THE IMPACT OF HONEY BEES ON
MONTANE ECOSYSTEMS WITHIN
TONGARIRO NATIONAL PARK

A thesis presented in partial fulfilment
of the requirements for the degree of
Masters of Science in Ecology
at Massey University

Claire Lisa Murphy
1996

ABSTRACT

A study of the effects of honey bees on montane ecosystems was conducted during the summers of 1993/1994 and 1994/1995 at Tongariro National Park. Three possible effects of the introduced honey bee were examined. The primary aims of the study were to identify areas with and without honey bees and to identify differences in the pollination success of a weed species, heather (*Calluna vugaris*) and a native species, the New Zealand flax (*Phormium tenax)* under different pollinator regimes, and to examine differences in the composition of native pollinator communities in these different bee areas.

The impact of honey bees on the reproductive success of heather, an important weed species in Tongariro National Park was examined over two flowering seasons. Insect visitation rates on heather flowers were low at each of the four study sites. Bagging plants to exclude insect flower visitors had little effect on female fitness. The potential of other pollen vectors, wind and thrips, as pollinators of heather was also examined. Both were determined to have a negative effect on several measures of female success, including pollen depostition, pollen tube formation, and pollination levels. However it appears that none of the pollen vectors (honey bees, wind or thrips) significantly effect the overall fitness of heather in terms of the viable seed produced.

The second part of the study examined the impact of honey bees on the pollination systems of a native plant species. Flax is thought to be predominantly bird pollinated, however, the floral resources are also utilised by a variety of native and introduced insect species. At some sites birds were either not present or rarely used the flowers. Seed set in flax was highest in heavily bird pollinated sites. The results also suggest, however, that flax has a flexible pollinating system that enables it to maintain a range of fruit and seed set levels under the different pollintor regimes.

The abundance and diversity of insect flower visitors on manuka and *Hebe* stricta, two common subalpine shrubs, was highly variable between sites, and between observation periods. Some of this variation may be described to differences in the weather or to altitude. However, I have shown that the abundance and diversity of diptera appears to be strongly influenced by levels of honey bee activity. This indicates that honey bees do play a role in determining the structure of pollinator communities and may be displacing a significant component of the native pollinating fauna.

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr Alastair Robertson, for his support and encouragement throughout the course of this study. Without him I would never have got to where I am today. Alastair was always there if I needed him, particularly over the last few months, and he never gave up on me, for that I am extremely grateful.

To the Department of Conservation, in particular, the Tongariro /Taupo Conservancy and the Science and Research Division, your contribution and support on this project was greatly appreciated. Funding was also provided by the Massey University Post-Graduate Research Fund.

I would also like to thank the staff and fellow post-graduates of the Ecology Department, Massey University for all their help, practical and emotional, in completing this thesis. To the staff of the Whakapapa Field Station, thank you for making field work not only tolerable, but also interesting.

I would like to thank my parents, Shirley and Craig , for their support over the past years, - I have finally finished!. And to my husband, Phil thank you for putting up with me and for keeping things going at home when I was too busy to be there.

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GENERAL INTRODUCTION

THE INTRODUCTION OF SPECIES AND COMPETITIVE INTERACTIONS

Human exploration and subsequent settlement of new countries has led to the introduction of foreign species to previously isolated ecosystems.. In an Australian study Fox (1990) suggests that the earlier invasions of "people from the north" introduced relatively few species and the lifestyle did not greatly affect the environment, although their use of fire would have altered vegetation types in some areas. The arrival of Polynesians to New Zealand around 1,000 years ago bought with them the Kuri or Maori dog (*Canis familiaris*) and the Kiore (*Rattus exulans*). The Maori used fire to clear land for crops and habitation. By 1840 forested land cover had been reduced from 78% to 53% of the land area (Atkinson and Cameron 1993). This resulted in large areas of land reverting back to tussocks (Salmon 1975). Fire may also have been used to hunt moa, a large flightless herbivore. Archaeological evidence suggests hunting by the Maori was the primary cause of extinction for moa (Atkinson and Cameron 1993).

The arrival of Europeans however resulted in a large changes to New Zealand's ecosystems. Forest coverage was further reduced to only 23% of the land area, while 90 species of vertebrates and 1,600 species of plants have become established since 1840 (Table 1) (Atkinson and Cameron 1993).

The introduction of exotic species results in the formation of novel interactions with native species. These interactions may include predation, parasitism and competition. Several definitions for predation have been proposed (Taylor 1984). For the purposes of this chapter I will use Taylor's first definition, "predation occur's when one organism kills another for food" (1984 p3). This is the most commonly used definition and includes not only animals as predator and prey but forms of herbivory as well. Parasitism, however, is excluded. Examples of introduced species preying on native species include, kiwi predation by dogs (Taborsky 1988), and cats preying on birds, lizards and weta (Karl and Best 1982, Fitzgerald and Veitch 1985, Taborsky 1988). Native birds, lizards and insects along with introduced rodents are eaten by Mustelids (Roser and Lavers 1976, King and Moody 1982, Moors 1983, Crouchley 1994).

Table 1. Numbers of endemic and established alien species in major groups in New Zealand (Adapted from (Atkinson and Cameron 1993))

Group	Endemic Species	Established Alien Species
Dicots	1 463	1 199
Monocots	473	380
Conifers	24	24
Ferns and Allies	106	20
Land Mammals	2	34
Resident Land Birds	60	33
Breeding Sea Birds	29	-
Reptile	60	1
Amphibians	4	2
Fresh Water Fish	23	20
Insects	c. 18 000	c. 1 500

Possums (*Trichosurus vulpecula*) have been shown to consume nesting birds and their eggs (Brown *et al.* 1993). The possum also feeds on fruit, bark, young shoots and leaves of many canopy plants. Overgrazing by possums can extensively damage large mature trees such as Rata (*Metrosoideros robusta, M. umbellata*), Pohutakawa (*M. excelsa*) and Fuschia (*Fuschia excorticata*) (Salmon 1975).

Large browsers such as deer (*Cervus* spp.) and goats (*Capra hircus*) can cause severe damage to native forests and may alter the composition of the forest when the most palatable plant species are also the most dominant (Parkes 1993). Regeneration of native forests is hampered by continual browsing of both seedlings and mature trees.

Competition occurs when two or more species utilize common resources such as food or nesting sites which are in limited supply, or when one species restricts another's access to that resource even when it is not limiting (Ford 1979). Competition between species may be direct (interference competition) or indirect (exploitative competition) (Gill 1978, Putman 1994). If two species coincide with their utilization of a common resource we may expect to see direct competition with one species actively restricting the other's access to the resource through aggressive or territorial behaviours. However if the species differ in temporal use of the resource we would expect to see indirect competition with one species restricting the other's access due to prior utilization of the resource.

Johnson and Hubbel (1974)ooked at direct competition for resources among five species of stingless bees in Costa Rica. The bees were observed on artificial bait stations designed to provide a constant and controllable food source. Aggression between the species was observed with *Trigonia silvestriana* and *T. corviva* being the most aggressive species and *T. latitarsus* the least aggressive. The level of aggression increased with increasing quality of the food source, and high quality resources were usually controlled by an aggressive species. Johnson and Hubbel suggest that the non-aggressive species may persist by being more efficient at discovering and exploiting resources.

Another means of examining competition in the field is to determine the range and activity of one species in the presence and absence of possible competitors. Ford and Paton (Ford and Paton 1976) examined the ecology of eight species of honeyeaters (*Meliphaga*) in South Australia. They looked at ecological differences between the species at three levels habitat, range and feeding ecology. Honeyeaters appear to be separated by differential use of resources in at least one of the three levels. The purple-gaped honeyeater (*M. cratitia*)exhibits a wider habitat range on Kangaroo Island in the absence of several potential honeyeater competitors than seen on the mainland. Ford and Paton suggest that this indicates strong but inferential evidence for interference competition, past or present, influencing the current ecological niches of the *Meliphaga*.

The honey bee (*Apis mellifera*) is indigenous to Europe and Africa where hives have been maintained for centuries (Martin, E.C. and McGregor 1973). With man's colonization of the world, the range of the honey bee has increased and now bees can be found in many different countries (Todd and McGregor 1960). According to Gojmerac (1988) (p14) "bees arrived in Australia by 1822, South America in 1839 and in New Zealand in 1842". The impact of honey bees on New Zealand's native flora and fauna has not been examined. Overseas studies however suggest that honey bees may compete with the native fauna for resources. Competition between Africanised honey bees (*Apis mellifera*) and the stingless bees of South America is likely, since they are both generalist feeders with an overlap in their range and time of activity (Roubik 1978). Roubik studied the impact of the introduced honey bee on native pollinators by manipulating the number of honey bees foraging on certain flowering plants. The number of stingless bees foraging on *Melochia villosa* was reduced with increasing numbers of honey bees. This trend was reversed when honey bee hives were removed from the area. The density of native pollinators on *Mimosa pudica* remained stable but the duration of flower visits increased when the hives were removed. Such changes in resource use in the presence of another species does not always imply competition, but when experimentally induced, do indicate that resources are limiting and may provide a basis for competition to occur.

Schaffer *et al.*. (1979) looked at competition between floral visitors of *Agave schottii* in Arizona. They determined that honey bees dominated at the most productive sites, bumble bees (*Bombus*) at the intermediate sites, while native bees (*Xylocopa*) predominated at the least productive sites. This system was then manipulated by removing ants as foragers of nectar (Schaffer *et al.* 1983). This led to an increase in honey bee numbers, no change to bumble bee activity and a significant increase in the number of small solitary native bees. The removal of honey bee hives led to an increase in the number of feral honey bees observed. This was associated with an initial increase and subsequent decrease in the numbers of both bumble bees and native bees as feral bees were recruited to the site. Schaffer *et al.*. believe that their data supports the hypothesis that competition for resources plays an important role in determining the extent to which various floral visitors utilize *A. schottii* flowers.

Competition is put forward as the reason why not all species are present in habitats that are potentially suitable for them. Where two species are ecologically identical one species may prevent the other from successfully invading and colonising the area.

The competitive displacement principle can be defined as "different species having identical ecological niches can not coexist for long in the same habitat" (DeBach 1966). In it's strictest form competitive displacement is an all or nothing situation. This principle has also been described as Gause's Law or Hypothesis, the Volterra-Gause principle and the competitive exclusion principle, and it has been defined in various ways (for references see DeBach 1966). Some ecologists consider competitive displacement to be rare, ambiguous and of little ecological significance. However De Bach (1966) suggests that it may be more common in nature than previously thought. Past cases of the principle can not be ascertained as one species has already disappeared but it may be observed when an ecological homologue of a species is introduced to the same area. For example one well documented case occurred in southern California between two species of Aphytis. Both are ectoparasites of the California red scale, *Aonidiella aurantii. A. chrysomphali* was accidentally introduced and became established around 1900. In 1947 *A. lingnanensis* was purposefully imported from south China. It became established and rapidly began to displace *A. chrysomphali* from all southern California except for a few small coastal pockets. Another homologue

A. melinus was introduced around 1956 which then proceeded to displace *A. lingnanensis* from the interior land areas (DeBach 1966). Nearly all future cases of competitive displacement will occur between an established species and an invader. For further discussion on the importance and validity of the competitive displacement principle in ecology see (Cole 1960, Hardin 1960, Patten 1961).

TONGARIRO NATIONAL PARK

National Parks- The concept of National Parks was first formulated late last century to protect the beauty and 'worth' of the natural environment for the benefit of all. The world's first National Park was established at Yellowstone, U.S.A in 1872.

New Zealand's National Parks Act (1980) states that these parks "contain scenery of such distinctive quality, ecological systems or natural features so beautiful, unique or scientifically important that their preservation is in the national interest" (section 4(1)). New Zealand has twelve National Parks, comprising of two million hectares of land, protected for scenic, scientific, recreational and cultural purposes. According to the National Parks Act these parks are to be maintained as much as possible in their natural state so that their value as conservation areas are maintained. Native flora and fauna are to be preserved and introduced species removed if their presence is in conflict with the basis of the Act. The Act allows for public access to the parks, subject to provisions and regulations, so that people may derive inspiration, enjoyment and recreation from the environment in it's natural state.

Tongariro National Park

With the European settlement of New Zealand, Chief of the Ngati Tuwharetoa, Te Heuheu was worried that Tongariro, his ancestor, would be divided and sold piece by piece to the pakeha, white man. On September 23rd 1887 Te Heuheu offered the mountains to the government as a national park. His sacred mountains would be the property of all the people of New Zealand. This made Tongariro National Park (TNP) New Zealand's first National Park and the 4th in the world. The park was formally established by parliament in 1984 and gazetted as such in 1907. The original gift by Te Heuheu consisted of the volcanic peaks Mt Ruapehu (2797m), Mt Ngauruhoe (2291m) and Mt Tongariro (1968m). In 1907 botanist Dr. Leonard Cockayne and Phillip Turner, an inspector of scenic reserves, were requested to survey the park and give proposals for expansion. They found that within the current boundaries the park was almost devoid of plant life and they saw a need to extend the park's boundary to include all the unique plant associations within the area. Following the recommendations of Cockayne and Turner the park was considerably enlarged and today covers more than 80,000 hectares.

Situated in the central North Island of New Zealand (39' lat, 175 long) TNP consists of volcanic craters, boiling lakes, snowfields, alpine scoria fields, beech forests, meadows and deserts, making it a highly varied landscape with complex interactions between ecosystems. The future of these native ecosystems is continually under threat with invasions of exotic species such as heather (*Calluna vulgaris*), lodgepole pine (*Pinus contorta*) and gorse (*Ulex europeaus*).

Another introduced species within Tongariro National Park is the European honey bee (*Apis mellifera*). The honey bee was previously thought to be beneficial by providing pollination services for native plant species. However Australian studies (Vaughton 1992, Carthe 1993, Paton 1993) suggest that honey bees may be inefficient pollinators of native plants and compete with other native pollinating species for resources. The impact of honey bees on New Zealand's ecosystems has not been previously examined, although the use of native plants by honey bees has been examined by (Donovan 1980, Butz Huryn 1995).

CHAPTER 1. HONEY BEES AND THEIR DISTRIBUTION WITHIN TONGARIRO NATIONAL PARK

INTRODUCTION

Bees belong to the superfamily Apoidea (Hymenoptera). There are around 20,000 species of bees worldwide, usually divided into 8 or nine families based on morphology. Bees range in size from 2 to 39mm in length (153). The breeding behaviour of bees ranges from solitary females to the complex interactions of eusocial bees. Of the 20,000 bee species, 3,000 are represented in the Australian fauna (19) while only 40 species are present in New Zealand. All New Zealand's native bees belong to the two primitive families, Colletidae and Halictidae.

Seven species of bees have been introduced and become established in New Zealand. Five of these species belong to the most advanced bee family, the Apidae. The introduced Apidae can be divided into four species of bumble bee (Bombinae) and one species of honey bee (Apinae). The honey bee (*Apis mellifera*) was introduced to New Zealand as early as 1839 (Donovan 1980). Honey bees continued to be introduced from different countries until the 1924 Apiaries Act prohibited the importation of bees or used equipment, in an attempt to exclude bee enemies not currently present in New Zealand (Donovan 1980).

The beekeeping industry fulfils two important functions -firstly, the production of honey and related products. In New Zealand the honey industry currently exports honey products worth over $8million worldwide. Secondly, the industry provides pollination services for many plant species, particularly for commercial crops (Todd and McGregor 1960, Martin, E.C. and McGregor 1973, Jay 1986).

Honey bees are important pollinators of many plant species and are highly adapted for the purpose. Complex pollen collecting hairs are concentrated on the hind legs, the corbiculae, and their mouthparts are specialised for imbibing nectar. Behaviourally, bees are also well adapted for pollination. Both the adult and juvenile stages of the honey bee feed on pollen and nectar. Foragers collect pollen and nectar in excess of their own requirements to feed young and to provision the nest for overwintering. Foragers constantly monitor the food sources available and recruit other colony members to the most rewarding food supply (Kevan and Baker 1983). Honey bees may forage over 10km away from the hive in search of an adequate food supply (Kevan and Baker 1983, Seeley 1985, Gojmerac 1988). Although honey bees will travel long distances in search of a food source studies have shown that 80-90% of foragers travel between 1-3km from the hive (Seeley 1985, Gojmerac 1988). Bees prefer to forage close to the hive reducing the energy and time wasted flying to and from the foraging site (Free 1982). When gathering pollen and nectar for the hive, travel time is very important. A honey bee can make 20 trips per hour if foraging 2-3km away but only 1 trip if the food source is 14km away (Kevan and Baker 1983). Within a foraging site individual bees do not forage at random, but limit their visits to comparatively small areas of 3-6 metre circles. Larger foraging areas may be observed in the absence of competition between bees, and smaller areas are associated with intense competition (Todd and McGregor 1960). Abiotic factors may also influence foraging behaviour amongst honey bees, for example workers seldom forage when the temperature is lower than 8 degrees celsius (Gojmerac 1988) or during strong winds (Kevan and Baker 1983).

Managed honey bees have escaped from commercial hives forming large feral populations around the world(Roubik 1978, Pyke 1990, Wills *et al.* 1990) and in New Zealand (Moller and Tilley 1989, Butz Huryn 1995). In Australia few areas are thought to be free of feral honey bees. These areas include the Australian Alps, where it is too cold and there is insufficient food in winter, and some desert areas where there is not enough water.

In New Zealand, the central North Island is an important area for the production of manuka and heather or ling honey. Until 1991 apiarists were allowed to place their hives within the boundaries of Tongariro National Park. The National Parks Act (1980) is the act which directly influences park management. Section 4(2) states that "National Parks shall so be administered and maintained... introduced plants and animals shall as far as possible be exterminated". Changes to the Department of Conservation's (DoC) Tongariro/Taupo Conservancy management policies were made to better enforce the regulations set down in the National Parks Act. These changes prevent hives being placed within Tongariro National Park. The hives are currently situated on either private or DoC administered lands just outside the park boundary. The change in management policies has not prevented honey bees from utilising park resources. The impact of these introduced honey bees on native insect species has yet to be determined.

Honey bees may affect native communities in at least three different ways:

1. Facilitation of weed dispersal by providing pollination services (Chapter 2)
2. Inefficient pollination of native flora (Chapter 3)
3. Competition with native fauna for resources (Chapters 3 and 4)

A review examining the contribution of honey bees to the reproduction of weed in New Zealand's protected natural areas (PNA's), was conducted by Butz Huryn and Moller (1995). Introduced weeds are important sources of both nectar and pollen for honey bees and the potential therefore exists for beekeeping to aggravate the problems already caused by weeds in PNA's. Weedy species tend to be characterised by their reproductive plasticity, including wind or unspecialised pollination systems, high germination potential or a high degree of vegetative reproduction. If honey bees are important pollinators of a weedy species, then regulation of bee numbers may limit seed set. However, if the weed can reproduce vegetatively, via self- or wind pollination, or has an unspecialised pollination system, and can be effectively pollinated by a variety of pollinator species, then regulation of honey bee numbers would have little or no impact on weed reproduction.

Of the 158 weed taxa surveyed in the PNA's, 65 were considered to be problem weeds (Butz Huryn and Moller 1995). These weed species are probably visited by bees for either nectar or pollen. Visiting species are not necessarily effective pollinators of the plants they visit, but visitation records can indicate potential pollinating species. The weeds known to be visited by honey bees were ranked on the relative importance of honey bees on the pollination or reproduction of the plant species. The ranking ranged from 'no influence' to a 'high influence' where honey bees were the main pollinator species visiting flowers. 43% of the weed taxa surveyed were potentially used by honey bees, 33% of which were considered to be problem weeds. Butz Huryn and Moller ~~(Butz Huryn and Moller~~ 1995) conclude that honey bees are probably not an important factor in the abundance and spread of the majority of problem weed species located in New Zealand's PNA's.

A review of current literature conducted by Butz Huryn (1995) shows the use of New Zealand's native plants by honey bees. The review indicates that honey bees collect nectar and/or pollen from 224 native plant taxa. This includes 188 species, 119 genera and 67 New Zealand families. The majority of species visited, however, are contained in only a few families including the Myrtaceae and Scrophulariaceae. Only 10% of all native plants have been noted for producing a surplus of honey. Myrtaceae account for more than one quarter of the surplus producers. The results of this literature search indicate that introduced honey bees use a very small proportion of the plant species available in a given area. Butz Huryn (1995) suggests that honey bees, and other introduced species, are unlikely to have a negative impact on the pollination of native plant species due to their relatively unspecialised pollination systems. She also suggests that honey bees may actually be more effective than native pollinators due to their high floral constancy whilst foraging.

Honey bees have been shown to compete with native floral visitors in French Guiana (Roubik 1978), North America (Schaffer *et al.* 1979, 1983) and Australia (Paton 1993). Their impact on New Zealand's native pollination sytems has not been previously examined. The effect of honey bees on the abundance and diversity of native floral visitors is examined in Chapters 3 and 4.

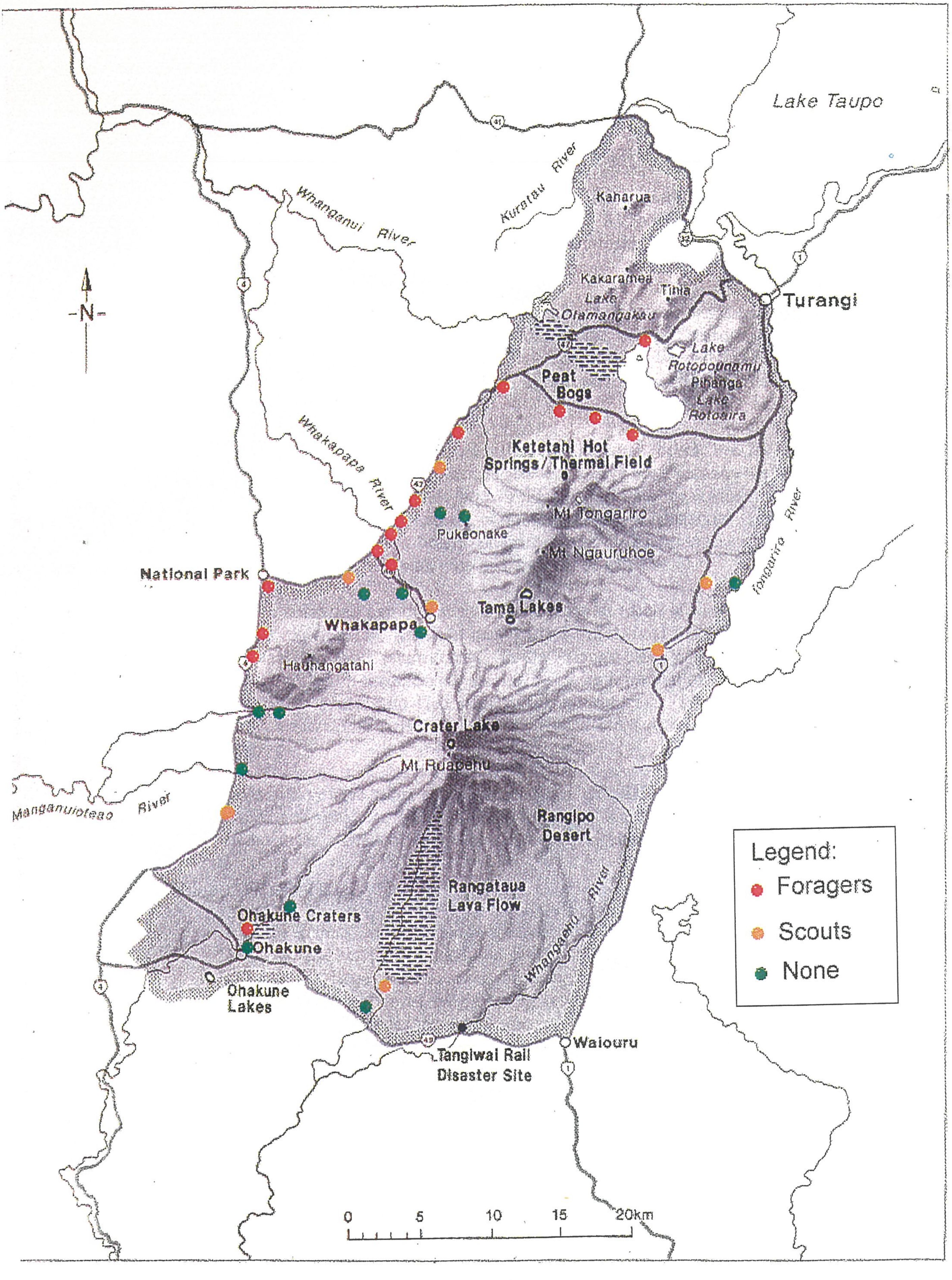
METHODS

Identification of Honey Bee Areas

Feeding stations were placed at various sites around the Tongariro/Taupo conservancy. The majority of feeding stations were placed within the Tongariro National Park boundary (Fig. 1). The feeding stations were constructed according to Danka *et al.* (1990). They consisted of a bright yellow 1kg honey container with snap on lid. The container was filled with a concentrated sugar solution (vol:vol) and small feeding holes were drilled above the rim (Fig. 2). Nectar guidelines were drawn towards each hole in black permanent marker pen. The feeding stations were placed upside down onto metal stakes. A large yellow lid was attached to the top of each feeding station to provide shade and protection from rain. Synthetic bee pheromone (1:1 citral:geraniol) was placed in a small vial attached to the feeding stations (Danka *et al.* 1990).

The feeding stations were revisited to determine the presence or absence of honey bees at each site. The number of bees observed and the amount of sugar solution remaining was recorded. The presence of other species at the feeding stations was also noted. The stations were refilled as required and later revisited.

Figure 1. The distribution of feeding stations and their utilisation by honey bees within Tongariro National Park. (Following page).


N
Lake Taupo
Kuratau River
Whanganui River
Kaharua
Kakaramea
Tihia
Lake Otamangakau
Turangi
Lake Rotopounamu
Pihanga
Lake Rotoaira
Peat Bogs
Ketetahi Hot Springs / Thermal Field
Whakapapa River
Mt Tongariro
Pukeonake
Mt Ngauruhoe
National Park
Tama Lakes
Whakapapa
Hauhangatahi
Tongariro River
Crater Lake
Mt Ruapehu
Manganuioteao River
Rangipo Desert
Rangataua Lava Flow
Whangaehu River
Ohakune Craters
Ohakune
Ohakune Lakes
Tangiwai Rail Disaster Site
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49
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Foragers
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None
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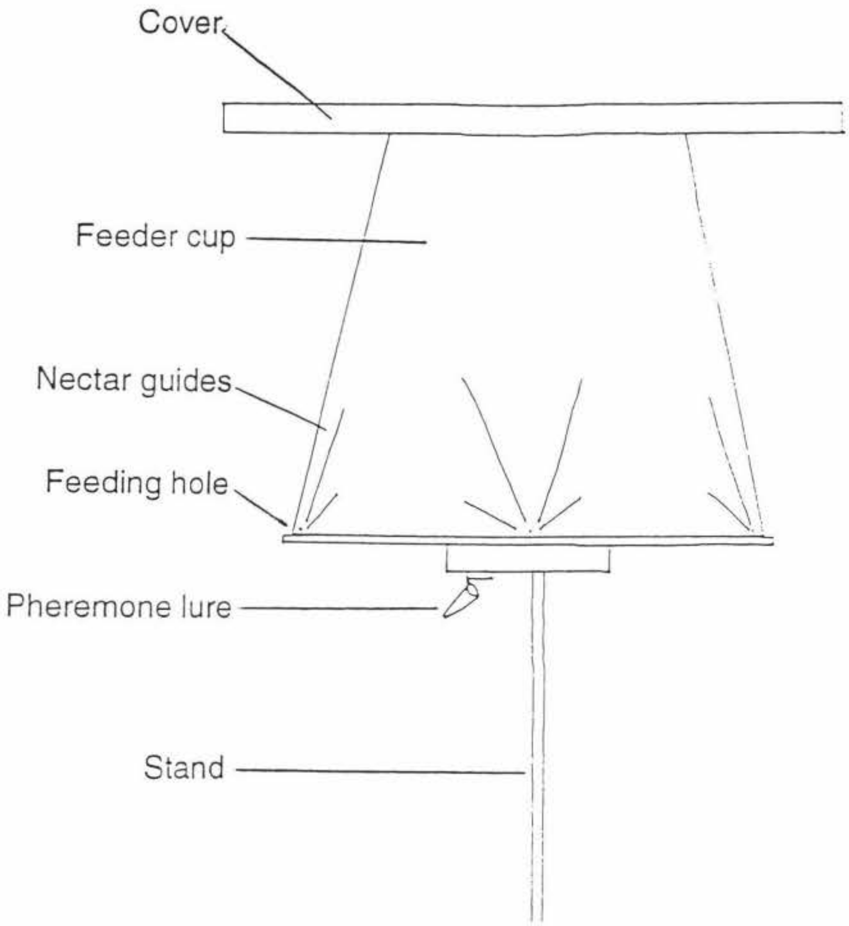


Figure 2. Feeding station design.

Feral Bees

During the 1993/94 season feeding stations were set out in groups of three. When satiated honey bees fly straight back to their hives. By identifying the return paths of foragers from the feeding stations and by using triangulation we hoped to identify the location of the source hives. Hives located within the park boundary would contain feral honey bees. Some of the feeding stations used to determine wether honey bees are present at each site were placed at least three kilometres inside the park boundary. Studies have shown that 80-90% of workers forage within three kilometres of their hives (Seeley 1985, Gojmerac 1988). As commercial hives are currently banned from TNP it was thought that high levels of recruitment to these feeding stations could indicate feral hives.

RESULTS AND DISCUSSION

Identification of Honey Bee Areas

Results from the feeding station experiments indicate that honey bees forage at least one kilometre inside the TNP boundary. This result is consistent with other studies on the foraging distances of honey bees (Kevan and Baker 1983, Seeley 1985, Gojmerac 1988). Data collected from the utilisation of feeding stations over both seasons has been consolidated and is presented in Figure 1. Sites represented by red circles indicate high utilization by honey bees. The most highly utilised feeding stations were located around the western boundary of TNP. This utilisation corresponds to the placement of commercial hives around the park. Hive placement does not remain static throughout the season, but follows changes in the flowering of the main nectar sources in the area (ie: manuka and heather). Small numbers of honey bees were observed at feeding stations indicated by the orange circles. These bees were thought to be 'scouts' and there was no evidence of further recruitment to the feeding stations. At sites indicated by the green circles, no evidence of honey bee activity was observed.

Feral Bees

There was no evidence for feral bee hives at any of the sites examined using feeding stations. Location of hives using triangulation was extremely difficult to achieve in the field and provided no information regarding the presence of feral hives in TNP. The few honey bees observed on feeding stations at least three kilometres inside the park boundary, were assumed to be 'scout' bees from commercial hives. The lack of evidence for feral hives within Tongariro National Park is thought to be due to low survival rates of overwintering bees (Pyke 1990)

CHAPTER 2. HEATHER POLLEN VECTORS AND FEMALE REPRODUCTIVE SUCCESS

INTRODUCTION

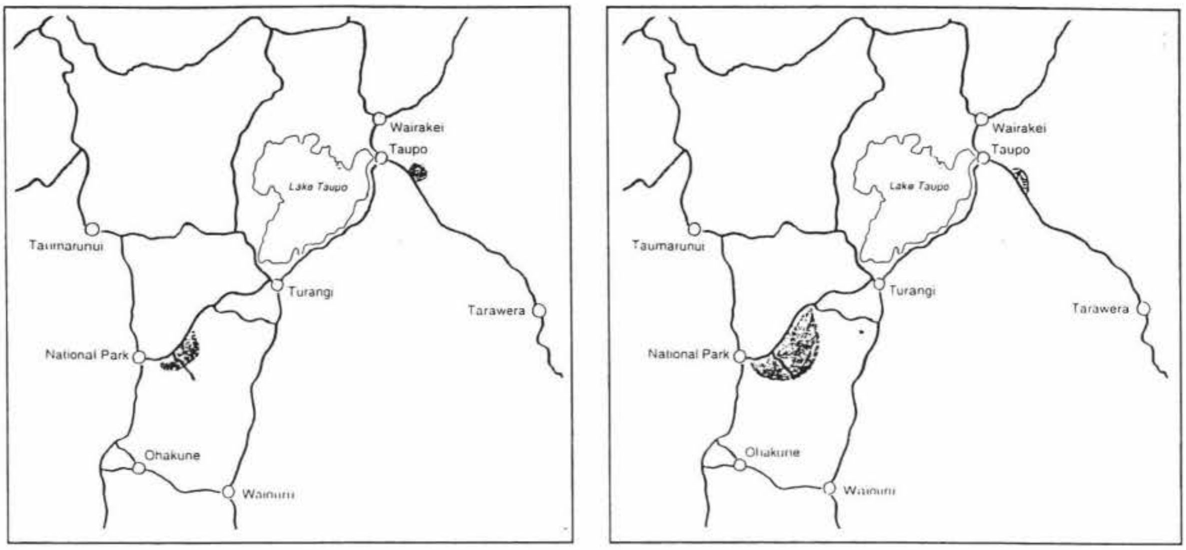
Heather, *Calluna vulgaris*, is a member of the family: Ericaeae, sub-family: Ericoideae. A low, much branched shrub, heather has evergreen sclerophyllous leaves (Gimingham 1960). *Calluna* is native to Europe and the United Kingdom where it is a heathland plant and a major constituent of dwarf shrub communities (Chapman 1984). Heather, was first introduced to Tongariro National Park (TNP) by John Cullen the honorary park warden. His plan was to develop a heather moor for the shooting of grouse and other gamebirds (Bagnall 1982, Chapman 1984, Williams and Keys 1993). Heather seed from New Zealand, France and the United Kingdom was used during the plantings from 1912-1921. By 1918 the range of heather within TNP was 25 sqkm. During the 1960's this had expanded to cover 80 sqkm and is currently over 6000 sqkm (Fig. 1).

The rapid expansion of heather, an exotic species, into new ecosystems has caused problems as it interferes with the natural processes of succession in tussock and shrublands. The introduction of heather has resulted in a reduction of indigenous species diversity in many ecosystems including tussocklands, alpine herbfields and wetlands (Williams and Keys 1993). The wide distributio of heather throughout Tongariro National Park can be explained by it's ability to adapt to a wide range of environmental conditions. Heather can act as a pioneer species in disturbed areas and becomes established far more rapidly than native species. In tussock grassland communities, heather acts as a more aggressive species entering via the inter-tussock spaces eventually excluding the tussock. At higher altitudes heather is a non-aggressive member of herbfields and scoria slope communities (Chapman 1984, May 1993). The majority of native plant species within Tongariro National Park are either totally eliminated in the presence of dense heather or are only able to remain in low numbers in the community.

The species most threatened by the heather invasion are inter-tussock and herb species, including *Coprosma cheesmanii*, *Coprosma perpusilla*, *Dracophyllum recurvum*, *Celmisia spectabilis* and *Helichrysum bellidiodes*.

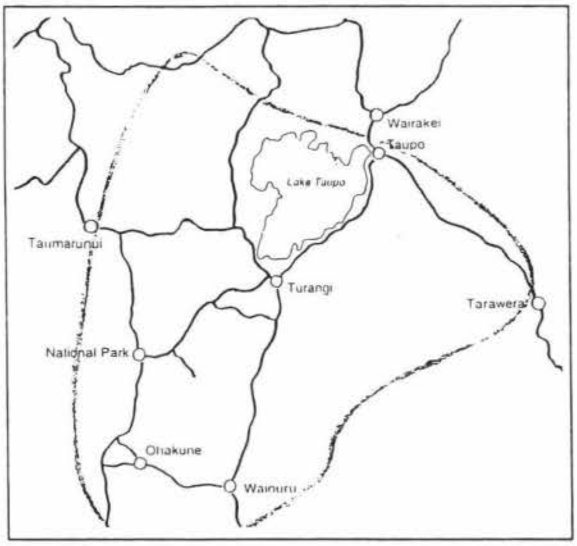
Control methods used to date have had little impact on heather spread. Mechanical controls such as hand pulling of isolated plants proved ineffective due to regrowth from remaining stem fragments and the reinvasion of heather into a disturbed area. Other control methods such as grazing, top dressing and herbicide sprays are inappropriate for most situations and are expensive. Possible exceptions may include outlying areas of heather to limit further range expansion. The Department of Conservation is currently examining the possibility of biological control using the heather beetle, *Lochmaea suturalis*. Both the adult and larvae of this species feed on heather foliage. In Europe beetle outbreaks have resulted in severe defoliation of heather moors. Host specificity tests have been conducted at the International Institute of Biological Control, Silwood Park, United Kingdom and at Lincoln University, Canterbury, New Zealand. A small test release was made in 1995, with plans for a larger scale release in 1996. If the heather beetle is proven suitable, it is expected to result in a reduction of heather growth rates, reproductive rates and dispersal. However it is not expected to eliminate heather, and heather will likely remain a significant component of the vegetation within Tongariro National Park.

European studies on the pollination of heather suggest that the honey bee is an important insect pollinator, although wind pollination is probably common (Gimingham 1960). A review of the contribution of honey bees to the reproduction of weeds in New Zealand has recently been conducted by Butz Huryn and Moller (1995). They proposed that honey bees may have a 'medium influence' on the pollination and reproduction of heather. Heather has been suggested to possess a variety of reproductive alternatives, including wind pollination, self pollination and vegetative spread (Butz Huryn and Moller 1995).



Range of heather, 1912-1921

Range of heather, 1960's



Range of heather, 1993

Figure 1. Range of heather expansion from 1912 to 1993 within the Tongariro/Taupo Conservancy, DoC. Heather indicated by ▨

With heather becoming an increasingly dominant feature within Tongariro National Park, this study aims to identify the effect of honey bees on heather pollination. By influencing the reproductive success of heather, honey bees may also be increasing heather's ability to disperse. The dependance of heather on honey bees for productive success was determined by measuring pollen deposition and seed set under differing pollinator regimes.

METHODS

Study Sites

Three sites were chosen along the Mangatepopo Road, which was the site for some of the first heather plantings. These sites were located at 0.2km, 3km and 5km in from the park boundary (Fig. 2). Altitudes at each site were 880m, 1000m, and 1080m respectively. A fourth site at 1200m along Mangatepopo Road was later selected to determine the influence of altitude on seed set in heather. A second location was chosen within the Tongariro National Park boundary opposite the Kapoors Road turn-off (Fig. 2). Both sites had honey bee hives placed just outside the park boundary. At the peak of the flowering season there were 56 hives opposite the Mangatepopo site and 89 opposite the Kapoors road site.

Floral Visitors

Patches of flowers were observed for 15 minute periods during February, 1994. After three observational periods, this time was extended to 30 minutes due to the initial low visitation rates observed. The number and type of each floral visitor was recorded as well as the number of flowers visited. At the end of each period the number of infloresences observed was counted. Approximately 20 random infloresences were collected and the number of flowers available to pollinators counted. An average number of flowers per inflorescence was used to give an indication of the total number of flowers observed.

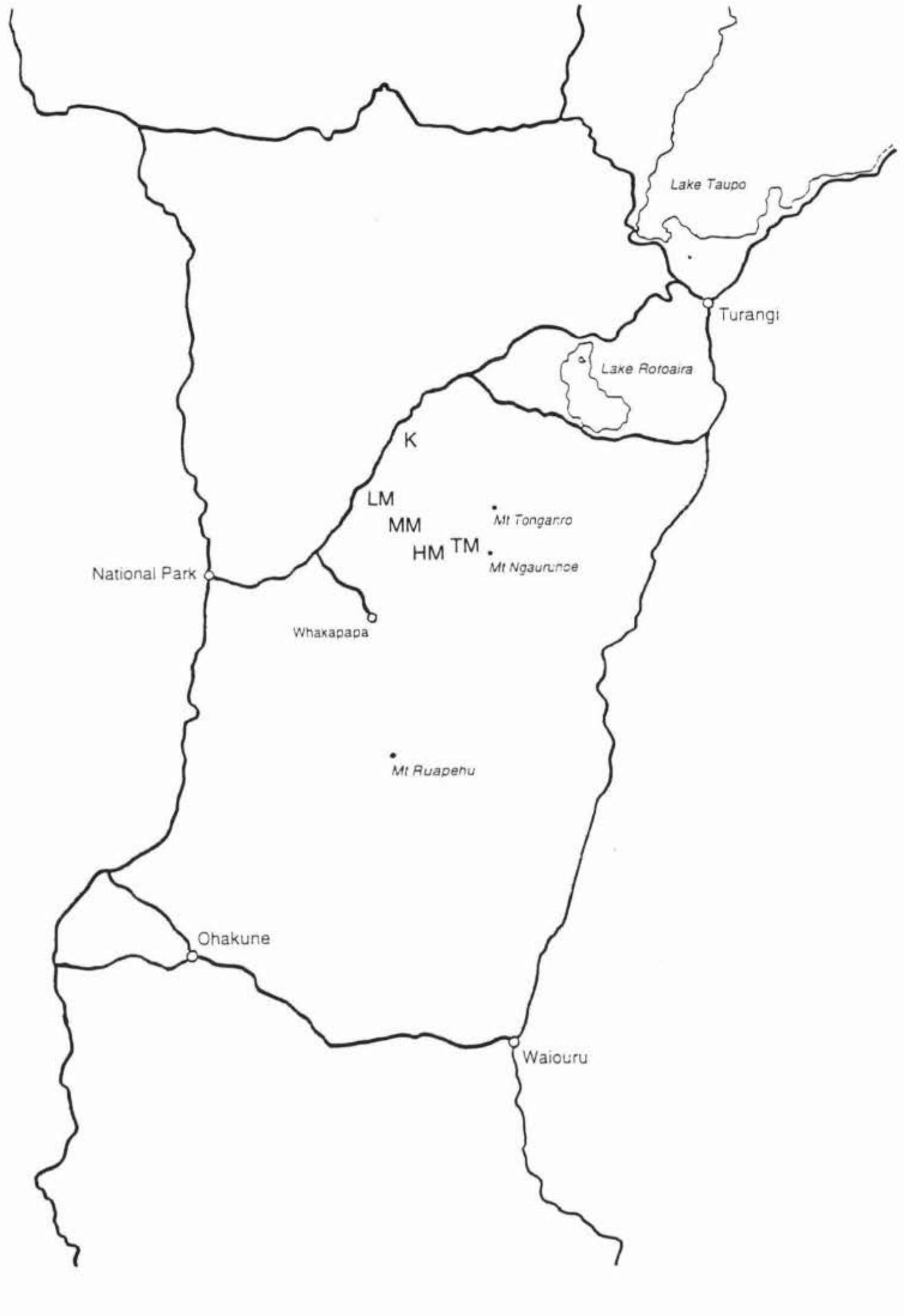


Figure 2. Map of Tongariro National Park showing the locations of heather study sites. (Note: LM= Lower Mangatepopo, MM= Middle Mangatepopo, HM= Higher Mangatepopo, TM= Top Mangatepopo, K= Kapoors Road)

Female Success

Female success of heather was assessed at four sequential stages;

i. Number of pollen grains deposited per flower

ii. Number of pollen tubes formed in the style

iii. Fertilisation rate (proportion of ovules pollinated)

iv. Seed set (proportion of ovules reaching full maturity)

Bagging Experiments, 1994 Flowering Season

In order to investigate the importance of honey bees and other large insects for seed set, plants were placed into one of two treatments;

i. bagged plants (n=5)

ii. open plants (n=5)

Ten plants were selected at three sites along Mangatepopo Road (Fig. 2) using random number tables to provide x and y co-ordinates. An open wire cage was placed around each plant and bagged plants were enclosed in mesh bags placed over the frame. The mesh was considered fine enough to prevent flying insects visiting the heather flowers. All plants were of similar size and phenological stage.

Bagging Experiments, 1995 Flowering Season

In 1995 the role of wind and thrips as pollen vectors for heather was considered. Twenty field plants whose flowers were uniformly infested with thrips, were selected at the lower Mangatepopo Road site and placed into one of two treatments:

i. thrips, wind (n=10)

ii. thrips, no wind (n=10)

Twenty plants from the same area were grown for several months at Massey University and were, at time of flowering, free of thrips. These plants were placed in the field in one of two treatments:

iii. no thrips, wind (n=10)

iv. no thrips, no wind (n=10)

Plants in the 'no wind' treatments were placed in large paper bags to prevent the transfer of air-borne pollen. All plants were placed inside fine mesh bags to prevent flying insects visiting heather flowers and to prevent thrip infestation of plants in the 'no thrip' treatments.

Pollen deposition, 1994 and 1995 Flowering Seasons

Ten infloresences from each of the above plant were tagged using wire wrap wire when all flowers were in bud. Five of these infloresences were collected during peak flowering to examine pollen deposition in each treatment. The remaining infloresences were left to set seed before they were collected. All samples were stored in 3:1, 40% alcohol:45% acetic acid solution (Dafni 1992). Stigmas were removed from open flowers and placed into a histokinette machine. They were washed twice in distilled water for thirty minutes each before being soaked in 1N NaOH for 12hrs. The stigmas were then rewashed 5x in distilled water for a total period of 2 1/2hrs to remove any remaining NaOH solution. Samples were placed in an aniline blue solution for at least 12hrs to stain (Martin 1959). They were then mounted on slides using a corn syrup: formalin mounting fluid and examined under ultra violet light using an epifluoresence microscope. The number of pollen grains present on the stigma were counted, as wall as the number of pollen tubes formed.

Seed Set, 1994 and 1995 Flowering Season

Seed capsules were dissected under a microscope and the number of seeds counted. Seeds were categorised as being;

i. **unpollinated ovules-** pale cream, small

ii. **aborted seed-** brown or dark cream, medium to large, shrivelled

iii. **set seed-** brown, large, plump

Statistical Analysis

All results were analysed using SAS's general linear models procedure (SAS Institute 1988). Hypothesis for mixed model ANOVA's were tested using the random effect as the error term for the fixed effects (Sokal and Rohlf 1981). In 1994, pollen tubes were, in many cases, too numerous to conduct an accurate count. Instead pollen tube numbers were estimated and assigned to frequency classes. An ANOVA was performed on these classifications. The proportion of seeds in each category, for both flowering seasons, were arcsine transformed to standardise their distribution before the analysis was conducted.

RESULTS

Flower visitors

In general, visitation rates to heather flowers in the field were low. Flies were the most common insect on plants (Table 1), but may have been using heather as a resting site rather than a source of food, although some flies were seen feeding. Honey bees were the only other insect observed on heather in this study. However bumble bees have been reported to forage on heather flowers (Cathy Lake pers.comm.).

Table 1. Insect Visitation Rates on Heather at four sites within Tongariro National Park. Visitation rates are expressed as visits/flower/hour. All observations conducted over 30 minute periods.

Site	Estimated Flower No.	No. Honey Bee Visits	No. Fly Visits	Bee Visitation Rates	Fly Visitation Rates	Total Visitation Rates	~No. Days till Pollination
LM	2925	0	4	0	0.0027	0.0027	30.47
LM	2111	0	11	0	0.0100	0.0100	7.99
LM	3276	0	1	0	0.0006	0.0006	136.5
UM	1638	0	0	0	0	0	∞
UM	1342	0	0	0	0	0	∞
UM	1933	1	1	0.0010	0.0010	0.0021	40.27
UM	3107	0	0	0	0	0	∞
HM	1758	0	3	0	0.0034	0.0034	24.42
HM	3014	0	0	0	0	0	∞
HM	1846	0	17	0	0.0184	0.0184	4.52
HM	2118	0	0	0	0	0	∞
HM	2020	0	0	0	0	0	∞
K	2705	1	9	0.0007	0.0067	0.0074	11.27
K	2697	0	0	0	0	0	∞
K	1359	20	0	0.0294	0	0.0294	2.83
K	1144	13	0	0.0227	0	0.0227	3.61
Total	34993	35	45	0.0020	0.0026	0.0046	18.23

The final column in Table 1 gives an indication of the number of days estimated to be required for each heather flower to be visited under the observed rate of visitation. This estimate assumes that there are twelve hours each day during which time pollinators are active.

Pollination, fertilisation and seed set, 1994 season

The average number of pollen grains deposited on the stigma per flower is shown in Table 2 for both bagged and unbagged plants, at each of the three study sites. There is no consistent effect of site on pollen deposition as an apparent increase in pollen with altitude in bagged plants is reversed in unbagged plants, resulting in a highly significant interaction between the site and bagging effects (Table 2).

Table 2. Pollen grain deposition under two pollinator regimes, 1994 flowering season.

	Bagged Plants		Unbagged Plants	
	Average	Range	Average	Range
Lower Mangatepopo	7.5	0-26	42.15	4-84
Higher Mangatepopo	14.40	0-60	19.87	1-191
Upper Mangatepopo	25.75	0-84	13.65	0-49

Source of Variation	DF	Mean Square	F Value	Pr > F
Site	2	618.72	1.00	0.384
Bagging	1	2410.01	3.88	0.061
Site*Bagging	2	5208.70	9.06	0.0003
Plant(Site Bagging)	23	620.66	1.08	0.384
Error	87	575.03		

The frequency of pollen tubes in each category are shown in Table 3 for each sites for bagged and unbagged plants. Bagged heather plants have significantly lower levels of pollen tubes than unbagged plants. The number of pollen tubes per flower is not significantly effected by the site in which the plant is located, as once again there is a strong interaction effect. Most tubes were recorded from the highest site for bagged plants, but from the lower site in unbagged plants.

Table 3. Frequency table showing number of pollen tubes formed at each site in bagged and unbagged heather flowers during the 1994 flowering season. (Medians are shown in bold).

	Frequency		Bagged			Unbagged	
Category	Class	LM	MM	HM	LM	MM	HM
0	0	**10**	9	4	0	5	5
1-5	1	3	**3**	4	2	**6**	**7**
6-10	2	0	1	1	1	1	1
10-20	3	3	6	**1**	3	5	4
20-50	4	0	1	**4**	**6**	2	3
50-100	5	0	0	4	8	0	0
100^+	6	0	0	2	0	1	0

Source of Variation	DF	Mean Squares	F Value	Pr > F
Site	2	6.18	1.87	0.177
Bagging	1	17.73	5.37	0.03
Plant (Site Bagging)	23	3.30	1.41	0.129
Site*Bagging	2	43.85	18.72	0.0001
Error	87	2.34		

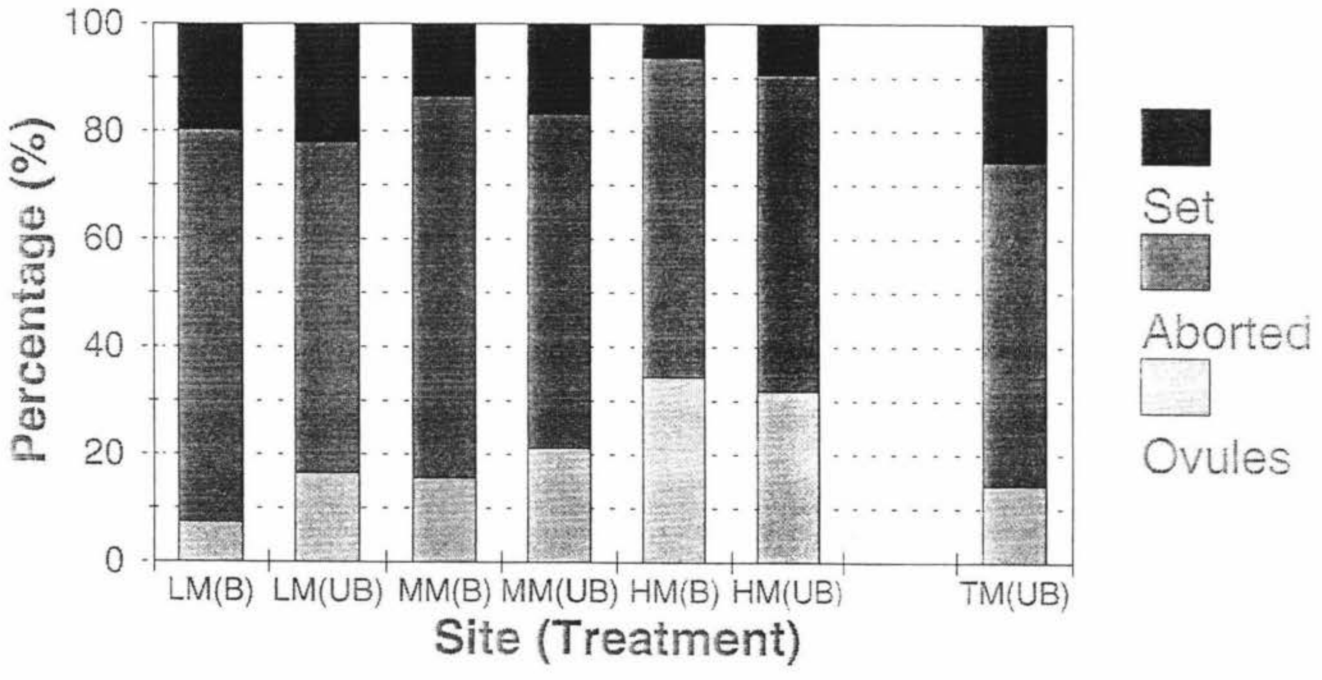


Figure 3. Proportion of set, aborted and unfertilised ovules, 1994 flowering season.

The number of heather seeds pollinated during the 1994 flowering season was estimated from an examination of ripe fruit. Pollination was apparently independent independent of the two treatments, site and bagging, whose effect on the proportion of ovules that were set, or appeared to be aborted rather than unfertilised was insignificant. The apparent increase in unfertilised ovules with altitude was not significant. Differences between individual plants, however, were highly significant (Table 4).

Table 4. ANOVA table showing the effects of site, bagging and individual plant variation on the proportion of heather ovules apparently fertilised, 1994 flowering season. (The proportions were arcsine square root transformed for analysis).

Source of Variation	DF	Mean Squares	F Values	Pr > F
Site	2	0.276	0.31	0.7365
Bagging	1	0.0057	0.01	0.9368
Plant(Site Bagging)	23	0.890	8.95	0.0001
Site*Bagging	2	0.253	2.54	0.0816
Error	176	17.50		

Similarly, seed set in heather did not differ significantly between treatments, with most of the variation occurring at the level of the plant (Table 5).

Table 5. ANOVA table showing the effects of site, bagging and individual plant variation on seed set in heather, 1994 flowering season. (The proportions were arcsine square root transformed for analysis).

Source of Variation	DF	Mean Squares	F Values	Pr > F
Site	2	0.355	2.58	0.0974
Treatment	1	0.001	0.01	0.9276
Plant (Site*Treatment)	23	0.137	3.10	0.0001
Site*Treatment	2	0.026	0.59	0.5535
Error	176	0.044		

Pollination, fertilisation and seed set rates, 1995 season

There was a significant difference in the number of pollen grains deposited in the two replicate trials conducted during the 1995 flowering season (Table 6). The second trial had higher pollen levels per flower. The effects of both wind and thrips on pollen deposition in heather are both significant with thrips highly so, pollen grain numbers were higher in the No Wind and No Thrip treatments in both trials.

Table 6. Pollen grain deposition under four pollination regimes, 1995 flowering season. (NTW= no thrips/wind, NTNW= no thrips/no wind, TW= thrips/wind, TNW= thrips/no wind)

	Trial 1				Trial 2			
	NTW	NTNW	TW	TNW	NTW	NTNW	TW	TNW
Average	3.50	5.77	2.30	1.80	10.20	20.67	2.90	3.70
Range	0-11	0-76	0-14	0-20	0-52	1-115	0-27	0-52

Source of Variation	DF	Mean Square	F Value	Pr > F
Trial	1	2226.50	25.23	0.0007
Wind	1	663.34	7.52	0.0228
Thrips	1	3307.84	37.48	0.0002
Plant	9	88.26	0.77	0.6437

The trial effect is highly significant with flowers in the second trial having higher numbers of pollen grains deposited per stigma (Table 6). Thrips have a highly significant, but negative effect on pollen deposition.

Table 7. Effects of trial, wind, thrips and individual plant variation on pollen tube formation, 1995 flowering season.

	Trial 1				Trial 2			
	NTW	NTNW	TW	TNW	NTW	NTNW	TW	TNW
Average	0.40	0.33	0.17	0.03	0.53	1.47	0.07	0.33
Range	0-3	0-5	0-3	0-1	0-4	0-5	0-1	0-4

Source of Variation	DF	Mean Squares	F Value	Pr > F
Trial	1	7.70	5.98	0.0371
Wind	1	4.54	3.52	0.0934
Thrip	1	19.84	15.39	0.0035
Plant	9	1.29	1.88	0.059
Error				

The trial effect is also significant for pollen tubes formation, with the second trial having higher numbers of pollen tubes formed. Thrips, again, have a significant, but negative effect on pollen tube formation.

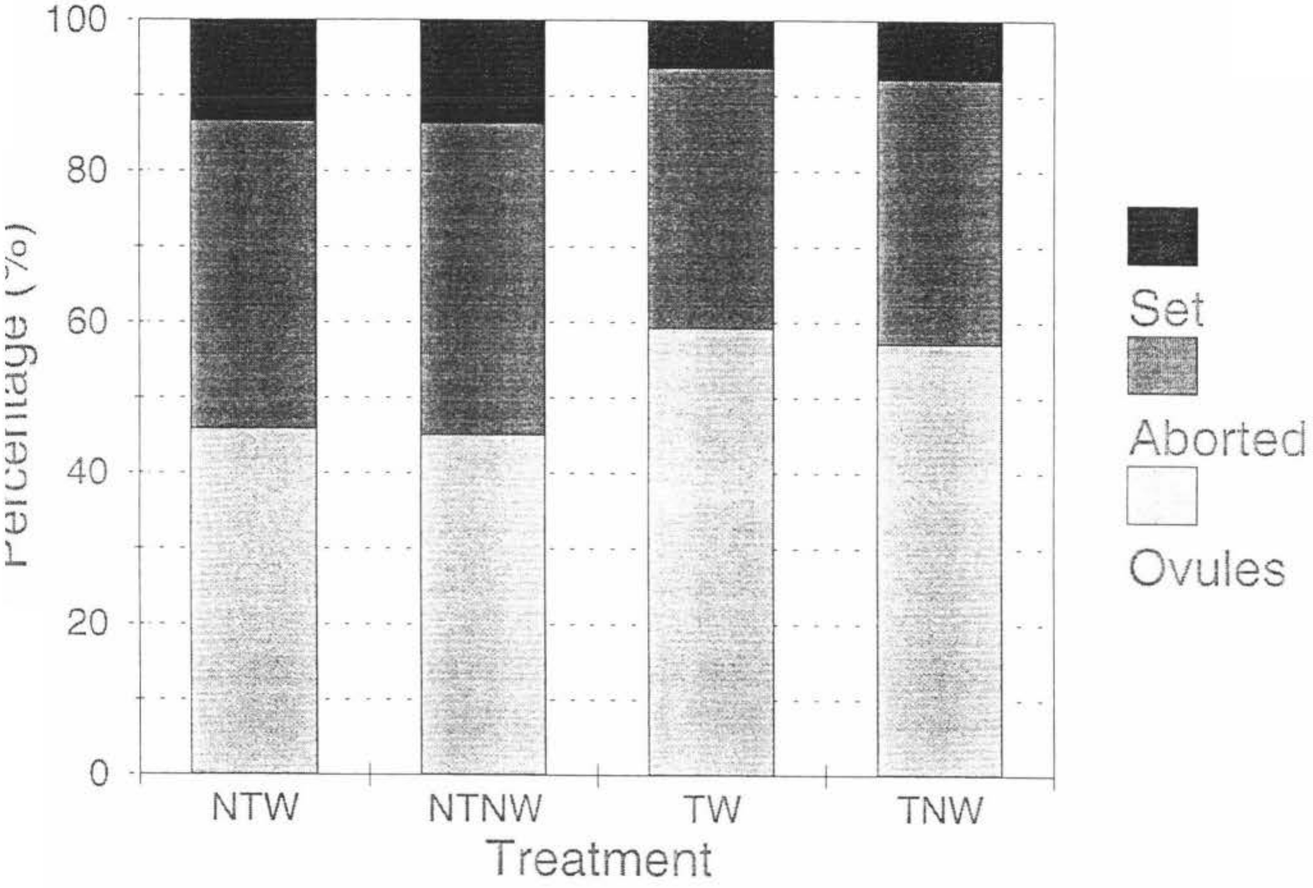


Figure 4. Proportion of set, aborted and unfertilised ovules, 1995 flowering season.

Table 8. ANOVA table showing the effects of wind, thrips and individual plant variation on the pollination of heather ovules, 1995 flowering season.

Source of Variation	DF	Mean Squares	F Values	Pr > F
Wind	1	0.00174	0.02	0.8816
Thrips	1	0.6356	8.58	0.0168
Plant	9	0.0741	0.93	0.5138
Error	40	0.08		

Table 9. ANOVA table showing the effects of wind, thrips and individual plant variation on seed set in heather, 1995 flowering season.

Source of Variation	DF	Mean Squares	F Values	Pr > F
Wind	1	0.0001	0.36	0.5645
Thrips	1	0.0008	1.65	0.2306
Plant	9	0.0005	1.85	0.0884
Error	40	0.0003		

Individual plant effects were not significant during the 1995 flowering season. The thrips were only significant in their effect on the pollination of ovules in the 1995 season.

DISCUSSION

Insect visitation rates were low at each of the four study sites. Native flies were the most common insect guild observed on heather. However, it is important to note that it was not always possible to distinguish between flies that were feeding or resting, the overall utilisation of heather by native fly species may actually be lower than has been reported here. Honey bees were the only other flower visitor observed during the study period although foraging by bumble bees on heather has been reported (Cathy Lake, pers. comm.). Table 1 also provides estimates for the number of days required, under observed visitation rates, for each flower to be visited. The average life span of heather flowers is approximately 4-5 days (pers. obs.). With an average of 18 days until visitation, it is likely that the majority of flowers will not be visited at all by insect vectors. Primack (Primack 1983) suggests that for some alpine species, periods of adverse weather conditions may extend the life span of flowers. If this is true for heather then the time available for flowers to be pollinated may actually be longer than this. Nevertheless it seems unlikely that all flowers will pollinated by insect vectors.

Although honey bees are thought to be important pollinators of heather in Europe, my study provides no evidence that honey bees influence the pollination or seed set levels of heather. Plants that were bagged to exclude honey bees, and other pollinators, did not differ significantly from open plants in terms of the number of pollen grains deposited per stigma, the number of ovules pollinated or seed set levels. Bagged plants did however, have slightly, but significantly, lower levels of pollen tubes than unbagged plants at each study site in 1994. This difference did not alter female fitness, however, as both treatments had similar seed set levels in that season.

Previous studies on heather (Chapman 1984) suggested that seed set levels decrease with increasing altitude. My data does not support this, with no significant site differences for any of the measures of female success. Unbagged flowers from the Top Mangatepopo site (1200m a.s.l) had no significant differences in seed set levels from the three other sites examined. This suggests that either altitude is not measurably affecting female success, or that any effects of altitude are not expressed over the range of sites studied. Chapman's (1984) highest sites, from 1500m a.s.l were considerably higher than the highest site studied here.

As I found no evidence of a requirement by heather, for pollination by honey bees, the potential for wind and thrip pollination was examined during the 1995 flowering season. The presence of both wind and thrips were found to have a negative effect on at least one measure of female fitness. Two replicate trials conducted, the first after a period of wet weather, showed a strong negative effect of thrips on pollination rate and a smaller effect of wind, again negative. The second trial was found to have significantly higher levels of pollen deposition and pollen tube formation. Rain was thought to have had a negative effect on the amount of air-borne pollen during the first trial. Wind had a significant effect on the amount of pollen received by flowers, with plants in the no wind treatments having higher levels of pollen deposition. This may be a side effect of the bagging treatment. The paper bags not only reduced air flow around the plant, but also protected flowers from any rain effects. Wind did not significantly effect any of the other measures of female success. Thrips on the other hand had significant effects on three measures of pollination rate, but not on seed set. Plants that were not infested with thrips had higher numbers of pollen grains per stigma, pollen tubes formed and a higher proportion of fertilised ovules. These results may, however, have been influenced by the quality of plants used for each treatment. Plants in the no thrip treatments were grown at Massey University in fertilised plant mix for several months before being placed in the field. The high level of nutrients available to these plants may increase their overall fitness, enabling them to produce more pollen and increase reproductive success. Another explanation for the observed thrip effect is the feeding behaviour of thrips. Thrips are pollen feeders (Dugdale 1975), so high infestation levels may reduce the number of pollen grains available to plants for fertilisation. Certainly no positive role in pollination of heather for thrips can be suggested.

Studies of heather pollination over two flowering seasons, 1994-1995, indicate that none of the potential pollen vectors (honey bees, wind or thrips) have a significant effect on the overall fitness of heather in terms of seed set. This suggests that heather has a flexible pollination system that enables it to maintain a constant level of seed set under a variety of pollination regimes. An overabundance of ovules allows heather to compensate for poor pollination rates. The two seasons differed in the rate of pollen receipt, but there was little or no effect on seed production from the differences in pollination rates.

CHAPTER 3. VARIABLE POLLINATOR REGIMES AND THEIR EFFECT ON FEMALE REPRODUCTIVE SUCCESS IN FLAX

INTRODUCTION

Flowering plants require pollination to ensure reproductive success. Pollination may be abiotic (ie: wind) or biotic, requiring animals or insects to transfer pollen from anthers to stigma. Biotic pollinators include small mammals (ie. bats), birds and insects from a variety of orders including hymenoptera, lepidoptera and diptera. Some plants are structurally adapted for specialised pollination relationships with a pollinating agent. For example tubular flowers, such as several orchid species, can only be fertilised by long tongued bees (Thomson 1880). This degree of specialisation can be circumvented by nectar 'robbers' which chew through the base of the corolla to reach the nectaries (Primack 1978, Dijkgraaf 1994). Other insects may also use this hole to obtain nectar, bypassing the anthers and stamen, and not facilitating pollination. Flower visitors may also be ineffective pollinators of some plant species if they visit only male phase flowers, fail to remove pollen or don't carry sufficient pollen between flowers, and if they fail to contact the receptive stigma (Armstrong 1979, Paton and Turner 1985, Vaughton and Ramsey 1991, Paton 1993).

Honey bees (*Apis mellifera*) can now be considered a commensal species, found in similar environments in different areas of the world. The introduction of the honey bee to new ecosystems has several possible implications including competition with native pollinators and ineffective pollination of native plant species. Many typically bird pollinated plant species are also visited by insects, both native and introduced species. Previously thought to be beneficial by providing extra pollination services, recent studies indicate they may be inefficient pollinators of bird pollinated species (Collins *et al.* 1984, Craig and Stewart 1988, Paton 1993). Paton's (1993) review of interactions between honey bees and native plant species in the Australian environment supports this idea. Studies on *Callistemon rugulous* show that foraging honey bees contact the stigma less often than honeyeaters. Nectar-feeding honey bees struck the stigma on 4.4% of all visits and pollen-feeding honey bees on 16.7% of visits. This is compared to honeyeaters which contact the stigma on more than 50% of all visits to flowers. *Correa reflexa* is pollinated by both honeyeaters and pollen feeding honey bees, however, fruit and seed production is significantly reduced when birds but not honey bees are excluded from flowers. These observations suggest that honey bee are less effective pollinators of Australia's native plant species. The effectiveness of honey bees as pollinators of *Banksia spinulosa* was examined by Vaughton (1992) and Carthew (1993). Honey bees were able to successfully pollinate 38% of flowers visited but they were only active at the latter part of the flowering season so that their overall success as pollinators was limited. Collins *et al.*. (1984) studied the pollination system of *Calothamnus quadrifus* (Myrtaceae). Floral visitors for the species included honeyeaters, honey bees, nocturnal moths and other invertebrates. The distance between the nectaries and anthers of *C. quadrifus* flowers suggests that honeyeaters were more important vectors of pollen than insects. However honey bees do contact the anthers on 42% of visits. Collins *et al.*. suggest that the relatively high abundance of honey bees near the flowers offsets their low pollen loads and individual visitation rates making the overall honey bee population an effective pollen vector for *C. quadrifus*.

The ineffectiveness of honey bees as pollinators of native species may be due in part to their foraging behaviour. They rarely move between plants, foraging in restricted areas, therefore not effecting cross pollination. Honey bee alsotend to visit male phase~~d~~ flowers, rich in pollen and nectar, avoiding the older female phase~~d~~ flowers and decreasing the chance of contacting a receptive stigma. Honey bees may also affect the pollination of plants by deterring native, potentially more effective pollinators, from flowers. This may be achieved by the removal of pollen and nectar resources (Carthe 1993, Paton 1993) or by their presence on flowers (Johnson and Hubbell 1974). Johnson and Hubbell (1974) noted that lone scout bees did not land on a food source when another bee species was present, even when no agonistic behaviour was shown by the current occupant. They suggest that there is some evidence for avoidance due to marking pheromones released by the first bee. In addition to removing resources which would otherwise be available to other pollinators, bees have also been shown to chase away competitors, such as hermit hummingbirds in Costa Rican rain forests (Gill *et al.* 1982)

New Zealand Flax (*Phormium tenax*) also has mixed pollinator regime. Flax is thought to be predominantly bird pollinated. On the mainland, floral visitors include native species such as tui (*Prosthemadera novaeseelandie*), bellbird (*Anthornis melanura*) and silver eye (*Zosterops lateralis*) and introduced species such as starlings (*Sturnis vulgaris*) and Indian mynas (*Acridotheres tristis*) (Craig and Stewart 1988). Tui and bellbirds are both honeyeaters (Melphagidae) and are common visitors to flax. Birds carry pollen on their foreheads and the stigma curvature ensures pollen is only deposited during the most receptive phase (Craig and Stewart 1988). Honey bees and native bees are also regular visitors on flax flowers in areas where their ranges overlap (pers obs.). However the physical positions of anthers and stigmas means that they are unlikely to be effective pollinators. An inflorescence that was bagged to prevent pollination by birds but allowed access by insects set <1% of it's flowers whereas infloresences available for pollination by birds and insects set around 20% of their flowers (Craig and Stewart 1988).

In flowering species, nectar production incurs a cost to the plant in terms of energy, carbon and water requirements. Nectar production may utilise up to 37% of a plant's daily energy availability as shown by Southwick (1984) for *Asclepias syriaca*. This cost to the plant may be expressed in terms reduced seed set (Pyke 1991). The plant must maintain nectar concentrations at a level to ensure that floral visitors do not become satiated before making sufficient visits to ensure pollination while providing sufficient reward to attract visitors to the flowers (Kevan and Baker 1983). After pollinator visits, plants may replenish lost nectar supplies (Corbett.SA and Delfosse 1984, Pyke 1991). In plants where nectar is stored close to the nectaries and where the nectaries remain attached to the plant after the corolla falls off, reabsorption may occur. Reabsorption has been shown in *Rubus*, *Trifolium*, *Eucalyptus*, *Brassica* (Burquez and Corbett 1991), and *Grevillea* (Nicholson 1995).

Despite the cost of nectar production, the ecological significance of nectar reabsorption has rarely been considered. Reabsorption is assumed to have the main function of retrieving valuable sugars not utilised by floral visitors. These resources are then made available to developing seeds and other flowers on the same plant (Burquez and Corbett 1991, Nicholson 1995). If continual probing for nectar after pollination increases the risk of destruction of the ovaries, thereby reducing seed set, it would be advantageous for the plant to remove the nectar via absorption or by allowing the nectaries to fall off with the corolla (Burquez and Corbett 1991). Nicholson (1995) suggests that reabsorption in *Grevillea* may also be important in maintaining a low nectar concentration in spite of evaporation.

Flax (*P. tenax*) is widely distributed throughout Tongariro National Park. The abundance of birds, particularly the honeyeaters tui and bellbird, however, is highly variable. The pollinator regimes are further influenced by the presence or absence of honey bees at various sites. The success of flax under these differing pollinator regimes is examined here. The effects of these differing regimes on female fitness of flax is determined by calculating pollen deposition, as well as fruit and seed set, at various sites. I also aim to identify the visitation rates of both birds and insects to flax, and to determine what impact visitation rate has on nectar standing crops. The potential for nectar replenishment and reabsorption under different pollinator regimes is also examined.

METHODS

Study Organism

Phormium tenax (Phormiaceae), the New Zealand flax is a large monocotyledon endemic to New Zealand. It can reproduce sexually and vegetatively by producing 'offshoots'. A typical plant may consist of tens of these offshoots including the original seedling (Craig and Stewart 1988). This 'plant' is presumed to represent a single genotype and crossing pollen between flowers of different offshoots results in selfing.

Infloresences are tall, up to 3m high and consist of a main branch or primary peduncle, and alternating secondary peduncles which carry the flowers (Fig. 1). Each inflorescence may consist of between 250-700 flowers (Craig and Stewart 1988, Becerra and Lloyd 1992).

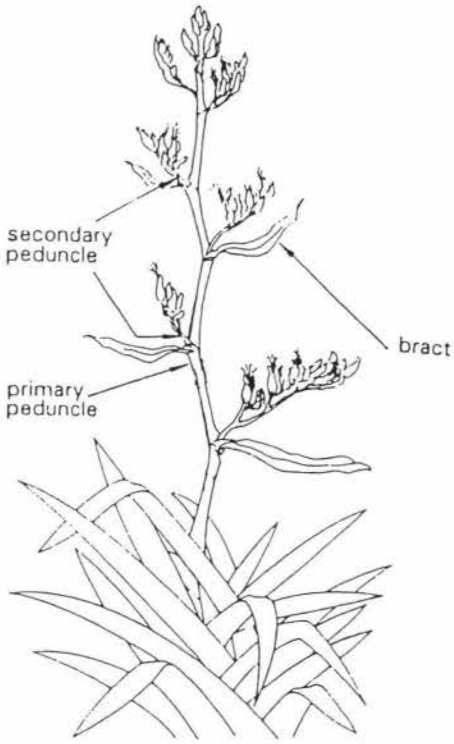
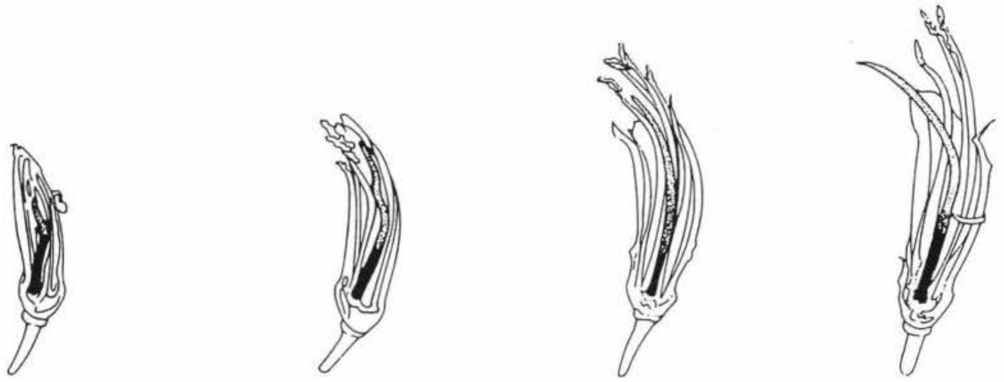


Figure 1. Diagramatic representation of flax (*P. tenax*)

All flowers are hermaphroditic and protandrous with the male and female phases being presented to pollinators sequentially (Craig and Stewart 1988). Flowers are approximately 5cm long with a diameter of 1cm (fig. 2). The colour varies from yellow-orange to deep red. Flowers produce abundant nectar and clumped pollen (Craig and Stewart 1988). Flax flowers irregularly with up to a 75-fold difference in flowering between good and bad years (Brockie 1986). Brockie suggests that high ambient temperatures during late summer early autumn initiate flowering in flax. Although *Phormium* provides an excellent nectar source for birds, due to it's periodic flowering capacity, it may prove an unreliable source with crops failing 3 out of 10 years.



Stage 0
Flowers closed

Stage 1
Anthers presented
Bright orange pollen

Stage 2
Pale yellow pollen
Most pollen removed

Stage 3
Female phase
Stigma curves away from anthers

Figure 2. Flowering stages of *P. tenax* , showing characteristics used to determine floral age.

Controlled pollination experiments were conducted by Craig and Stewart (1988) using pollen from a variety of sources. In the 1982/83 trials pollen from the same inflorescence and from different plants were used. Only the cross-pollinated flowers set seed. In 1984/85 all flowers set some seed, although seed set in self-pollinated flowers was low. Craig and Stewart suggest that flax is not strictly self-incompatible but that it preferentially sets outcrossed seed. The relative success of fruit set in crossed and self-pollinated flax flowers was also examined by Beccerra and Lloyd (1992). Trials were conducted during the 1988-89 season. Three different pollination treatments were used:

1. Infloresences receiving only self-pollination
2. Infloresences receiving only cross-pollination
3. Infloresences receiving mixed-pollination

For infloresences in the mixed pollination treatment, individual flowers were either selfed or cross-pollinated. The frequency of fruit set among infloresences in treatment 1 and 2 were not significantly different suggesting that flax is self-compatible. However on infloresences receiving mixed pollination, treatment 3, significantly more cross-pollinated fruits were maintained when compared with self-pollinated fruits. Where the two pollination types compete for limited resources cross-pollinated fruits are preferentially retained. Competition between crossed and self-pollinated flowers is stronger when the flowers are closer together on the inflorescence.

Craig and Stewart (1988) recognise three types of flax seed. Outcrossed seeds are large with a fully developed embryo and have a large attached wing presumably for dispersal. Seeds selfed from the same inflorescence are small with little endosperm. The small seeds are assumed to be inviable and to represent aborted zygotes or unfertilised ovules (Craig and Stewart 1988, Craig 1989a). Self-pollination between infloresences on the same plant result in an intermediate form with a large seed and little endosperm. In addition, up to 10% of all zygotes are apparently aborted to allow the pod to remain vertical (Craig 1989b).

Study sites

Seven sites were selected within the Tongariro/Taupo conservancy, predominantly around the Tongariro National Park boundary (Fig. 3). The sites are listed as follows:

1. Mangawhero Campsite (MW)
2. National Park Corner (NP)
3. State Highway 48 (SH48)
4. Erua (E)
5. Mangahuia Campsite (MH)
6. Lake Rotoaira (LR)
7. Whakapapa Village (WV)

Figure 3. Map of Tongariro National Park and surrounding areas. (Site abbreviations shown in methods)

Floral Visitors

Preliminary observations of bird and insect visitation to flax flowers were conducted at each site. Insects were collected from flowers for easy identification in the field. They were then pinned out for proper identification. A video camera was set up at each site where bird foraging was previously noted to determine the rate of floral visitation by birds. The video tapes were later viewed to determine the number of flowers visited by each bird species. The number of flowers available for foraging were counted and the length of the observation period recorded. The number of flowers visited during each foraging bout was also calculated. The video camera was also used to determine the rate of insect visitation in the same way. In addition, a census of insect abundance and diversity at each site were conducted by recording the number and type of each insect observed on flax flowers over a 10-15 minute random walk through the site.

Nectar standing crops

These were determined by collecting one stage 2 flower (Fig. 2) from twenty random plants at each of the seven study sites. The volume and concentration of nectar was recorded to determine an average standing crop for each site. Nectar samples were collected using capillary tubes. The amount of nectar collected was measured and the sugar concentration determined using a refractometer (Bellingham and Stanley close-set 0-50% sugar refractometer). Refractometers express results of sucrose equivalents as milligrams of sugar per 100 milligrams of solution. These measurements were then converted to milligrams of sugar per flower by converting the measured refractometer reading into grams per litre and multiplying this value by the volume of nectar. These figures were adjusted using conversion tables for the density of sucrose at the observed concentrations (Dafni 1992).

Nectar Production

Secondary peduncles (Fig 1) on six plants at the Lake Rotoaira and Erua sites were bagged in fine mesh to prevent nectar consumption by birds or insects. Flowers reaching stage 2 (Fig. 2) were selected for nectar replenishment/reabsorbtion studies.

Two bagged and two unbagged flowers on each plant were sampled every 24 hours for three days. A further set of two bagged and two unbagged flowers were only sampled on the third day to determine whether or not nectar removed on days one and two was replenished. Flowers were later studied at SH48 to further examine the potential for nectar replenishment and nectar reabsorption in flax. Six flowers on one inflorescence were bagged on each of six different plants. All flowers were tagged at the stage 0 (Fig. 2) and were placed into one of three treatments.

> Treatment 1. Day 1 flowers- sampled at four hourly intervals from 8am-8pm. Resampled after 24 and 48 hours.
>
> Treatment 2. Day 2 flowers- sampled at 8am on day 2. Resampled after 24 hours.
>
> Treatment 3. Day 3 flowers- sampled at 8am on day 3.

Pollen Deposition

Stigmas were collected from the same flowers sampled for determining nectar standing crops at each site and stored in a 3:1, 40% alcohol:45% acetic acid solution until required (Dafni 1992). In the laboratory, the stigmas were placed into a histokinette machine where they were washed twice in separate distilled water baths. The stigmas were then placed in 2M NaOH solution to soften for 12 hours. The stigmas were then rewashed 5x in distilled water for a total period of 2 1/2 hours to remove any remaining NaOH solution. Samples were placed in an aniline blue solution for a minimum of 12 hours to stain. The stigmas were mounted on to slides using a corn syrup and formalin mounting fluid and examined under an epifloresence microscope at 340nm. The number of pollen grains on the stigma were counted as well as the number of pollen tubes formed.

Fruit Set and Seed Set

Fruit set was determined by counting the number of pods formed on twelve random plants at each site. Two stalks were selected from each plant. The number of pods formed and flowers aborted were recorded. Evidence of aborted pods was provided by the retention of petioles. Two pods were collected off each inflorescence and counted to determine seed set. The incidence of insect damaged pods was also noted.

Statistical Analysis

All statistical analysis of the data was conducted using SAS's general linear models (GLM) procedure (SAS Institute 1988). Hypotheses for mixed model ANOVAS's were tested using the random effect as the error term for fixed effects (Sokal and Rohlf 1981).

RESULTS

Floral Visitors

Birds were only observed foraging on flax flowers at four of the seven sites- Lake Rotoaira, Erua, Mangawhero and Whakapapa Village. However at Erua, tui were only observed at the bushline, on plants that were inaccessible for closer observation and the collection of samples. Tui were the most common bird visitor to flax at each of the four sites, whilst bellbird were also observed at Lake Rotoaira and Mangawhero. On one occasion silvereyes were observed foraging on flax at Lake Rotoaira.

Floral visitation rates were calculated as the number of flowers visited over the total number of flowers observed divided by the length of the observational period. This figure was then expressed as visits/flower/hour and is shown in Table 1. Insect visitors were divided into five different guilds for ease of video identification. The guilds include honey bees, native bees, nectar feeding native flies, pollen feeding syrphids (Holloway 1976, Hickman *et al.* 1995) and other, including bumble bees and wasps. Total insect visitation rates varied greatly between sites (Table 1). Some of the insect guilds observed foraging on flax during video analysis were not recorded as being present in the census findings (Table 2).

Table 1. Flax flower visitation rates, expressed as the number of visits/flower/hour, for (a) insects arranged by guild and (b) birds at six sites around Tongariro National Park. (Site abbreviations shown in methods, the number suffix representing separate sampling occasions).

(a) Insect visitation rates

Site	MW1	MW2	LR	MH1	MH2	SH1	SH2	E	NP1	NP2
Date	11/2	12/2	25/1	29/1	10/2	31/1	31/1	10/2	29/1	10/2
Time(min)	32	31	29	66	31	27	29	32	34	35
Flower No.	17	23	27	25	31	19	16	21	21	11
Honey Bees	0.11	0.75	0.23	0	0.43	0	1.30	0.18	0.08	1.89
Native Bees	0	0	1.47	0	0.50	0	0.26	0.53	0	0
Native Flies	0.89	0	1.08	0.29	0.56	0	0.91	0.09	0.92	1.72
Syrphids	0	0	0.46	0.07	0	0	1.20	0	0.25	0
Other	0	0	0.08	0	0.25	0	0	0.45	0	0
Total	1	0.75	3.32	0.36	1.74	0	3.67	1.25	1.25	3.61

(b) Bird visitation rates

Site	LR1	LR2	LR3	LR4	MW1	MW2	E1
Date	20/1	21/1	25/1	25/1	9/2	9/2	21/1
Time(min)	118	140	119	96	121	115	34
No. Flowers Observed	1635	1292	479	646	455	883	365
No. Flowers Visited	0	0	120	0	113	452	0
Visistation Rate	0	0	0.13	0	0.46	0.26	0

Table 2. Census results for insects, expressed as encounter rates/minute of flax floral visitors.(Site abbreviations shown in methods, number represents separate sampling ocas~~s~~ions)

Site	MW	LR1	LR2	NP1	NP2	MH1	MH2	SH1	SH2	E1	E2
Date	9/2	21/1	25/1	29/1	10/2	30/1	10/2	31/1	31/1	24/1	9/2
Time(min)	8	14	15	18	16	12	12	12	10	13	16
HBee	-	0.43	0.20	1.17	2.06	0.17	0.08	2.17	3.50	0.38	0.50
Lg		1.57	0.80	0.56	-	2.00	-	1.08	0.4	0.77	0.94
Sm	-	2.00	0.93	0.06	-	2.25	-	0.83	0.20	0.31	0.13
Wasp	-	0.07	-	-	-	-	-	-	-	-	-
BBee	0.13	0.14	0.33	-	0.06	-	-	-	-	0.23	0.06
Tach	-	-	0.27	-	-	-	-	-	-	-	-
Csyr	0.63	-	-	0.78	0.38	0.33	-	1.75	1.10	0.15	0.31
Blue	-	-	-	1.56	0.63	-	-	-	-	-	-
Smfl	-	-	-	0.28	0.38	-	0.75	-	-	-	-
Babd	-	-	-	-	-	0.50	0.17	0.33	0.40	-	0.06

Nectar Standing Crops

The standing crop of Stage 2 flowers for each study site is shown in Fig. 4. The mean nectar concentration for flax flowers was determined to be 18.09% (Table 3). With an average volume of 179.85 æl the mean amount of sugar per flower was calculated at 35.18mg (Table 3). These values for flax flowers were then compared to other bird pollinated species (Table 4).

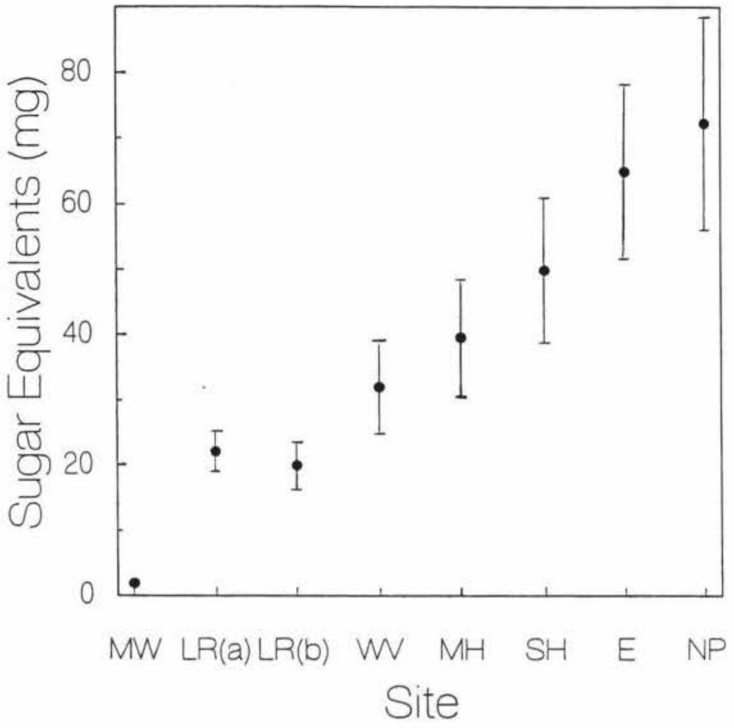


Figure 4 . Nectar Standing Crops (mean ± s.e) of Stage 2 flowers, expressed as milligrams sugar equivalents.

Table 3. Nectar Standing Crop (n=204)

	Volume (μl)	% Sugar	mg Sugar
Mean	179.85	18.09	35.18
Median	159	18	29.77
Maximum	802	23	164.23
Minimum	0	6	0

Table 4. Comparisons of mean nectar production in bird pollinated species. Arranged in decreasing order of milligrams sugar produced per flower.

Plant spp.	Bird spp.	Volume (µl)	% Sugar	mg Sugar
Phormium tenax	Honeyeater	179.85	18.09	35.18
Meterosideros excelsa[b]	Honeyeater	-	-	7.54
Lobelia laxiflora[a]	Hummingbird	28.8	23.1	7.26
Salvia fulgens[a]	Hummingbird	23.2	24.1	6.16
Meterosideros fulgens[b]	Honeyeater	-	-	4.60
Salvia spp.[a]	Hummingbird	12.6	28.7	4.05
Castilleja tenuiflora[a]	Hummingbird	2.9	41.6	1.43
Campsis spp.[a]	Hummingbird	4.7	23.2	1.19
Dysoxylum spectabile[b]	Honeyeater	-	-	1.02
Castilleja integrifolia[a]	Hummingbird	1.6	33.4	0.61
Salvia iodantha[a]	Hummingbird	2.1	25.3	0.59
Fuschia exorticata[a]	Honeyeater	-	-	0.52

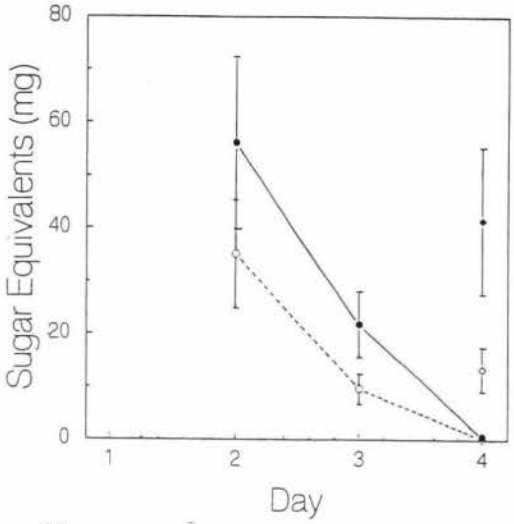
[a] Heyneman 1983

[b] Castro and Robertson in prep. Flowers were bagged for 24 hours to accumulate nectar. This may underestimate total nectar production.

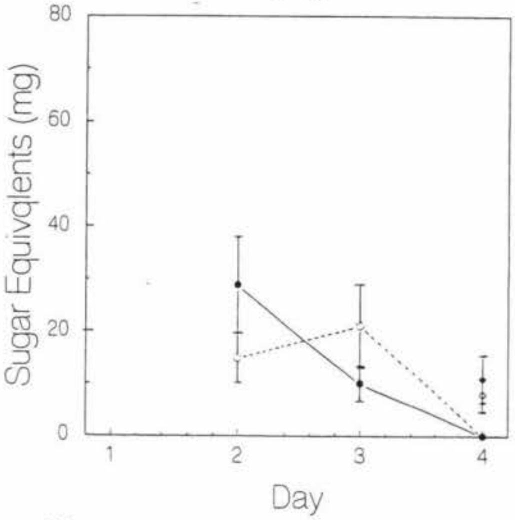
Nectar Production

The amount of sugar produced over a three day period at two sites, Erua and Lake Rotoaira is shown in Fig. 5(a) and 5(b) for bagged and unbagged flowers. The initial sampling of mean sugar production at each site indicates that more sugar was available at Erua (22.82mg) than at Lake Rotoaira (14.38mg). Bagged flowers has lower standing crops than open flowers at Erua suggesting low rates of nectar cropping and a small but insignificant negative effect of bagging on nectar production. There was a low standing crop of nectar at Laek Rotoaira, even in bagged flowers, but as the flowers were not bagged until stage 2, much of the nectar may have already been removed by the active bird presence at the site. The results also indicate that more nectar is available in younger flowers at Erua (Fig. 5(a)) and that this amount decreases with floral age, levelling off at days 2 and 3. This provides evidence for nectar reabsorption in flax flowers when nectar is not removed by foragers. This trend significant for Erua (Table 5(a)). Replenishment of low floral nectar resources is indicated at Lake Rotoaira in bagged flowers, where more nectar is available at Day 2 than Day 1. This difference however is not significant ($P>0.4$). Nectar replenishment was also evident at State Highway (Fig. 5(c)) where small quantities of nectar were produced in flowers after initial sampling. The levels of nectar replenishment were insignificant when compared to the initial levels of nectar production. The amount of nectar available to foragers however is significantly higher ($P<0.005$) at Day 1 than in flowers first sampled at Days 2 and 3 (Fig. 5(c)). In this light, the nectar standing crops for each site (Fig. 4) taken from stage 2 flowers may have missed the peak in nectar levels.

5(a) Erua



5(b) Lake Rotoaira



5(c) State Highway

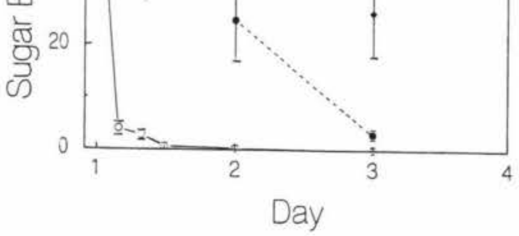


Figure 5. Nectar production (mean ± s.e) of bagged (●) and unbagged (○) flax flowers at Erua and Lake Rotoaira. Nectar is expressed as milligrams sugar equivalents. All flowers were bagged at State Highway (○ represents flowers sampled every 4 hours between 8am and 8pm on Day 1, and every 24 hours thereafter. ● represents flowers first sampled on Day 2 and resampled after 24 hours. ♦ represents flowers sampled once on Day 3).

Table 5. ANOVA showing the effects of day, bagging and individual plant variation on nectar sugar(mg) production at three study sites.(Note: All flowers were bagged at State Highway)

5(a) Erua

Source of Variation	DF	Mean Square	F Value	Pr > F
Day	1	4539.25	14.11	0.013
Bagging	1	4543.42	5.07	0.074
Plant	5	672.32	0.96	0.531
Day*Bagging	1	6.41	0.01	0.932
Day*Plant	5	321.81	0.38	0.858
Bagging*Plant	5	896.39	1.05	0.415
Day*Bagging*Plant	4	700.78	0.82	0.526
Error	20	851.11		

5(b) Lake Rotoaira

Source of Variation	DF	Mean Square	F Value	Pr > F
Day	1	841.67	3.67	0.1137
Bagging	1	221.77	0.85	0.3981
Plant	5	584.26	3.13	0.1880
Day*Bagging	1	18.32	0.17	0.6917
Day*Plant	5	229.65	2.09	0.1506
Bagging*Plant	5	260.05	2.36	0.1157
Day*Bagging*Plant	3	186.40	1.69	0.2307
Error	10	109.99		

5(c) State Highway

Source of Variation	DF	Mean Square	F Value	Pr > F
Day	2	3227.35	7.60	0.014
Plant	4	1151.16	3.35	0.038
Day*Plant	8	424.59	1.23	0.345
Error	15	343.86		

Pollen Deposition

The numbers of observed pollen grains observed on flax stigmas under the epifluoresence microscope were very low. Some pollen may have been lost during preparation for the staining procedure. Accordingly, I decided to use the number of pollen tubes forming on the stigma as the indicator for pollen deposition on the stigma (Table 6). Flax plants at Whakapapa Village had higher levels of pollen tubes than the other sites, while Lake Rotoaira had the lowest observed level. The remaining five sites had similar numbers of pollen tubes formed per stigma. However, the flowers used in this analysis were subsequently determined to have been sampled prior to stigma receptivity, which occurs during stage 3 (Craig and Stewart 1988). This may explain the low levels of pollen deposition and tube formation observed for flax. Consequently no further analysis was conducted on this data.

Table 6. Mean and range of pollen tubes formed per stigma for each site.

	MW	LR	MH	SH	E	NP	WV
Average	7.8	4.7	7.65	8.75	8.85	9.2	27.35
Maximum	15	11	20	39	21	19	200
Minimum	3	1	0	2	3	3	4

Fruit and Seed Set

Fruit and seed set averages are shown for each site in Figures 6 and 7 respectively. The maximum level of fruit set observed was 40.24% for one plant at Erua, the minimum was 0.87% at National Park. There were significant site differences in fruit production however, most of the variation occured at the plant level (Table7). The average seed set at each site was more variable (Fig. 7). The maximum seed set of 100% was observed on some plants at Lake Rotoaira and at Mangahuia. The lowest level of seed set, 7.08%, was recorded at Erua. Seed set also differed significantly between sites and individual plant variation was again significant (Table 8).

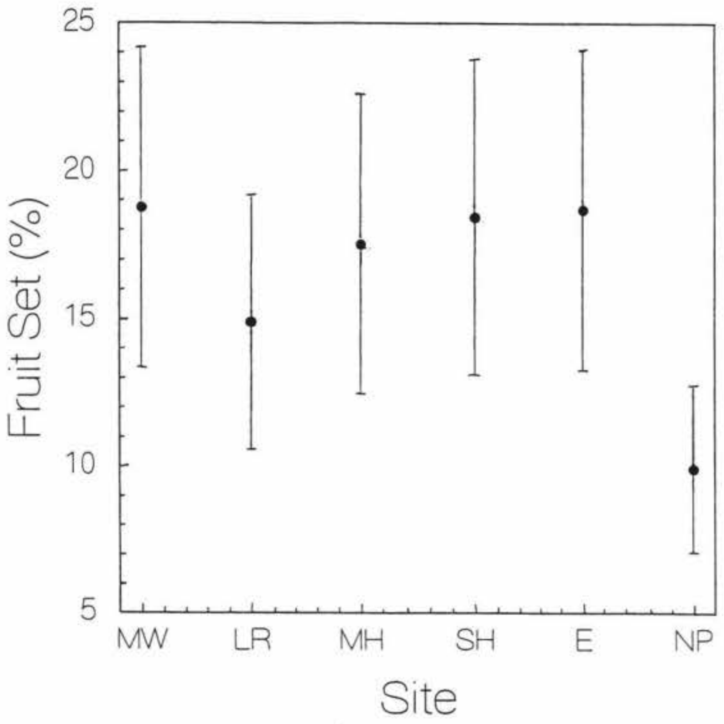


Figure 6. Fruit set (mean ± s.e) at each site, calculated as a proportion of total flower production.

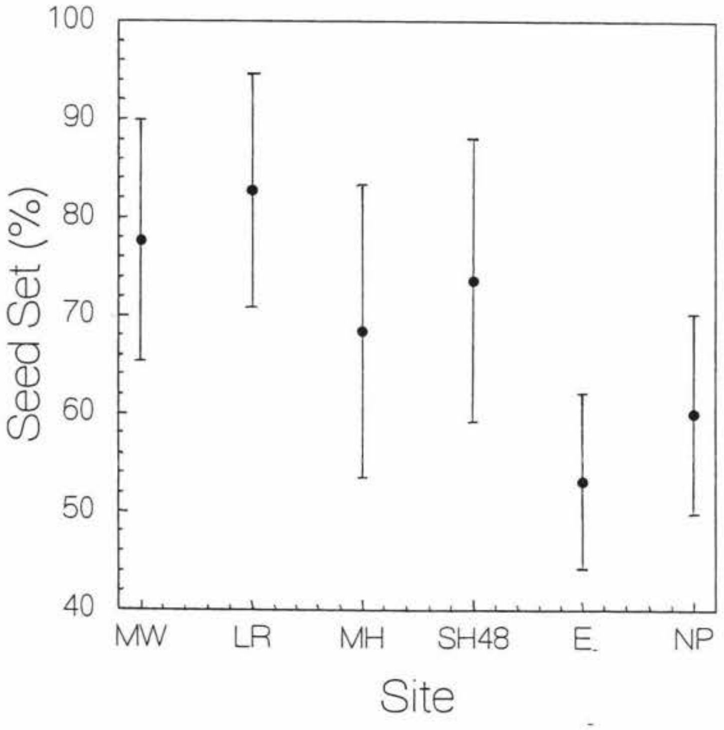


Figure 7. Seed set (mean ± s.e) at each site, calculated as the proportion of large seeds produced.

Table 7. ANOVA showing the effect of site and individual plant variation on fruit set at six study sites.

Source of Variation	DF	Mean Square	F Value	Pr > F
Site	5	0.066	2.78	0.024
Plant (Site)	66	0.024	5.09	0.0001
Error	72	0.33		

Table 8. ANOVA showing the effect of site and individual plant and infloresence variations on seed set at six study sites.

Source of Variation	DF	Mean Square	F Value	Pr > F
Site	5	0.546	3.93	0.004
Plant (Site)	61	0.139	2.10	0.003
Infloresence (Site*Plant)	52	0.066	1.27	0.158
Error	87	0.052		

The levels of fruit and seed set at each site were further influenced by predation of the developing fruit. Insect damaged pods were not included in the fruit or seed set analysis. The mean levels of insect damage on plants at each site are shown in Figure 8. These values represent the incidence of insect predation of developing seeds observed in pods collected to determine seed set. Damage ranges from 0-100% for some plants at State Highway and Mangahuia. An analysis of variance shows there is a significant (P <0.0001) difference in the levels of insect predation at each site.

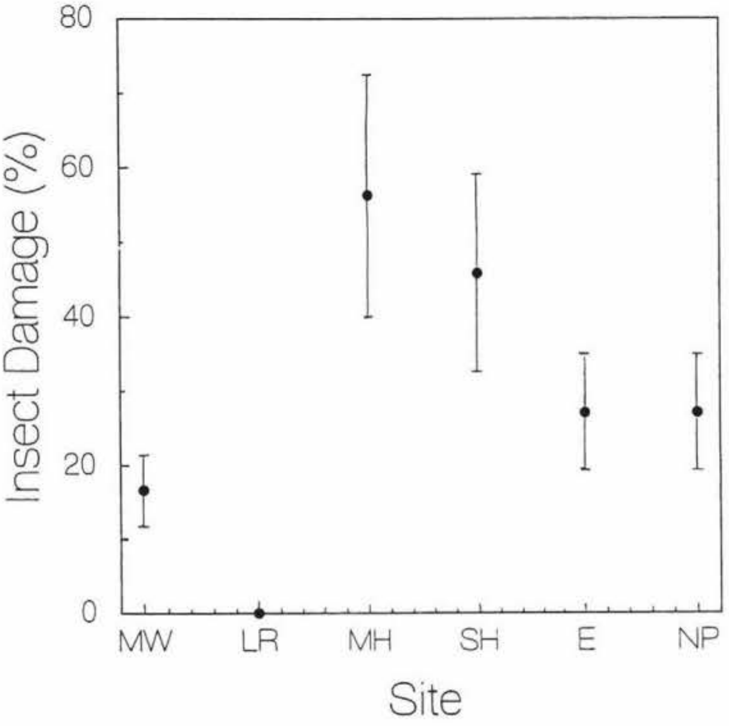


Figure 8. Insect damaged pods (mean ± s.e) at each site.

Table 9. ANOVA showing the effect of site variation on insect damage at six study sites.

Source of Variation	DF	Mean Square	F Value	Pr > F
Site	5	0.066	2.78	0.024
Plant (Site)	66	0.024	5.09	0.0001
Error	72	0.33		

DISCUSSION

Observations of flax visitation rates indicate that flax flowers are visited by a variety of bird and insect visitors. The abundance of these visitors, particularly birds, varies between the sites. The effectiveness of these species as pollinators of flax may vary, so that in turn, the sites may be expected to vary in female success. The levels of fruit and seed set, however, are not strongly related to the pollinator regime at each site. The inherent flexibility within the flax pollination system may enable selective retention of cross-pollinated flowers.

The honey eaters, Tui and Bellbird, were only ever observed foraging on flax flowers at sites where flax plants and the native bush line met. These sites included Lake Rotoaira, Erua, Mangawhero and Whakapapa Village. This suggests that the bush provides other resources, such as shelter and nesting sites, important to both Tui and Bellbird. The sites where birds were not seen may have been too far away for foraging on flax to be profitable. For example those Tui that were observed at Erua restricted their foraging on plants closest to the bushline even though their were other flowers available at the site. The higher rate of visitation observed at Mangawhero under video analysis may reflect the timing of observations. The site was not discovered until late in the flowering season when most of the plants were past peak flowering. This meant that there were fewer flowers available for foraging and these were concentrated on a small number of plants. One effect of this timing was that Tui were observed defending patches of flax. This territorial behaviour was not observed at Lake Rotoaira where flowering was abundant. A second explanation may be that the dense bush surrounding the Mangawhero study site can support a higher resident tui population.

Craig and Stewart (1988) suggest that open infloresences of flax typically set about 20% of their flowers, which is consistent with the data obtained from my sites, with an average of 16.5% fruit set. Low flower to fruit ratios are reportedly common in outcrossing hermaphroditic species (Lloyd 1980, Sutherland and Delph 1984). This low fruit set could be due to selective abortion, resource limitation or through additional flowers acting only as pollen donors. The lower fruit sets recorded at Lake Rotoaira (14.9%) and National Park (9.9%) are unlikely to be due to low pollination rates because of the high rates of visitation observed under video analysis. Resource limitation is proposed, not only to set upper limits on a plants ability to set fruit, but also to explain the low levels of fruit set at some sites. Resource limitation as a means for explaining low fruit set in flax can only be confirmed by supplementary hand pollination experiments.Seed set, calculated by determining the percentage of large, fully developed seeds, was more variable between sites than fruit set. Lake Rotoaira had a lower fruit set level compared with the majority of sites examined yet had the highest seed set. Mangawhero and Lake Rotoaira, the only sites with observed bird visitation, also had the highest seed set levels. It is possible that pollen limitation may be occuring at the other sites, but this can only be confirmed by futher study. Erua, however, had a comparable fruit set level with other sites, but had only 53.45% seed set. The levels of fruit set and seed set at each site were not significantly related to any of the variables examined, including visitation rates and nectar standing crops but were negatively correlated with each other, with a significance level of $P<0.05$. This suggests that fruit and seed set levels are somewhat interdependent.

The size and structure of flax flowers (Craig and Stewart 1988, Craig 1989a) conform with Raven's (1972) ideas on vertebrate pollination systems. Raven states that flowers attracting mainly vertebrate visitors with high energy requirements must produce larger amounts of nectar than those flowers visited by insects. Plants presumed to be adapted for bird pollination have dilute nectar concentrations (20-30%) compared with insect pollinated species (40-60%) (Mitchell and Paton 1990). These values compare well with the nectar standing crop results presented here, which give an average nectar concentration of 18.09%. However the large nectar volumes provided by flax flowers (179.85æl) mean that vary large quantities of nectar sugars per flower are available to foragers. The amount of sugar (35.18mg) provided by flax is considerably larger than that from other bird pollinated species (Heyneman 1983)Castro and Robertson, in prep. Some plant species with small flowers cluster them together to form large, conspicuous infloresences. These infloresences may then provide sufficient reward for larger pollinators. Studies on *Banksia ericifolia* (Paton and Turner 1985), a species visited by birds, small mammals and insects, show that total nectar production is equivalent to 194.8 mg sugar per inflorescence. The low nectar concentrations for birds are predicted under the biophysical theory and have been confirmed in Mitchell and Hubbell's (1990) studies of nectar feeding in Meliphagidae. The availability of this floral resource to less effective pollinators must be restricted if outcrossing is desired. This can be achieved by making the nectar inaccessible to illegitimate visitors, often associated with deep tubular corollas. Bird pollinated flowers tend to be odourless as birds do not primarily respond to olfactory cues. The flowers of bird pollinated species are often orange or red, colours which are conspicuous to birds but less so to insects. Stiles (1978) suggests that large pollinators, ie: birds and bats, have a greater potential for mobility, and that this, combined with higher energy requirements may result in birds foraging on several widespread plants during a single foraging period. If outcrossing is important in the successful reproduction of flax as suggested by Craig (1989a) and Craig and Stewart (1988), then birds would presumably be more effective as pollinators, due to their foraging behaviours. Genetic studies of outcrossing rates in areas with and without birds would be useful.

The findings of insect visitations, both under video analysis and during census', were also highly variable. Insect behaviour is highly dependant on weather conditions and adverse conditions limit their activity. Primack (1978) suggests that the relative abundance of flower visitors may change rapidly depending on the environmental conditions. He studied insect pollination of New Zealand's alpine flora. Unlike Heine (1938) who recorded a paucity of insect pollinating fauna, Primack (1983) noted large numbers of insects foraging on warm sunny days. The highly variable weather patterns in mountainous areas may result in surveys being conducted during periods of inappropriate conditions for insect foraging. Primack's (1983) studies on alpine flora suggest that native bees are more affected by the weather than most other groups of insect foragers. Honey bee activity is also highly dependant on the appropriate weather conditions, workers seldom forage at temperatures lower than 8°C (Gojmerac 1988) or in strong winds (Kevan and Baker 1983). The higher visitation rates observed at some sites were not reflected in higher fruit or seed set levels at these sites. This suggests that other factors such as pollen transference or resources may limit these measures of female fitness.

The average standing crop of nectar at each site was highly variable with significant differences between site groupings. Although one may expect an inverse relationship between visitation rates and the standing crops, this was only observed for bird visitation. The two sites with observed bird visitation had the lowest nectar standing crops, however when insect visitations were also included there was no observed relationship. This suggests that only birds are significantly cropping flower nectar levels. Nectar standing crops give an indication of the level of resources available at a given point in time. These levels may be affected by previous weather conditions. When pollinator visitation rates are dependant on favourable weather conditions, bad weather prior to sampling may have limited pollinator activity, resulting in higher standing crops for that site than if the weather had been fine.

My studies on flax nectar production at three sites, Erua, Lake Rotoaira and State Highway indicate that higher levels of nectar sugar are available in younger, stage 1 flowers. Nearly 50% of that nectar is reabsobed by stage 2. This implies that flax has the ability to reabsorb unutilised floral resources. This ability may have evolutionary signficance given the uncertainty of vistation during stage 1 and the cost assocaited with such a large volume of nectar. The studies also show that if nectar is removed by foragers small quantities may be replenished.

Pyke (1991) examined nectar production in Christmas Bells (*Blandfordia nobilis*). Nectar was removed from half the flowers sampled using capillary tubes. The remaining flowers were probed using blocked capillary tubes to prevent nectar removal. On the fourth day nectar from all flowers was removed. Pyke determined that flowers which had their nectar removed daily produced three times as much nectar than flowers only sampled on the fourth day. He concluded that removed nectar was replenished at a cost to the plant. There is a trade off between increasing nectar production and attracting more pollinators and the costs which can be measured in reduced seed set. Nectar production in *Ipomopsis aggegata* was examined by Pleasants (1983). His studies showed that repeated sampling of nectar over a 24hr period had no impact on total nectar production, in contrast to Pyke's (1991) studies, when compared to flowers whose nectar had accumulated over the same period. The effect of nectar removal on total nectar production has been studied for 12 species (Pleasants 1983), 5 of which showed a positive effect, 2 species showed a negative effect and 5 species showed no effect of nectar removal on total production. Pleasant (1983) found no evidence to suggest that nectar sugars were reabsorbed during the active life of *I. aggegata* even when nectar was left to accumulate.

Although the majority of flax flowers produce no seed, they may have an important role in male fitness. Craig and Stewart (1988) suggest that the low flower to fruit ratios observed in flax indicates that many flowers act solely as pollen donors. Flower function is not predetermined but reflects the quality of pollen received by individual flowers (Becerra and Lloyd 1992). Stanton *et al.*. (1986) suggests that resources often limit fruit and/or seed set, so increased visitation by pollinators doesn't always result in increased female fitness. This has led to the idea that a plants ability to attract pollinators is primarily important in increasing male fitness. This idea has been supported by experimentation with the pollination of *Raphanus raphanistrum* (Stanton.ML *et al.* 1986). This species has two distinct colour morphs, white and yellow. *R. raphanistrum* is visited by a number of generalist pollinators including bumble bees, honey bees, pierad butterflies, syrphids and solitary bees. Pollinator visitations are strongly biased towards the yellow flowers. Homozygote populations of each colour morph were used during experimental pollination trials. Pollinator preferences had no impact on maternal fitness however yellow flowers were visited more often and were more successful as pollen donors than the white colour morph. The relatively constant output of seed from flax plants seen may mask variability in pollen movement occuring under the differing pollinating conditions that exist at different sites. Only a genetic study can reveal such patterns.

Flax provides large quantities of nectar sugars (35.18 mg) to pollinators, suggesting that birds are primary pollen vectors for flax. However, floral resources are also utilised by a variety of native and introduced insect species. The effect of different pollinator regimes at each site on female fitness was significant for both fruit and seed set. Although plants experiencing bird visitation were more likely to have higher seed set levels, overall these results suggest that flax has a flexible pollinating system that can maintain a range of fruit and seed set levels under different pollinator regimes. Thus I have no evidence to suggest that honeybees are negatively effecting female success in flax in Tongariro National Park, nor that they deplete the resources sufficiently to signifcantly effect use by native birds.

CHAPTER 4. THE INFLUENCE OF HONEY BEE ABUNDANCE ON NATIVE POLLINATOR COMMUNITIES

INTRODUCTION

Insect pollination of flowering plants was not recognized until 1652 when it was discovered that pollen must reach the stigma for the flower to set seed (Martin, E.C. and McGregor 1973), and with this discovery came recognition of the insect's role in cross pollination.

Plants pollinated by insects are termed entomophilous. Structurally such plants are adapted for fertilization by insects, with some species adapted to the extent that only certain insects can effectively fertilize them. For example, tubular flowers, such as several orchid species can only be fertilized by long tongued bees (Thomson 1880). Open, simple flowers tend to be visited by a variety of small unspecialised insects. In general 'bee' flowers tend to exhibit bilateral symmetry (zygomorphy) and are strong with areas suitable for landing. Nectar guides are often present with nectar hidden in moderate quantities. Flowers may also have great depth effect. However 'fly' flowers are often regular with no depth effect. Nectar guides may be present but the nectar is open and easily obtainable (Faegri and van der Pijl 1979).

The colour of flowers is also designed to attract insects. Flower colour may be perceived differently by insects who are sensitive to ultra violet light. However, in general, blue and purple flowers are associated with long tongued bees and lepidoptera. Yellow and white flowers are often highly reflective and attract a variety of insect visitors, including short tongued bees, flies and beetles. Green flowers are very effective in attracting pollinators, particularly Diptera (Thomson 1927, Heine 1938, Norton 1984).

Within the New Zealand flora red, blue and purple flowers are rare compared with the rest of the world (Norton 1984). Red flowers are generally large and adapted for pollination by birds, while blue and purple flowers are small and adapted for pollination by short tongued bees. Over 60% of New Zealand's entomophilous flowers are white, compared with the British Isles where only 25% of flowers are white. This is the colour that is most attractive to the majority of New Zealand's native insects. It attracts large numbers of bees, flies, beetles and more lepidoptera than any other colour (Norton 1984).

Plants that require insect vectors for the transfer of pollen often provide 'rewards' for this service in terms of pollen and/or nectar (Jay 1986). Nectar is mostly sugar in aqueous solution and provides carbohydrate fuel for flight. The sugar concentration of nectar generally varies between 25-75%. Low nectar concentrations (20-30%) are often associated with bird pollinated species while those flowers pollinated by insects have higher nectar concentrations (40-60%) (Mitchell and Paton 1990). The chemoreceptors of pollinating insects are extremely sensitive to sugar, with a threshold level of less than 10%. Low sugar concentrations mean less food (energy), but may provide insects with a valuable water source. Concentrations and quantities of nectar are important in the energy budgets of pollinators. But nectar is not a pure carbohydrate solution, and contains varying amounts of amino acids and lipids. Pollen is also a rich supply of food, providing essential proteins and amino acids. Analysis of pollen grains gives 16-30% protein, 1-7% starch, 0-15% sugars, 3-19% lipids and 1-9% ashes. Pollen may be eaten directly (chewed) or indirectly (digested by infusion) (Faegri and van der Pijl 1979). The effectiveness of insect pollination may be determined by floral structure, nectar volumes and concentrations and by the distribution of nectar among flowers (Kevan and Baker 1983).

The pollination ecology of New Zealand plants is unusual due to the absence or rarity of specialized pollinators such as long tongued bee and lepidoptera. The pollination of New Zealand's entomophilous flowers is carried out by relatively few insect species compared to the pollination of flowers worldwide. Heine (1938) comments on the paucity of our insect fauna and the unusual proportions of insect orders found in New Zealand. Proportionally there are one third the number of hymenoptera and twice the number of diptera to be found in New Zealand's pollinating fauna than can be found any where else in the world. Pollinators available to the native New Zealand flowering flora include birds (7 spp.), bats (1 spp.), native bees (~ 40 spp.), butterflies (16 spp.) and numerous moths, flies and beetles (Godley 1979). Our native bees are all solitary species and include the short tongued Colletidae and the small tongued Halicitidae. There are no native long tongued bees. Thus there are four main insect orders visiting flowers in New Zealand, Diptera, Hymenoptera, Lepidoptera and Coleoptera. Thompson (1927) suggests that the diptera are the most numerous flower visitors and carry out the functions performed by hymenoptera in other parts of the world.

Montane and alpine plant species in many parts of the world are pollinated by specialized insects including honey bees, bumble bees and butterflies (Primack 1978). New Zealand's pollinator assemblages lack native long tongued bees and other specialized pollinators are not abundant. Thompson (1927) and Heine (1938) both concluded that New Zealand plants lacked specialized pollination systems and that insects in general, but particularly hymenoptera, were scarce as pollinators. Later studies of montane and alpine pollination systems indicate a greater abundance of native pollinators than previously thought. However, there is no evidence that any native insect species forages exclusively on any one plant species (Primack 1983). Of 82 plant species observed, 75 were visited by insects from two or more orders. Plants then, receive visits from a multiple range of species whose composition may vary between sites and from day to day. The presence of insects in alpine regions depends greatly on the ambient temperature, wind speed and light levels (Primack 1978, 1983, Inouye and Pyke 1988). The abundance of native bees appears to be more affected by the weather than other insect orders (Primack 1983).

Arroyo *et al.*. (1982, 1985) studied entomophilous plants in the Chilean Andes at altitudes of 2200-3600m. They found that the most important pollinators were hymenoptera and diptera, pollinating 50% and 46% of plant species respectively. However the significance of bees as pollinators decreased with increasing altitude and the proportion of fly pollinated plants increased, with approximately 70% of all species studied pollinated by flies at the higher altitudes. Another study by Moldenke and Lincoln (1979) in Colorado found that 62% of the entomophilous flora was visited by hymenoptera in particular bumble bees and solitary bees. Flies were the next most important order, visiting 31% of all plant species.

The flora and fauna of alpine Australia resembles that of New Zealand in that there are no native social bees and many plant genera are common to both countries. The most common flower colour in both alpine communities is white, a colour typically associated with nocturnal and fly visitations. A predominance of white flowers in alpine flora could then be expected where the pollinating fauna consists mainly of flies (Inouye and Pyke 1988). A study of visitation rates of alpine flowering plants by different insect species was conducted by In~~n~~ouye and Pyke (1988) in the Snowy Mountains of Australia. 62.3% of all visits on flowers were by diptera, 30.8% by hymenoptera, 11.2% by diurnal lepidoptera and 1.9% by coleoptera.

The pollinator assemblages for alpine communities in the Southern Alps of New Zealand were examined by Primack (1978, 1983). He determined that 71% of all floral visitors were diptera, comprising of 25% syrphids and 46% muscid and tachinid flies. Only 12% of all visitors were native bees, 8% coleopotera and 7% diurnal lepidoptera. New Zealand montane and alpine plant species have typically generalized pollination systems. Of 82 plant species examined only 4 exhibited specialized pollination relationships with an insect order (Primack 1983). Three species showed no insect visitation and the remaining 75 species were pollinated by insects from 2 or more orders. At least 45 insect species were collected foraging on manuka. Diptera, particularly tachinids and syrphids, visit a wide range of plant species. Primack's (1978, 1983) studies show no evidence of native pollinators foraging exclusively on one plant species.

This chapter seeks to determine the abundance and diversity of insect foragers on two native plant species manuka (*Leptospermum scoparium*) and *Hebe stricta*. Foraging activity of the introduced honey bee (*Apis mellifera*) was examined to determine whether or not honey bees effect native pollinator assemblages.

Methods

Manuka

A member of the family Myrtaceae, manuka (*Leptospermum scoparium*) is a small tree or shrub. Manuka is widespread throughout New Zealand, it tolerates a wide range of habitats from peaty bogs to lowland and alpine shrublands (Poole and Adams 1964, Ronghua *et al.* 1984). Manuka flowers are typically white, with five petals. An andromonoecious species, it produces both male and hermaphrodite flowers. Manuka flowers are visited by a wide range of insects, including solitary native bees, lepidoptera, beetles and flies (Primack and Lloyd 1980a, b, Primack 1983)

Hebe stricta

A member of the family Scrophulariaceae, *Hebe stricta* is a small tree or shrub. *Hebe stricta* is distributed throughout the North Island and in Malborough, mainly in lowland and montane habitats (Poole and Adams 1964). *Hebe stricta* flowers are small and clustered into spiked infloresences. These infloresences can be quite large, 10-12 cm, with 80-120 florets (Kristensen 1989). A variety of insect species have been recorded visiting *Hebe* spp. (Thomson 1927, Heine 1938, Primack 1983, Kristensen 1989), including native bees and flies, with tachinid and syrphid flies accounting for over half of the visits to *Hebe* (Primack 1983).

Study Sites

A total of four study sites were selected for each plant species within the Department of Conservation's Tongariro/Taupo Conservancy. Three of these study sites were within the boundary of Tongariro National Park, while the remaining site was located at Lake Rotoaira. Location of the study sites are shown in Figure 1.

Manuka	***Hebe stricta***
Lake Rotoaira (LR)	Lake Rotoaira (LR)
Mangahuia (MH)	Mangahuia (MH)
Taranaki Falls (TF)	Mangawhero (MW)
Silica Rapids (SR)	Ketetahi (K)

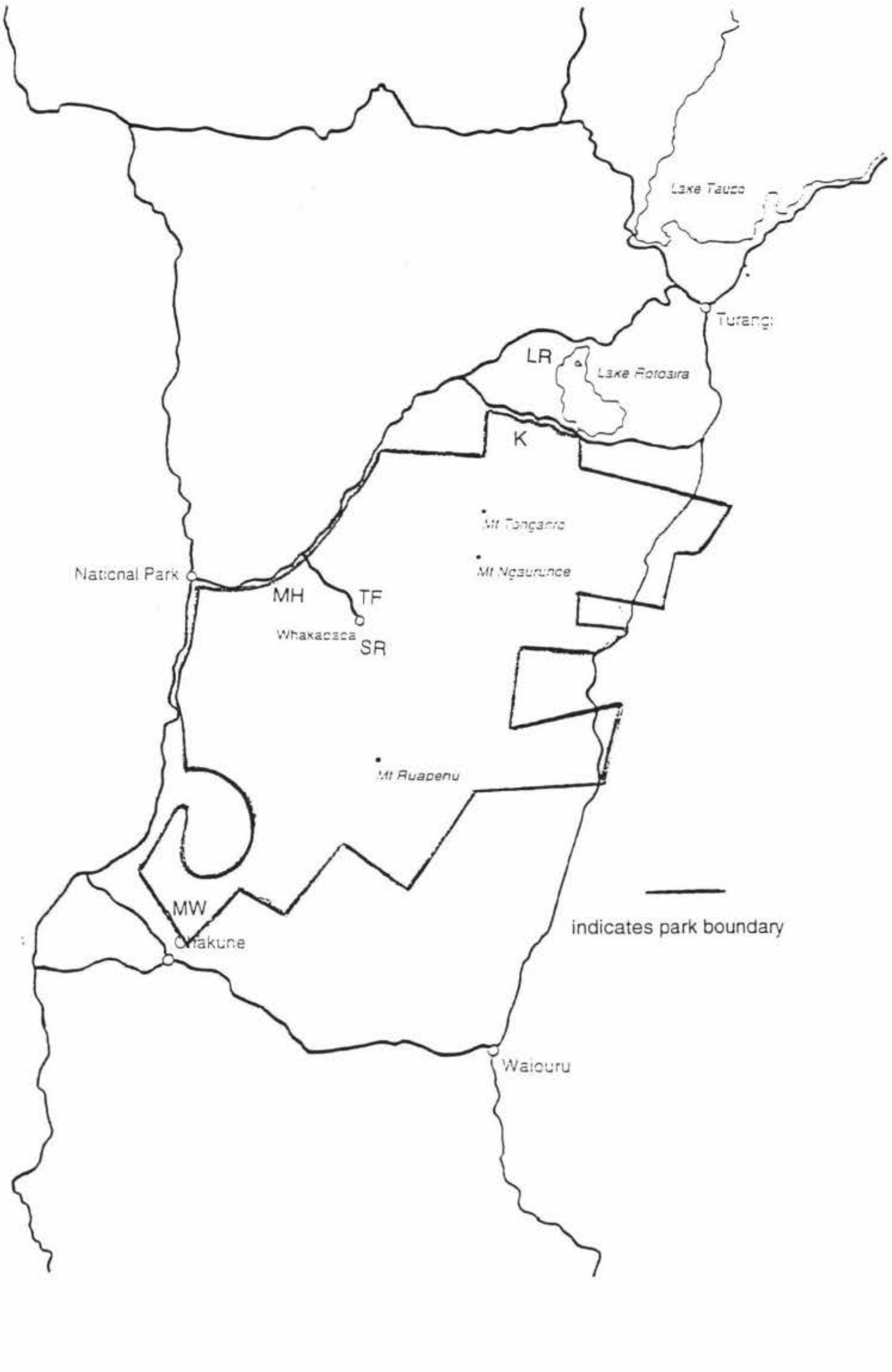


Figure 1. Tongariro National Park and surrounding areas, showing location of study sites. (Site abbreviations shown in methods)

Floral Visitors

Preliminary observations for both species were conducted at each study sites. Insects observed foraging on flowers were collected for field identification. The insects were then pinned out for identification to species. A census of insect abundance and diversity at each site were conducted by recording the number and type of each insect observed foraging on flowers over a 10-15 minute random walk through the site. The census data, collected for each site, is expressed as encounter rate per minute of observation. In addition, a video camera was set up at each site to determine flower visitation rates for each species. The number of flowers available to foraging insects were counted, and the length of the observation period recorded. Floral visitation rates for manuka were calculated as the number of flowers observed divided by the length of the observational period. This figure was then expressed as visits/flower/hour. The small size of *Hebe stricta* flowers meant that visits to individual flowers were difficult to detect on film, so the number of visits per infloresence was used as an index for visitation rates.

Statistical Analysis

The diversity and variability of the pollinator assemblages for both species was such that it was felt a community analysis might reveal communities that are sensitive to the presence of honey bees. Ordination procedures, for the insect range of each plant species and for sites, were conducted using a detrended, correspondance analysis and employing reciprocal averaging, in Multivariate Statistical Package (MVSP) computer software.

Results

Floral Visitors

The abundance and diversity of insect floral visitors for both species was examined under different honey bee densities. Overall manuka had the widest range of flower visitors, with 32 insect species observed. A total of 23 insect species were observed foraging on *Hebe stricta*. The insects were classified into five guilds, these included the introduced honey bee, native bees, nectar feeding flies, pollen feeding syrphids

(Holloway 1976, Hickman *et al.* 1995) and other. Species in this last guild included bumble bees (*Bombus*), wasps (*Vespula*) and for *Hebe stricta* the copper butterfly (*Lycaenidae*). The number of species observed in the three main native guilds are shown in relation to honey bee densities at each site (Table 1).

Table 1. Flower visitor diversity for two plant species (a) manuka and (b) *Hebe sticta* in relation to honey bee densities at each study site.

(a) Manuka

Site	Honey Bees (No./min)	Native Bees	Native Flies	Syrphids	Total
Lake Rotoaira	1.26	2	3	3	11
Mangahuia	0.05	2	11	5	20
Taranaki Falls	0.02	2	5	3	12
Silica Rapids	0	2	14	2	19
Total	-	2	22	5	32

(b) *Hebe stricta*

Site	Honey Bees (No./min)	Native Bees	Native Flies	Syrphids	Total
Lake Rotoaira	2.14	1	4	1	8
Mangahuia	2.20	2	4	0	9
Ketetahi	1.00	1	7	1	12
Mangawhero	1.34	1	9	2	15
Total	-	2	15	2	23

During the initial sampling period at Mangawhero honey bees were not present in high numbers. However when I returned to the site three weeks later large numbers of honey bees were seen foraging at the site. The increased encounter rate of honey bees (Table 2) was associated with a decrease in the number of native insect pollinators observed.

Table 2. Temporal changes in flower visitor diversity for *Hebe stricta* at Mangawhero

Date	Honey Bees (No./min)	Native Bees	Native Flies	Syrphids	Total
11 February	0.18	1	9	1	14
14 February	0.87	1	7	2	13
8 March	5.50	1	0	0	3
Total	-	1	9	2	15

Table 3. Insect visitation rates by guild on manuka flowers, expressed as the number of visits/flower/hour, at four sites around Tongariro National Park. (The number suffix representing separate sampling occasions).

Site	LR1	LR2	MH1	MH2	TF	SR1	SR2
Date	25/1	25/1	28/1	28/1	28/1	31/1	1/2
Time(min)	35	31	29	30	32	34	28
Flower No.	47	33	39	46	31	28	36
Honey Bees	1.37	1.13	0.21	0.43	0	0.08	0
Native Bees	0.95	1.06	1.30	0.97	0.53	0.27	0.42
Native Flies	0.69	0.86	0.78	0.56	1.86	2.11	1.73
Syrphids	0.26	0.43	0.59	0.20	1.45	0.25	0.99
Other	0.58	0.62	0	0.01	0	0.07	0
Total	3.85	4.10	2.88	2.17	3.84	2.78	3.14

4.4

Table 3. Census Results for Manuka, expresses as encounter rate/minute of floral visitors.

Site	LR1	LR2	LR3	LR4	LR5	LR6	MH1	MH2	MH3	MH4	TF1	TF2	TF3	SR1	SR2	SR3
Date	21/1	21/1	25/1	25/1	25/1	25/1	21/1	28/1	28/1	28/1	26/1	28/1	28/1	31/1	01/02	14/2
Time	25	15	11	12	14	11	15	15	12	20	13	16	15	27	22	17
honey	0.96	1.27	0.82	1.92	1.86	0.91	-	0.07	0.17	-	-	-	0.07	-	-	-
bumble	-	-	0.09	-	-	0.09	-	-	-	-	-	-	0.07	-	-	-
largenat	0.8	1.67	0.27	3.33	0.93	0.09	1.33	1.13	1.58	0.75	0.46	0.94	0.87	1.33	0.64	0.71
smallnat	-	0.07	-	0.08	0.29	0.09	-	-	-	0.05	-	0.13	0.13	0.19	0.05	-
creamsyr	0.12	0.2	-	0.33	-	-	0.13	0.47	0.5	0.55	0.08	2.38	1.2	0.48	0.68	0.47
goldsyr	0.12	0.2	0.36	-	0.07	0.18	0.07	-	-	-	-	-	-	-	-	-
y/bsyr	0.08	-	0.09	0.33	-	0.09	0.13	0.07	0.08	0.25	-	0.19	-	-	-	-
w/bsyr	-	-	-	-	-	-	-	0.07	-	-	-	0.13	-	0.04	-	-
bluesyr	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-
?syr	-	-	-	-	-	-	-	-	-	-	-	0.13	-	-	-	-
tachinid	-	0.2	0.09	0.25	-	0.36	0.27	0.13	0.42	0.1	-	0.06	-	-	-	-
tabanid	0.08	-	-	-	0.14	-	-	-	-	-	-	-	-	-	-	-
bluefly	-	-	0.09	0.17	0.07	-	1.33	0.13	0.42	0.4	0.46	0.38	0.8	1.07	6.09	0.65
bronzefly	-	-	-	-	-	-	-	0.2	0.42	0.85	-	-	-	-	-	0.06
checkerfly	-	-	-	-	-	-	0.13	0.13	-	0.1	-	-	-	-	-	0.18
orangefly	-	-	-	-	-	-	-	0.07	0.17	-	-	-	-	0.04	-	-
antjefly	-	-	-	-	-	-	-	0.13	0.25	-	-	-	-	-	-	-
greenmet.	-	-	-	-	-	-	-	-	0.08	0.05	-	-	-	-	-	-
chfly	-	-	-	-	-	-	-	-	-	0.1	-	-	-	-	-	-
b/cfly	-	-	-	-	-	-	-	-	-	-	-	0.13	0.13	-	-	-
greyfly	-	-	-	-	-	-	-	-	-	0.25	-	-	0.2	-	-	0.18
hairyfly	-	-	-	-	-	-	-	-	-	-	-	0.06	-	-	-	-
longbrown	-	-	-	-	-	-	-	-	-	-	-	-	-	0.11	-	-
polkadot	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04	-	-
littleblack	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04	-	0.06
blue/gold	-	-	-	-	-	-	-	0.07	0.25	0.5	-	-	-	-	0.05	0.06
brown/b	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.05	-
stripedabd	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.12
blackfly	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.41
y/brownab	-	-	-	-	-	-	-	-	-	-	-	-	-	0.56	0.23	0.29
?fly	-	-	0.27	0.25	0.21	0.09	-	-	0.33	0.35	0.08	0.38	0.33	0.11	0.05	0.12
ichneum	-	-	-	-	0.07	-	-	-	0.08	-	-	-	-	0.22	-	0.35

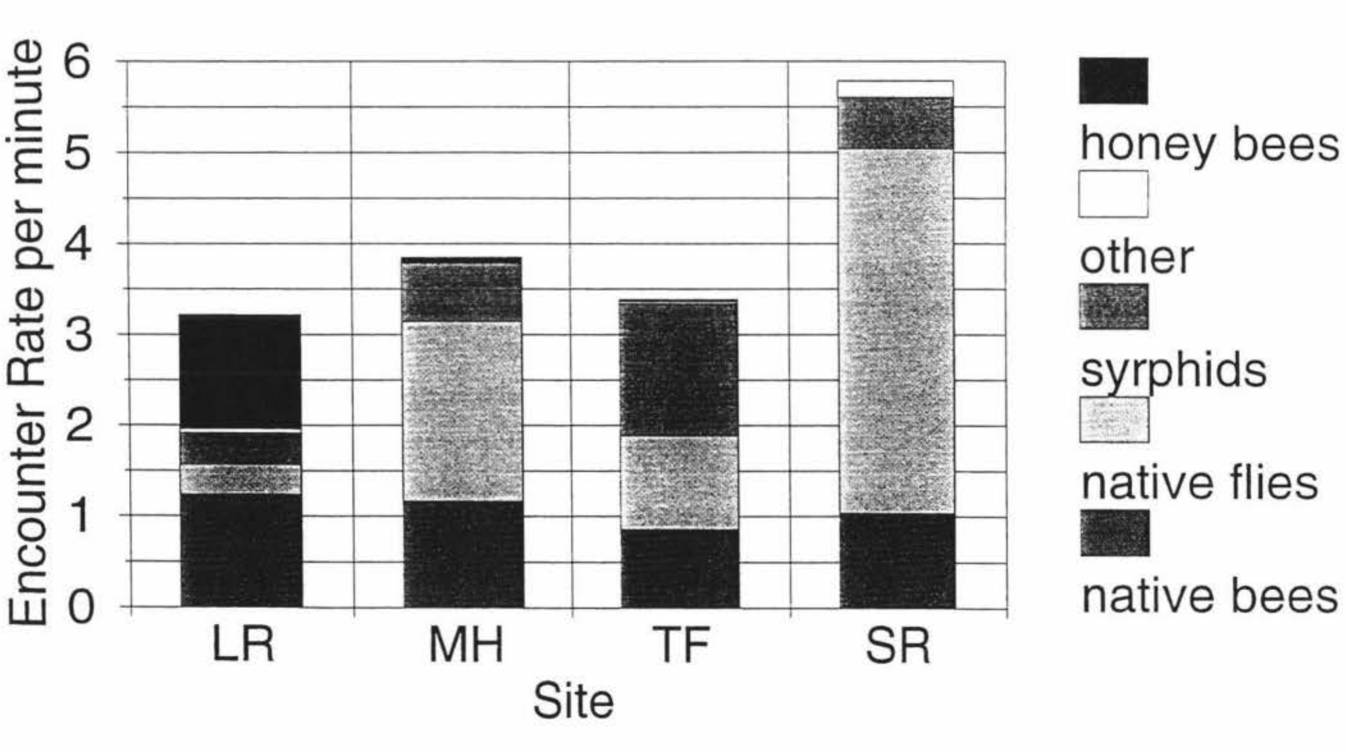
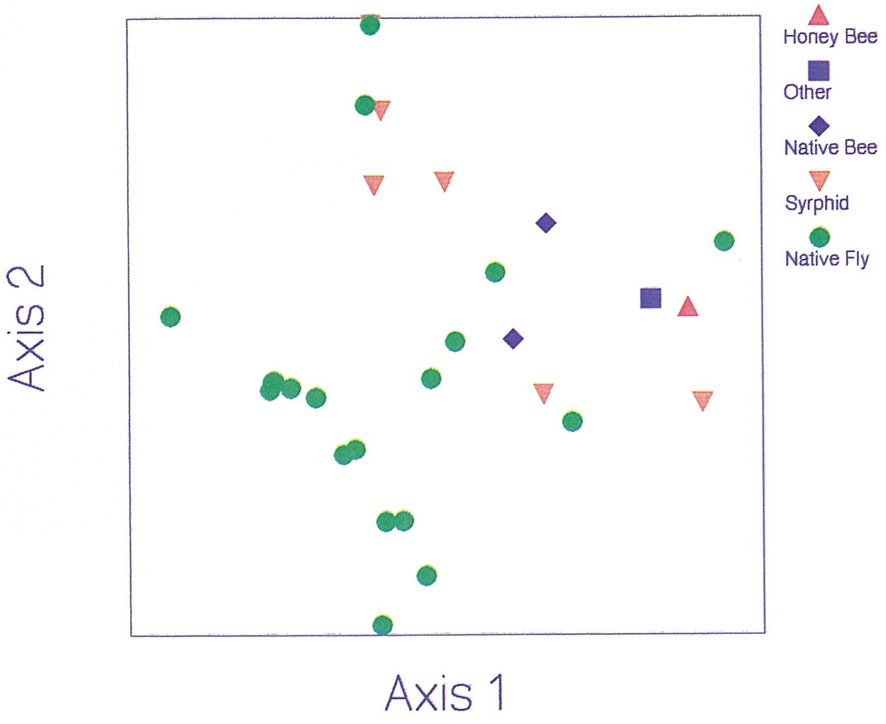


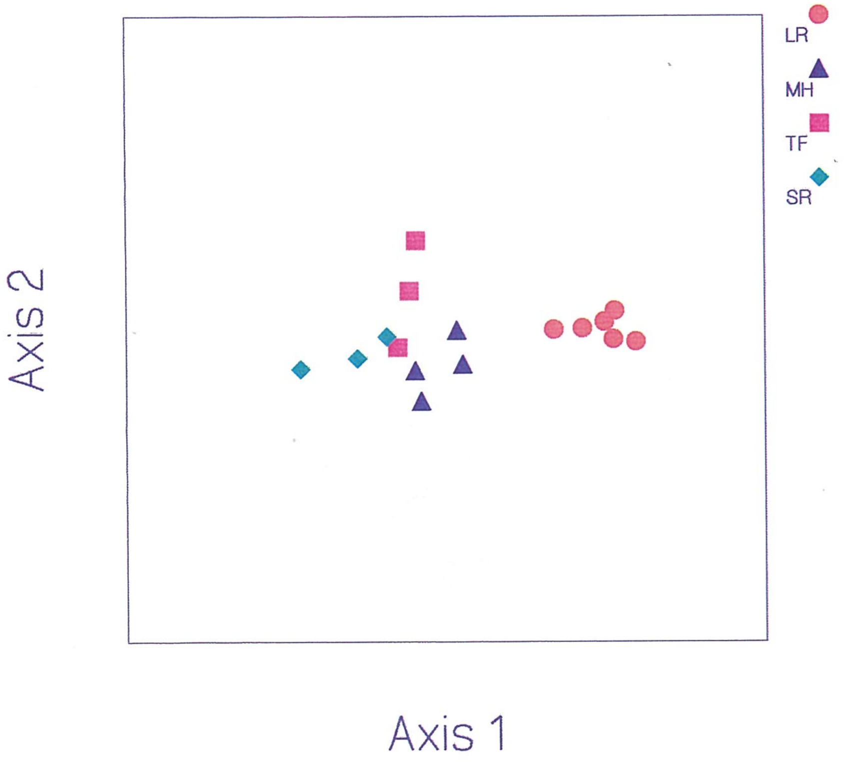
Figure 2. Census results for manuka, expressed as encounter rate per minute of flower visits by guild. (Site abbreviations shown in methods)

Table 4. Census results for Hebe stricta, expressed as encounter rates/minute

Site	LR1	LR2	LR3	LR4	MW1	MW2	MW3	MW4	MW5	K1	K2	K3	K4	MH1	MH2	MH3
Date	17/2	17/2	2/3	9/3	11/2	11/2	14/2	14/2	08/03	17/2	9/3	15/3	18/3	17/2	17/2	18/2
Time	15	14	17	11	14	19	14	17	12	12	13	10	13	17	13	19
honey	1.67	2.21	3.88	7	0.14	0.21	0.43	1.24	5.5	4.5	5.46	2.5	9.38	3.76	5.38	4.11
bumble	0.6	0.43	2.59	0.18	1	0.21	0.57	1.18	4.08	0.17	-	0.9	0.92	-	0.08	0.16
largenat	2.87	2.57	2.06	0.73	0.43	0.58	2.79	2.47	0.33	1.75	1.23	0.2	0.69	0.65	1.23	4.21
smallnat	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.08	-
creamsyr	0.07	0.07	0.12	-	0.43	0.21	0.79	0.88	-	-	0.15	0.6	0.46	-	-	-
honeysyr	-	-	-	-	-	-	0.21	0.12	-	-	-	-	-	-	-	-
orangestr	0.27	0.14	0.06	-	-	0.32	1.29	0.76	-	-	0.08	0.3	0.23	-	-	-
whitestr	0.13	-	0.18	-	-	0.37	0.21	0.12	-	-	-	-	-	-	-	-
b/cfly	0.07	0.07	-	-	-	-	-	-	-	-	-	-	-	0.06	-	0.06
blackfly	-	0.07	-	-	0.71	0.21	0.14	-	-	-	-	-	0.15	-	-	-
tachinid	-	-	-	-	0.14	0.16	-	-	-	-	-	-	-	-	-	-
tabanid	-	-	-	-	-	-	-	-	-	-	-	0.1	0.23	-	-	-
bronzefly	-	-	-	-	0.07	0.11	0.07	0.29	-	-	-	-	-	0.06	0.08	-
longbrown	-	-	-	-	0.21	-	-	0.06	-	-	-	-	-	-	-	-
blue/gold	-	-	-	-	0.07	0.32	0.5	0.35	-	-	-	0.1	-	-	-	-
lgstr	-	-	-	-	0.43	0.21	0.14	-	-	-	-	0.1	-	-	-	-
y/strgold	-	-	-	-	-	0.21	-	-	-	-	-	-	-	-	-	-
smblack	-	-	-	-	-	-	-	-	-	-	-	-	0.08	-	-	-
bluefly	-	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-
b/ostrabd	-	-	-	-	-	-	-	-	-	-	-	-	-	0.06	0.08	-
metstr	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.05
?fly	-	-	-	-	0.21	0.11	-	0.18	-	-	-	0.1	0.08	-	-	-
copperbut	-	-	-	-	0.14	0.11	0.07	-	-	-	-	-	-	-	0.08	-



Insect Ordination



Site Scores

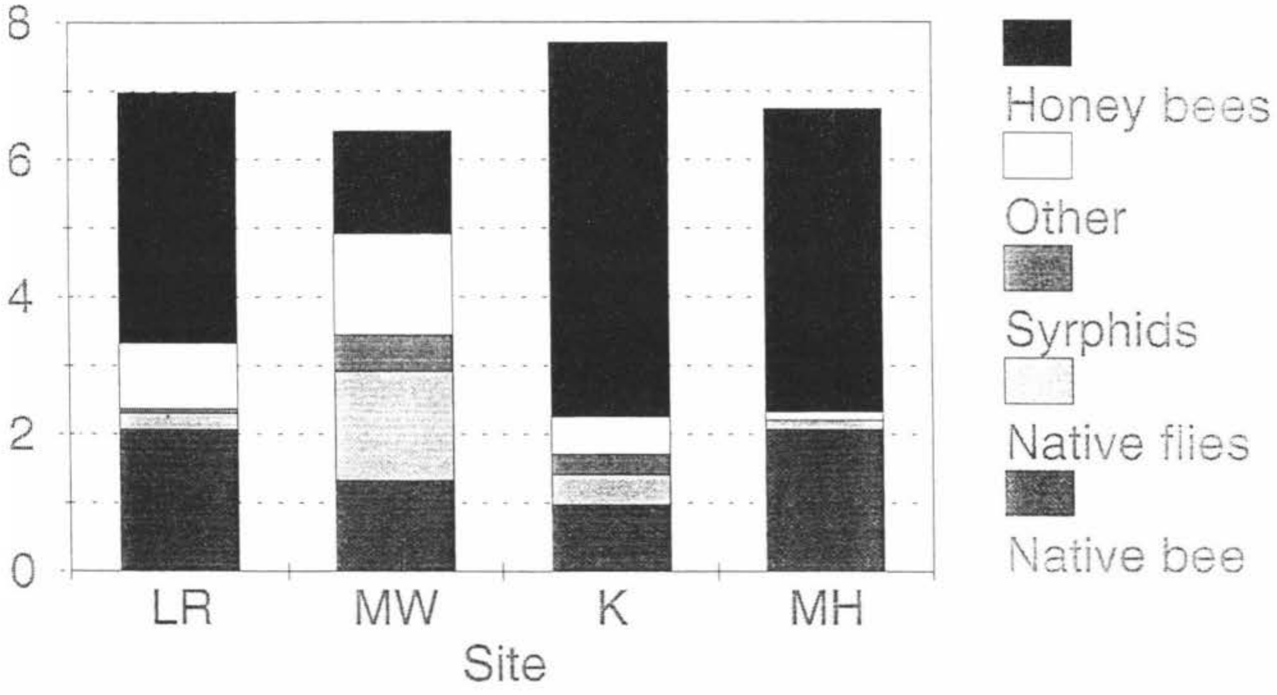


Figure 4. Census results for *Hebe stricta*, expressed as encounter rate per minute of flower visits by guild. (Site abbreviations shown in methods)

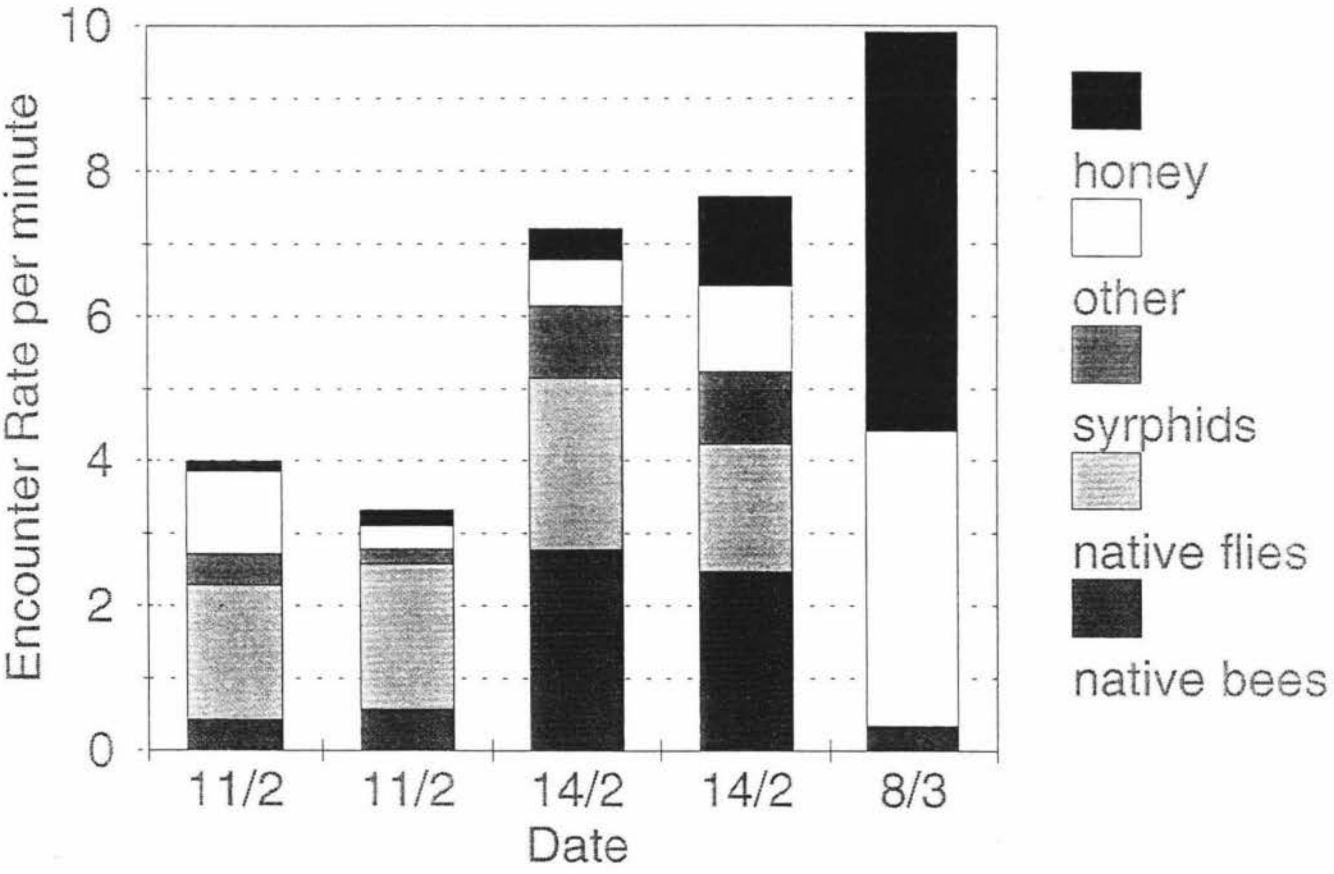
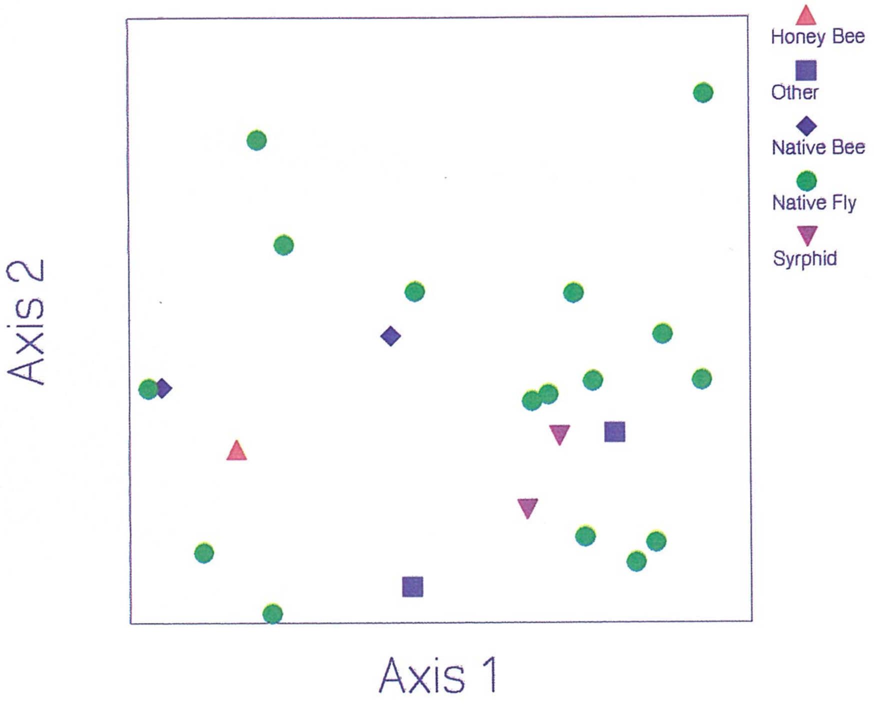
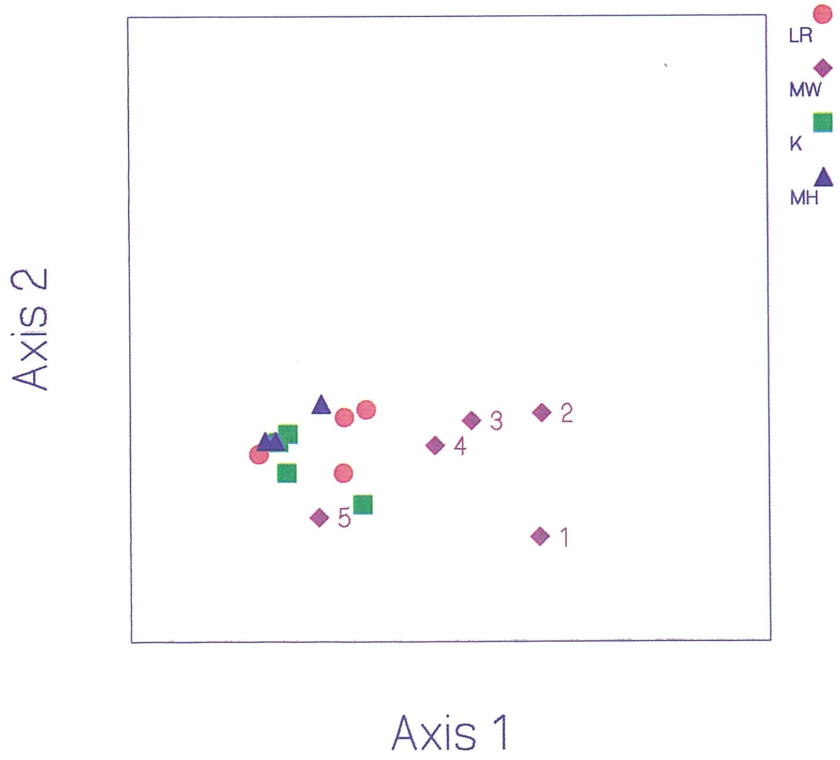


Figure 5. Census results for *Hebe stricta* at Mangawhero, expressed as encounter rate per minute of flower visits by guild, showing changes in pollinator communities over time.

Hebe



Insect Ordination



Site Ordination

DISCUSSION

Many native New Zealand plant species have generalised pollination systems and are visited by a wide variety of insects. Here, Manuka and *Hebe stricta* were both visited by a wide range of insect species from different orders. Manuka had the most diverse set of flower visitors (n=32), while *Hebe stricta* was visited by 23 different insect species. Previous studies on the pollinator assemblages of New Zealand's alpine flora have also shown that many plants are visited by a range of non-specialised insect foragers (Primack 1978, 1983).

The diversity of insect pollinators may vary dramatically between sites, day and the time of observation (Primack 1983), these differences may be related to temperature (Primack 1983, Arroyo *et al.* 1985, Gojmerac 1988), wind (Kevan and Baker 1983) or altitude (Arroyo *et al.* 1982). However, analysis of the pollinator assemblages of manuka and *Hebe stricta* suggests that some of the observed differences may be particularly associated with honey bee densities. Butz Huryn (1995) suggests that native flower visitors are limited more by weather conditions than the presence of honey bees on flowers, and that honey bees merely represent an addition to pollinator assemblages. However, I have shown that the abundance and diversity of diptera appears to be strongly influenced by increased honey bee activity. This trend is most apparent for *Hebe stricta* at Mangawhero where honey bee numbers in the area dramatically increased over a three week interval. When honey bee activity in the area was high (encounter rate 5.5 bees per minute), no diptera, either native fly or syrphid guilds, were observed foraging on *Hebe stricta.* This indicates that honey bees may have the greatest effect on dipteran pollintors which play an important role in the pollination of many New Zealand plant species (Thomson 1927, Heine 1938, Primack 1978, 1983).

Honey bees apparent ability to alter pollinator assemblages on different plant species may be due to their utilisation of a limiting resource which makes foraging inefficient for other insect species, or to agonistic behaviours directed towards other potential competitors. Competition between the honey bees and native insects is likely as they are both generalist feeders, visiting a wide variety of plant species and are active during the same periods of the day. Roubik (1978) studied the impact of the honey bee on native pollinators in South America. As the number of honey bees foraging in the area increased, the number of native bees was reduced. This trend was reversed when honey bees were removed from the area. Similar studies were conducted by Schaffer *et al.*. (1979, 1983). Honey bees were found to dominate at the most productive sites while native bees predominated at the least productive sites.

Manipulation of honey bee densities within Tongariro National Park would be useful in determining what aspects of honey bee activity are importent in determining the structure of the native pollinator communities.

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