the sun came out.

#### HABITAT AND POLLINATORS

Populations of the same plant species may show differences in their pollinator assemblages if species of flower visitors have a more limited geographical distribution or ecological amplitude than the plant species. Every habitat in which a plant grows will have a different microclimate, which varies in its suitability for insect flower visitors.

At the base of Cass Hill, large individuals of the shrub Wild Irishman, *Discaria toumatou* (Rhamnaceae), are contained in a gully which is protected from the wind and is consequently far warmer than the exposed grassland in the vicinity. In the gully, the

small cup-shaped white flowers of this species were visited by a great variety of dipteran species, and also many species of beetles, bees and wasps. When the weather was sunny, tremendous numbers of the small, black, solitary bee, *Lasioglossum sordidum*, began foraging on the *Discaria* flowers, at times constituting more than 90% of the pollinator community. Just 100 m from the gully on the windy, colder slopes of Cass Hill, there was a population of small, scattered *Discaria* individuals. Species of hairy, medium-sized, grey tachinid flies accounted for 71 % of the 65 flower visitors observed under a variety of weather conditions at this locality. The number of solitary bees foraging on these plants did not increase as the weather became sunny. Apparently such scattered, small plants represented a nectar resource which tachinid flies could forage on profitably, while the remaining insect species could forage profitably only on large, concentrated masses of flowers.

Solitary bee species often have special requirements for a particular soil type in which to nest (Donovan, 1974). These special requirements, and the tendency of solitary bees to nest gregariously, result in local concentrations of each species as foragers on flowers. For example, the solitary bees on the manuka flowers at Cass Hill were predominantly individuals of *Leioproctus* 'E', with occasional individuals of *Leioproctus boltonii*, *Leioproctus imatatus*, and *Hylaeus relegatus*. In contrast, individuals of *Leioproctus boltonii* were the only solitary bees visiting the manuka flowers at the Goldney Saddle, only 3 km from the Cass Hill area. Along the main West Coast Road in the Broken River Basin at the turn-off for the Craigieburn Ski Club, about 15 km away, *Leioproctus imatatus* was the only solitary bee visiting the manuka flowers.

#### DIEL VARIATION IN POLLINATOR ACTIVITY

In New Zealand, butterflies, advanced flies (Brachycera and Cyclorrhapha), beetles, hymenoptera, hemiptera, and birds visit flowers during the day, while moths, crane flies, and gnats visit flowers at night. However, grass moths (Pylalidae) occasionally forage during the day as well. In the alpine areas, moths visit flowers during the day only, an apparent adaptation to the rapid drop in temperature at nightfall.

In the flowering population of manuka at Cass Hill, a daily cycle of flower visitation was seen during January 1977. With the first light of dawn, the larger tachinid and calliphorid flies began visiting the flowers. With increasing light and temperature, a great variety of flies, in particular syrphids, became active. If the day was sunny, large masses of bees

began to arrive on the manuka flowers between one and two hours after sunrise, depending apparently on air temperature, wind, and moisture conditions. The pollinators continued foraging until the late afternoon, when first the bees and then the other insects ceased foraging. In the late afternoon insect activity on the manuka flowers was quite low.

However, with the last light of day in calm, overcast weather, clouds of moths began emerging from the edge of the *Nothofagus solandri* var. *cliffortioides* forest, flying out into the grassland. Any breeze seemed to slow down this movement, but moth activity resumed with each subsequent pause in the wind. Moth activity was often quite high with over 50 moths present on large, individual manuka bushes. A wide variety of moths was present on the flowers, mainly species of Pyralidae, Geometridae, and Noctuidae, with each type of moth showing different foraging patterns. The pyralids foraged very slowly, spending up to several minutes on each flower, probing the flower from the side through the filaments, and not usually contacting the anthers or the stigmas. The geometrids foraged in a manner similar to the pyralids, but more frequently flew between plants, presumably giving a higher degree of cross-pollination if they contacted the anthers and stigma. The noctuids were the least common type of moth, but since they clambered around on the flowers, and frequently flew strongly between plants, they must be counted as important pollinators. Also, at night, many species of crane-fly (Tipulidae) visited manuka flowers. On certain nights both moth and crane-fly activity was quite high, but on other nights either moths or crane-flies, or sometimes both groups, were not abundant on the manuka flowers.

On flowering plants of manuka, as well as on many other montane shrubs in New Zealand, such as *Hebe salicifolia* (Scrophulariaceae), *Pimelea traversii* (Thymelaeaceae), and *Hoheria lyallii* (Malvaceae), there appears to be a day-active and a night-active group of flower visitors. The day visitors are probably more important than the night visitors as pollinators of these shrub species because of the great abundance, high levels of activity, and pollen-collecting activities of the day-active visitors. However, since the activity of the day visitors is so often limited by weather conditions, night visitors may often be important as a secondary force effecting pollination.

The daily patterns of foraging activity are often matched by periods of nectar flow, anther dehiscence, and scent production by the flowers of a plant species (Percival, 1955). Information is needed on the times of anther dehiscence, stigma receptivity, and nectar

production for all New Zealand plants. Studies would be particularly interesting on a genus such as *Dracophyllum*, which includes species pollinated during the day (*D. pronum*) as well as species pollinated at night. In a hybrid population of *Dracophyllum acerosum* and *D. uniflorum* (Epacridaceae) on Cass Hill, the flowers are visited during the day only by occasional flies and solitary bees which feed on pollen and do not probe into the tubular flowers. At night, beginning at dusk, a strong sweet smell is emitted from the flowers, presumably aiding to attract moths which actively forage on the flowers.

#### PLANT MATING TYPES AND POLLINATOR ASSEMBLAGES

Individuals of different mating types in dioecious plant species may differ in a wide range of secondary sexual characteristics related to their mating type (Lloyd and Webb, 1977), such as the number of flowers produced per plant, and the length of time over which the flowers are presented. With the high number of dioecious plant species present in the New Zealand flora (Godley, 1975), and the frequently skewed sex ratios of particular populations (Godley, 1976; Lloyd, 1973), investigations of different roles of mating types in populations of New Zealand plants are particularly appropriate.

Seven flowering plants of the spaniard, *Aciphylla scott-thomsonii* (Umbelliferae), at tree-line in the Craigieburn Range were examined on a sunny afternoon in late January 1977. The three female plants had five, four, and four flies per plant which were collecting nectar from the female flowers and the small sterile flowers at the centre of the umbels. In order to reach the sterile flowers, the flies had to climb into the flower umbel, contacting the stigmas. In contrast, the four male plants had 19, 40, 46, and more than 200 insects foraging per plant. These insects, which included tachinid flies, solitary bees, calliphorid flies, and beetles, were collecting both pollen and nectar from the male flowers. The flowers on the male plants open progressively over several weeks, providing a continuous supply of pollen. Hence, the male plants provide pollen and nectar rewards for a large number and variety of insects, but only relatively few insects leave this abundant resource to seek food on the female plants, in the process effecting cross-pollination. A similar difference in the rewards provided by male and female plants is apparent in a population of another spaniard, *Aciphylla divisa*, observed in the Sealy Range of Mt. Cook National Park, in which many flies were foraging on the flowers of each male plant, but no flies were seen on the flowers of any female plant.

## COMPETITION AMONG POLLINATORS

Competition may determine patterns of foraging activity of flower visitors. Less aggressive species or individuals may be restricted to certain times of the day (Kikuchi, 1962, 1964), to certain less desirable plant species (Kikuchi, 1962, 1964), to isolated plants (Linhart, 1973; Feinsinger, 1976), or to particular parts of a plant (Primack and Howe, 1975) by the territorial activities of dominant species or individuals. Species of colonial bee, in particular species of stingless *Trigona* bees, may be important on certain tropical trees in forcing weaker insects to leave a nectar resource and search for another flowering plant (Frankie *et al.*, 1976; Johnson and Hubbel, 1974).

Such competitive interactions are not readily apparent in the pollinator assemblages on New Zealand plants. Pollination systems in the tussock grasslands and the alpine areas in particular seem to involve abundant flowers and large populations of pollinators. Access to these flowers is more limited by the weather than by other flower visitors. Frequently days go by during which weather conditions are unsuitable for foraging activity. When the weather turns warm and calm, foraging activity commences with few apparent animal interactions. Several dozen insects may forage at the same time on an individual flowering shrub. The concentrated, constant nectar resource which an individual can defend at an energetic profit, and aggressive insect species which might defend it, seem to be lacking in the New Zealand montane and alpine regions. Two quite isolated cases of competitive interactions were observed, however. Firstly, a large syrphid fly foraging on a patch of the alpine herb, *Euphrasia revoluta* (Scrophulariaceae), in the Craigieburn Range was observed to fly at and chase away two small syrphid flies which flew within a few centimetres of the *Euphrasia*. Secondly, a tachinid fly foraging on the mountain daisy, *Celmisia spectabilis* (Compositae), in the alpine region of the Craigieburn Range, was observed to fly repeatedly over the flowers in a patch, dropping onto any other insects visiting the flowers and thereby causing the intruders to leave the vicinity. This limited number of observations of competitive interactions in three months of detailed field work clearly suggests that competitive interactions of flower visitors on New Zealand montane and alpine plants are rare or very subtle.

## SEX OF INSECTS IN RELATION TO POLLINATION

Specific pollination relationships exist between the males of certain social bees and specific species of plants. For example, males may try to copulate with

flowers which resemble female bees or males may gather fragrances produced by flowers as an integral part of their mating display (Dodson, 1975). Such extreme co-evolutionary relationships are not obvious in the New Zealand flora, but concentrations of flower-visiting insects with biased sex ratios are commonly seen, and this can be related to the biology of the insect species.

Mating swarms of male march flies, *Philia* sp. (Bibionidae), gather about 0.5 m above widely scattered manuka bushes at Cass during mid-summer. Distinguishing between the sexes of this species is quite simple; males have a black thorax and females a red thorax. The males spend most of their time flying in swarms, occasionally leaving the swarm to forage on manuka flowers. Females are only rarely seen on the manuka plants, during which time they forage on the flowers, usually with a male riding on their back. At dusk, particular scattered manuka bushes are covered with numerous male march flies 'foraging' in the flowers, apparently as a result of a mating swarm breaking up and the individual flies feeding on the flowers of the shrub below.

Solitary bees in the genera *Lasioglossum* and *Leioproctus* often reach a very high density on the flowers of many species of New Zealand montane and alpine plants. Deviations from equal numbers of males and females among the solitary bees collected visiting flowers over the summer of 1976-77 in the vicinity of Cass and the alpine regions were examined using Chi-square tests. Significantly more females than males were collected of *Leioproctus boltonii* (13 out of 14), *Lasioglossum sordidum* (53 out of 53), and *Lasioglossum* 'A' (26 out of 26). Significantly fewer females than males were collected of *Leioproctus* 'E' (0 out of 23). Roughly equal numbers of females and males were collected of *Leioproctus fulvescens* (12 out of 25) and *Leioproctus* 'A' (18 out of 29).

These biased sex ratios of foraging bees are related to the differing life histories and roles in reproduction of male and female solitary bees (Donovan, 1974). The females of species in these genera collect pollen on a region of their back legs, the scopa. The pollen is used to form a pollen ball in the nest tunnel, after which an egg is laid and the tunnel sealed. The pollen ball represents the only food source for the growing bee larva. While the females must gather quantities of pollen to provision their young and nectar and pollen for their own needs, male bees need forage only for themselves. Consequently, female bees may need to forage for longer on plants with more abundant pollen and so be more conspicuous and important as pollinators than males. The differing life histories of male and

female bees in these genera result in biased sex ratios at times in the overall population. In the genus *Lasioglossum* only fertilized females overwinter, so that females predominate in the spring and early summer. New male and female bees are produced during the summer, so that the proportion of male bees in the population increases. Male bees predominate in the population by the end of the summer, since they live longer than the females.

#### DISCUSSION

Flowering plants in the New Zealand montane and alpine flora are characterized by general pollination systems (Heine, 1937; Primack, unpublished), with only a very few species showing specific floral syndromes associated with particular pollinators. That such diverse pollinator assemblages on single plant species exist in other regions of the world is evident in the large lists of animal visitors on many temperate plant species (Knuth, 1906). In South Australia, a wide variety of bird species visits the flowers of many plant species, with many insect species recorded as visitors as well (Paton and Ford, 1977). Such diverse pollinator assemblages are not restricted to the temperate regions of the world, but are found in the tropics as well. In wet lowland forests in Costa Rica, about 70 % of the tree species show a period of massive flowering in which a great array of opportunistic insects are attracted to the flowers, though fewer massively flowering species were found in the understory (Frankie *et al.*, 1974; Frankie, 1975). In a Costa Rica dry forest, opportunistic pollination systems were also quite common among tree species (Frankie, 1975). Nectar-feeding tropical birds seem to show little specificity in the tree species on which they feed (Terborgh and Diamond, 1970; Feinsinger, 1976). It is clear that the New Zealand montane and alpine plants are not exceptional in possessing mainly generalized pollination systems.

Research in the field of pollination ecology has emphasized floral syndromes as adaptations to ensure pollination by particular types of pollinators. Perhaps, relative to their proportion of the world flora, an undue amount of attention has been focussed on spectacular and unusual pollinator-plant systems. However, such examples are valuable in showing the degree to which animals and plants can evolve in response to one another. The most detailed and elaborate co-evolutionary relationships between plants and animals appear to be in the understory of the humid, lowland tropics; for example, orchids and bees (Dodson, 1975) and the plants associated with *Heliconius* butterflies (Gilbert, 1975). Detailed examples of specific pollinator-plant relationships

are known as well for temperate groups (Grant and Grant, 1968) and groups occurring in both tropical and temperate regions (Simpson *et al.*, 1977). More survey work needs to be done on the relative frequency of specialized and generalized pollination systems in different tropical and temperate ecosystems such as cloud forests, alpine areas, deserts, and grasslands. Only then will comparisons of tropical and temperate, and continental and island community structure be valid.

Plants possessing flowers visited by a wide range of animal species can have pollination activity take place under a wider range of weather conditions and habitats than plants with specialized pollinator systems. Further, plants with general pollination systems retain the flexibility to extend their ranges, taking advantage of the pollinating animals of the new area. As an example, Mexican plants with flowers specifically adapted for hawkmoth pollination appear to be limited in their altitudinal distribution by the inability of hawkmoths to forage at low temperatures (Cruden, 1976). Similarly, by being able to obtain rewards from the flowers of many plant species an animal is not as vulnerable in a poor flowering year of a particular plant species.

Many New Zealand alpine and subalpine plant species have evolved from plant species dispersing across the sea (Raven, 1973), leaving their previous pollinators behind. The flowers of these species were visited by the great diversity of New Zealand pyralid moths, tachinid flies, and solitary bees, resulting in seed production and population establishment. No species of flower-visiting insect was so abundant or unusual as to result in a specific relationship with a plant species. On the contrary, the diversity of alpine flower-visiting insects is so great that selection appears to be operating to make flower types generalized enough to take advantage of a wide range of insect pollinators.

Adaptation of local plant populations to the local pollinating fauna may occur if certain pollinator types are abundant in one locality but rare in another. Studies on *Metrosideros collina* in Hawaii show that certain red-flowered populations appear to be adapted for bird pollination while other yellow-flowered populations are adapted for insect-mediated self-pollination (Carpenter, 1976). Such local adaptations to particular pollinators are not readily apparent in New Zealand montane and alpine plants, possibly due to the unreliability and low numbers of any single element of the pollinating fauna. Additional studies should further reveal the underlying principles governing this neglected area of the pollination ecology of New Zealand plants with many pollinators.

## ACKNOWLEDGEMENTS

I thank P. Johns, T. McIntosh, and the officials of Arthur's Pass and Mt. Cook National Parks for assistance with the field work and D. Lloyd, B. Donovan and R. MacFarlane for helpful comments on the manuscript. B. Donovan, J. Dugdale, P. Johns, and R. MacFarlane helped in identifying insects. A Post-Doctoral Fellowship from the Miss E. L. Hellaby Indigenous Grasslands Research Trust and the United States-New Zealand Cooperative Science Program of the National Science Foundation made this work possible.

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