

INTERACTIONS BETWEEN NATIVE AND INTRODUCED BEES IN NEW ZEALAND

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SUMMARY: There are about 40 species of native bees in New Zealand, all belonging to the two most primitive bee families. Seven species have been introduced and established, five of which belong to the most advanced family of bees.

All bees exploit similar resources such as nest sites, pollen, and nectar, so the question arises as to whether native and introduced bees are competing for these resources. Similarly, are native or introduced bees affected by the pathogens of newly contacted bee species?

Although basic data on many native bee species are scarce, wide differences in nest site requirements suggest that competition for nest sites does not occur, except for a slight overlap between large Hylaeinae and introduced Megachilinae. Many native bees and introduced honey bees forage on the same flowers, but honey bees from commercial hives, bumble bees, alkali bees and leafcutting bees forage primarily on introduced plants. Native bees frequently outnumber honey bees on native and some introduced plants. Peak native bee foraging occurs during the "honey flow" when pollen and nectar are abundant, thus competition between species for food is reduced. Leafcutting bees are attacked by native bee parasites but the converse is not known.

It is concluded that some of man's activities such as destruction of native flowers, introduction of new flowers and unintentional creation of nest sites, have probably had more impact on native bees than any competition from introduced bee species. Some native bees have competed successfully with honey bees for about 140 years and for a lesser time with other introduced bee species, which suggests that competitive success should continue. The status of those native bee species which are uncommon cannot be estimated until basic biological data become available.

INTRODUCTION

Bees belong to the Apoidea (Hymenoptera). According to Michener (1974) "they are a group of flower-visiting wasps that has abandoned the wasp habit of provisioning nests with insect or spider prey and instead feeds its larvae with pollen and nectar collected from flowers or with glandular secretions ultimately derived from the same sources". Bees also possess morphological characteristics not found in sphecoid wasps from which they were apparently derived.

The bees of the world constitute a group of about 20 000 species which is usually divided into 8 or 9 families based mainly on morphology. Bees range in size from 2 to 39 mm in length. Behaviour of females ranges from construction of nests without co-operation with other females (solitary state) to complete co-operation with other individuals of the same species (eusocial state).

The basic similarity in the life cycle and resource requirements of bee species implies that if those which evolved apart were brought together, competition for one or more resources may be detrimental to one or more species. Competition might occur primarily for nest sites, and / or pollen

and nectar, but resident species also could possibly be attacked by bee enemies transferring from introduced species or vice versa. The level of competition could be influenced by the distribution and seasonal abundance of each species. Seasonal abundance in turn may depend upon the type of social organisation.

Studies of the interactions of bee species under natural conditions are few. However Eickwort and Ginsberg (1980) in reviewing the influence of honey bees on other bees concluded that there is strong evidence that honey bees influence the foraging patterns of native bees. In French Guiana, Roubik (1978) found that if the density of introduced honey bees on flowers being visited by native meliponine bees was increased by moving in honey bee hives, stingless bees became less abundant. In New Zealand, Wratt (1968) observed the displacement of pollen collecting *Bombus ruderatus* from red clover as the number of honey bees increased with rising temperature. On the other hand Menke (1954) in Washington State noted that as the number of native alkali bees foraging on lucerne increased, introduced honey bees were displaced.

New Zealand possesses both native and introduced

bee species. Little is yet known of the biology of many native species. It is the aim of this paper to review what is known, however incomplete, with a view to evaluating any interactions with introduced bees, and especially any detrimental effects on native bees. Aspects that could be profitably studied to further delineate the effect of interactions may be indicated.

NATIVE BEES

A systematic revision of native bees now in progress indicates that the fauna consists of about 40 species, about 36 of which belong to the Colletidae, and 4 or 5 to Halictidae. These families were considered by Michener (1944) to be the most primitive families based on morphology. In comparison with that of many other regions New Zealand's bee fauna is depauperate in both number of species and families. For example about 1 630 species in 6 families have so far been described from Australia (Michener, 1965) and the total may number about 3000 (Michener, 1970). About 251 species in 8 families are known in Britain (G. Else, pers. comm.).

Colletidae

The Colletidae in New Zealand is divisible into three distinct subfamilies, the Colletinae (about 30 species), the Euryglossinae (1 species) and the Hylaeinae (about 5 species). The Colletinae are robust, hairy, black bees (one species is orange-yellow) that range from 5 mm to 12 mm in length. Females carry pollen externally on scopae (pollen carrying hairs) on the hind legs. The Euryglossinae and Hylaeinae are slender and mainly black with



FIGURE 1. Cell of *Leiproctus fulvescens* (Smith), showing a larva lying on a pollen mass. Dillons Point, Blenheim. 8 January 1980. Photograph: B. J. Donovan.

sparse hairs, and with a range in length from 2.5 to 9 mm. Females carry pollen internally in a crop. Life cycle

Colletidae overwinter as diapausing prepupae in cells in nests. In spring prepupae develop to adult bees which emerge from September to December. After mating, females begin nesting while males continue mating attempts. Females individually construct cells, provision each cell with pollen and nectar, lay one egg per cell and seal the cell entrance. In about 3 days eggs hatch to small larvae which consume all stored food in about 10 days (Fig. 1). Within a month from oviposition larvae become prepupae which diapause until the following spring.

Female bees can probably construct and provision at least one cell daily in suitable flying weather. Individual bees may possess the capacity to produce about 30 cells in their lifetime of about 6-8 weeks, but because of inclement weather and other factors a mean production of about 10 cells per female seems likely. Most male bees die within a few weeks of emergence.

Nest sites

Natural nest sites of Colletinae are bare and semi-bare areas of ground that are free of excess moisture during the nesting season, and in which the substrate is of such a consistency that nests can be excavated without difficulty. Nests consist of branching tunnels which at a depth of about 200-500 mm terminate in oval cavities (cells). Strong preferences for certain physical features of nest sites are exhibited by some species. *Leiproctus metallicus* (Smith) nests only along the upper ocean beach line in dry, shifting sand or fine gravel in areas that are inundated by spring tides (Fig. 2).



FIGURE 2. Nest site of *Leiproctus metallicus* (Smith) in the sandy upper beach at Conway Flat, North Canterbury. 22 December 1977. Photograph: B. J. Donovan.

Several species nest in different strata in near-vertical sandstone cliffs along the shorelines of waterways. *L. fulvescens* (Smith) prefers compacted dry soils with a high clay content, but will sometimes nest in dry parts of silty alkali bee nest sites.

Most known nest sites of the majority of species have been made by activities of man. Roadside cuttings or earth bared by machinery, ground maintained weed free by herbicides, and soil in animal tracks frequently harbour bee nests.

Only one nest site of Euryglossinae is known. At Nelson *Euryglossina proctotrypoides* Cockerell nested in tunnels of the house borer beetle *Anobium punctatum* (De Geer). Nests of Hylaeinae have been found in galls of *Morova subfasciata* (Walk.) (Lepidoptera) on *Muehlenbeckia* sp. (Gourlay, 1928, in stems of *Lupinus* sp., *Linaria* sp. and *Digitalis purpurea* L (Fig. 3) (P. Quinn, pers. comm.) and in grooved board nest holes of the lucerne leafcutting bee *Megachile rotunda* (F.).

Flower relationships

The Myrtaceae appears to be the primary flowering host family of most Colletinae. *Leptospermum*, *Metrosideros* and *Lophomyrtus* are visited for pollen and nectar by many *Leioproctus* species, especially *L. metallicus* (Smith) and *L. imitatus* Smith, plus several undescribed species. At least two species, one of which is *L. vestitus* (Smith) visit primarily leguminous genera such as *Carmichaelia*, *Chordospartium* and *Notospartium*. *L. fulvescens* and one or two undescribed species visit only Compositae both native and introduced. On the basis of flower visiting preferences most Colletinae can be divided into three groups: those that visit Myrtaceae, Leguminosae, or Compositae. Species

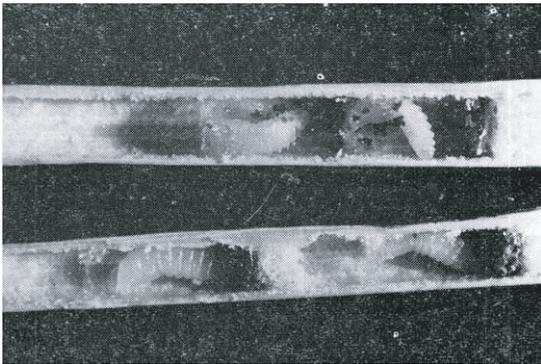


FIGURE 3. *Prepupae* of *Hylaeus capitosus* (Smith) in cells in plant stems. Lake Tekapo, 25 November 1977, collected by P. Quinn. Photograph: J. Cocks.

that visit flowers of one of these groups have rarely been collected on flowers of the other two groups. Other species have been captured in some abundance collecting pollen from *Cordyline*, *Hebe*, *Raoulia*, *Cotula*, *Celmisia*, *Selliera*, *Discaria* and many other genera.

Several species are successfully exploiting some introduced flowering plants. Two that visit native legumes have been captured collecting pollen from lucerne (*Medicago sativa* L) and sweet clover (*Melilotus* spp.) (Donovan, 1974). In Otago, Canterbury and Marlborough *L. fulvescens* collects pollen from *Achillea millefolium* L and yellow-flowered weedy composites. In the Bay of Plenty, at least three species of *Leioproctus* collect pollen from kiwifruit flowers (*Actinidia chinensis* Planch.). Euryglossinae and Hylaeinae have been captured on *Leptospermum* flowers, and Hylaeinae on *Hebe*, *Raoulia*, *Taraxacum*, *Eucalyptus* and others. More details on flower relationships of Colletidae will be presented elsewhere.

Distribution and abundance

Colletidae occur throughout vegetated areas, but most species are restricted in their distribution and some are known from only one or several specimens. Some, e.g. *L. metallicus*, *L. vestitus* and *L. fulvescens* can be extremely abundant on their particular host flowers. Native bees often greatly outnumber honey bees on most Myrtaceae, many Compositae and Leguminosae, and numerous other plants both native and introduced. Peak abundance generally occurs during November and December. Most Colletidae are scarce prior to late October and after early February.

Parasites and diseases

A *Hyptiogaster* (Hymenoptera) parasitoid of *Leioproctus* spp. has been collected from flowers or nest sites throughout New Zealand. Near Auckland 8.8% of cells were successfully attacked. In the same nest site 2.8 % of cells were infected with a chalk brood fungus, *Ascospaera* sp. (Donovan, 1967). Pyemotid mites were present in some cells and were phoretic on some bees but appeared to be non-pathogenic. The pollen mould fungus *Bettsia alvei* (Betts) Skou 1972 (= *Ascospaera alvei* (Betts) Olive and Spiltoir 1955) caused mycosis of a *Leioproctus* pupa collected near Auckland (Thomas and Poinar, 1973). Prepupae of Hylaeinae have been parasitised by the chalcidoid *Melittobia* sp. and at least one unidentified chalcidoid wasp. At Whataroa, Westland, prepupae of *Hylaeus relegatus* (Smith) in nests were attacked by the hymenopterous parasitoid *Gasteruption* sp.

Halictidae

New Zealand Halictidae belong to the Halictinae. All four or five species are moderately to sparsely hairy, black or greenish, and range from 4 to 8 mm in length. Females carry pollen externally on scopae on the hind legs, laterally on the thorax, and to some extent ventrally on the abdomen. The possession of an acute glossal apex distinguishes these bees from Colletidae where the glossal apex is bifid.

Life cycle

Fertilised females remain quiescent in nests in soil during most of May, all June and July, and most of August. When the soil begins to warm in early spring females emerge, feed, and begin renesting, possibly in the maternal nests but often in new nests. Several females of *Lasioglossum sordidum* (Smith) may forage from the same nest. Evidently some form of social organisation exists, probably at the primitively eusocial level. Males and females appear to be produced throughout the summer and autumn, but individuals probably do not live more than 6-8 weeks.

Nest sites

L. sordidum nests in fine-grained bare soil with a level to vertical surface. By far the greatest concentrations of nests have been found in soil maintained bare by man's activities. At Lincoln near Christchurch fence lines and horticultural land sprayed annually with weedicides supports numerous *L. sordidum* nests. Near Blenheim stop-banks and ditch sites above water level provide many suitable sites. A second species nests in nearly vertical sandstone cliffs on the shores of the Waitemata Harbour.

Nests of *L. sordidum* consist of a tunnel 3 mm in diameter that penetrates up to 400 mm into the substrate. Cells open almost directly from the tunnel in all directions.

Flower relationships

The lengthy nesting period of Halictinae means that a demand for pollen and nectar exists through much of spring and autumn and all summer. *L. sordidum* females appear to be broad generalists in their foraging habits. An extremely wide range of both native and introduced plants (about 80 species) are visited. Marked preferences are not obvious, and females appear to collect pollen from almost any flower in which it proves to be accessible. In addition to numerous native flowers *L. sordidum* females have been collected on introduced *Prunus*, *Pyrus*, *Ceanothus*, *Taraxacum*, *Achillea*, *Brassica*,

Daucus, *Cucurbita*, *Cytisus*, *Medicago*, *Actinidia*, *Phebalium*, and many others.

Distribution and abundance

Halictinae range throughout most of vegetated New Zealand, but are more numerous in the drier eastern and south-central regions of the South Island. Female numbers increase rapidly from August. Males first appear in early summer, and by late summer may form mating swarms over flowering *Hebe* or other vegetation near nest sites. Females decrease in abundance as winter approaches, and males disappear with the onset of frosts. During peak abundance in late spring and early summer female Halictinae often outnumber other bees, both native and introduced, on some flowers. However, because of their small size Halictinae are less obvious than most other bees.

Parasites and diseases

Enemies of Halictinae are unknown.

INTRODUCED BEES

Seven species of bees have been purposely established in New Zealand since the advent of European man. An eighth species, the pumpkin bee (*Peponapis pruinosa* (Say)) has been recently released but as establishment is uncertain it will not be dealt with here.

Five of the established species belong to the Apidae, and one each to the Halictidae and Megachilidae. Introduced bees are present in all vegetated areas. Several species are still expanding their ranges, aided and abetted by man for economic reasons. The Megachilidae was considered by Michener (1944) to be more advanced than the Halictidae. The Apidae are generally believed to represent the apex of bee evolution because of several features considered to be advanced, including the complexity of their social structure and the use by honey bees of a "language" to transmit information between individuals.

Apidae

Introduced Apidae can be divided into Apinae (one species of honey bee), and Bornbinae (four species of bumble bees). Females carry pollen in corbiculae (pollen "baskets") on the hind legs.

1. *Apinae*

The first documented introduction of *Apis mellifera* L. was in 1839 when hives from England were landed at Hokianga (Hopkins, 1911). By 1848 many hollow trees at the Bay of Islands had been 'occupied by honey bees, and hives were evidently

being kept at Auckland, Coromandel, Waikanae and elsewhere (Cotton, 1848). Importations from many geographical regions of hives and queen bees with attendant worker bees continued until early this century. The Apiaries Act of 1924 prohibited the importation of honey bees or used hives and equipment in an attempt to exclude bee enemies not yet present in New Zealand. However, it is rumoured in beekeeping circles that honey bee queens and attendant workers have been imported illegally in recent years.

Worker honey bees are about 12-13 mm long, and in colour range from golden yellow to black. Black honey bees are similar in general appearance to the largest *Leioproctus* species, but can be distinguished by the presence of short hairs throughout the compound eyes.

Life cycle

Honey bees are highly social (eusocial) in that individuals live permanently in co-operative groups. In winter a hive consists of one fertilised queen, up to 20000 worker bees and few immatures (brood). Since flowers are usually very few and flying hours are restricted because of short days and low temperatures, the bees depend for food almost entirely on pollen and honey (produced from nectar) stored during the previous summer. From mid winter, if food supplies both stored and collected are adequate, brood rearing expands rapidly. By early summer the hive population will have increased to about 60000 workers, plus several hundred to several thousand male bees (drones). Food stores are depleted during population build-up in early spring, but by late spring stores are replenished as brood rearing levels off and the proportion of foraging bees to brood increases. At this time many flowers begin producing large quantities of nectar—the "honey flow" as it is termed by beekeepers. Hive reproduction by swarming is greatest just prior to or as the honey flow begins, but swarms can be produced from spring until autumn. New queens are produced at swarming and at other times when old queens fail. Brood rearing declines rapidly after early summer to be followed 6-8 weeks later by a parallel decrease in the worker bee population. Drones are expelled from the hives as winter approaches, and in early winter brood rearing usually terminates although in vigorous hives some brood may be reared throughout the winter.

The continuous presence of active adult bees throughout the year and the almost continuous brood rearing means that the demand for pollen and honey is also continuous. The quantity of honey

stored during the honey flow varies greatly among hives but at least 20 kg is probably required in most districts to sustain hives through winter and early spring. Vigorous hives may store in excess of 150 kg, plus several kg of pollen. During a year many times more pollen and honey is consumed within the hive than is stored. Beekeepers have accentuated the honey storing trait of their bees by selective breeding. Feral honey bees probably store much less honey per hive than do bees in commercial hives.

Nest sites

Honey bee hives consist of parallel combs of beeswax hanging from the ceiling of a dry cavity well protected from wind, rain and extremes of temperature. Natural nest sites are commonly hollow trees and to a lesser extent hollows in rock formations. At Ithaca, New York, the modal volume of 49 cavities (21 in trees) occupied by feral honey bee colonies was 30 to 40 litres; 80% of the nest sites were from 20 / to 100 / in volume (Seely, 1977; Seeley and Morse, 1976).

In New Zealand, cabbage trees (*Cordyline australis* (Forst. f.) Endl.), white pine (*Dacrycarpus dacrydioides* (A. Rich.) de Laubenfels) and willows (*Salix* spp.) are frequently occupied. Although nest cavity size has not been measured it probably approximates that of nest cavities in the United States. Honey bees maintained by beekeepers are housed in moveable frame (comb) hives manufactured expressly for this purpose.

Flower relationships

The number of species of flowering plants visited by honey bees is probably greater than that visited by any other species. Continuous adult bee activity, and almost continuous brood rearing coupled with the drive to store surplus pollen and honey stimulates foraging whenever weather is suitable for flight. Walsh (1978) listed numerous native and introduced plants as good nectar and pollen sources for honey bees, but many more species must supply lesser quantities. Commercial hives produce about 8000 tonnes of honey annually (Mr C. Wicht, N.Z. Honey Marketing Authority, pers. comm.). At least 80% of 6000 tonnes supplied to the Honey Marketing Authority is derived from introduced clovers and pasture weeds (Mr C. G. Rope, Honey Grader, MAF, pers. comm.). The quantity of honey stored by wild hives cannot be assessed but it must be considerable.

Distribution and abundance

The Ministry of Agriculture and Fisheries

recorded 226 870 registered bee hives in 1979 (Mr J. Smith, Apicultural Instructor, MAF, pers. comm.). Numerous wild hives must exist in almost all vegetated areas. On days suitable for bee flight, worker honey bees appear on attractive flowers throughout the country. Honey bee numbers are lowest in winter and highest in summer. Honey bees are probably one of the most common and continuously present insects in New Zealand.

Parasites and diseases

Palmer-Jones (1964) listed seven organisms as enemies of honey bees in New Zealand: two external acarine mites, *Acarapis externus* Morgenthaler and *A. dorsalis* Morgenthaler, the protozoan, *Nosema apis* Zander, the amoeba, *Malpighamoeba mellifica* Prell., the bacillus, *Bacillus larvae* White, a virus that causes sac brood disease, and the chalk brood fungus, *Ascosphaera apis* Maassen ex Claussen (Olive et Spiltoir). In addition, Clinch and Ross (1970) reported the presence of *Acarapis vagans* Schneider.

2. *Bombinae*

Four species established from bumble bee queens collected in England and liberated in 1885 and 1906. The aim was to improve pollination and therefore seed production of red clover (*Trifolium pratense* L.), (Hopkins, 1914). However, although this aim was achieved by the establishment of the long-tongued *Bombus hortorum* (L), *B. ruderatus* (F.) and *B. subterraneus* (L), the short-tongued *B. terrestris* (L) also established (Gurr, 1957). Bumble bees are characterised by their bulky size (12-25 + mm long), densely hairy bodies, prominent black, yellow and white colouration, and loud buzzing when flying.

Life cycle

Bumble bees are primitively eusocial in that for part of their life cycle queens are solitary. New queens and males are produced in nests from spring to autumn but mainly during summer. Mating usually occurs in the field although in *B. subterraneus* it may occur in the nest. After mating, new queens usually return to nests for a few days to feed and build fat reserves for winter hibernation. As nests decline new queens leave to search for winter hibernation sites. After selecting an area of soil which is generally partly shaded, lightly vegetated and angled so water will be shed, new queens dig up to 100 mm into the soil in a few minutes. A torpid state is then entered which is maintained until the soil warms in spring. However, many *B. terrestris* queens and some *B. hortorum*

queens remain on the wing through the winter (Donovan and Wier, 1978).

In spring emergent queens feed for several weeks then begin nest site searching. Within a month of nest founding the first worker bees emerge and from then on if conditions are favourable nest growth is rapid. About three months after founding, a thriving nest may have produced several hundred worker bees and several score males and new queens. Nest decline usually begins about this time. New queens leave the nest, brood rearing decreases, and workers, males and foundress queen eventually die. Nest remnants are soon destroyed by invading insects, mites, slaters and / or rodents.

Nest sites

Of 28 naturally occurring nests studied by Donovan and Wier (1978) 50% were in abandoned rodent nests. Prospective nest sites appeared to have to possess an enclosed dry space, at least a small amount of fibrous material, drainage for faeces, and ventilation, to be acceptable to nest site searching queens.

Mature nests consist of small waxen cups containing eggs, larger waxen ovoid cells enclosing larvae, large fibrous cocoons containing pupae, and fibrous cocoons from which new bees have emerged which may contain pollen or honey. Nest constituents are piled one on the other to form a mass which may reach up to 300 mm across and 120 mm high (Macfarlane, 1976; Donovan and Wier, 1978). Hives designed to house bumble bee nests are beginning to be used by farmers in an effort to increase pollination of certain crops (Macfarlane, 1976; Donovan and Wier, 1978).

Flower relationships

As a group the four bumble bee species visit a wide range of introduced plants and a more restricted number of native plants. *B. hortorum*, *B. ruderatus*, and *B. subterraneus* prefer flowers with long tubular corollas such as red clover, broad beans (*Vicia faba* L), and runner beans (*Phaseolus coccineus* L). Macfarlane (1976) reported the short-tongued *B. terrestris* visiting 400 introduced and 19 native flowers. *B. terrestris* prefers shallow flowers and is an excellent pollinator of lucerne (*Medicago sativa* L) (Gurr, 1955) on which it sometimes occurs in high numbers. Many other introduced plants are also pollinated (Macfarlane, 1976). However, *B. terrestris* often robs nectar from flowers with long corollas (e.g., Kowhai (*Sophora* spp.), bean and red clover flowers) by biting holes near the base and so gaining direct access with its short tongue to the nectar. Flowers so robbed of

nectar are not pollinated by the robbing bee because the stigma is not contacted. However, pollination will occur if a bee subsequently visits a flower "legitimately".

Distribution and abundance

B. hortorum was restricted to Canterbury, Otago and Southland, but has been recently established at Palmerston North (Gurr, 1964; 1972). *B. subterraneus* is confined to the inland eastern half of South Island, but *B. ruderatus* and *B. terrestris* range throughout the two main islands. The latter is established on Stewart Island and *B. ruderatus* appears to have colonised Chatham Island after liberation of queens in 1976 (Macfarlane, 1980).

Seasonally, bumble bees are very few throughout winter, but with rising spring temperatures the number of emerging queens and foraging workers increases rapidly. Later, queens become less common as foraging workers further increase in abundance. Males and new queens soon appear and by mid-summer may outnumber workers. By autumn workers and males are few and queens become scarce as hibernation is entered with the approach of winter.

Parasites and diseases.

A parasitic nematode *Sphaerularia bombi* Dufour, an internal mite *Locustacurus buchneri* (Stammer), two external mites *Pneumolaelaps* sp. and *Kuzinia laevis* (Dujardin), a protozoan and possibly viral, fungal and bacterial diseases are present on or in overwintering queens (Macfarlane, 1975; 1976). *Melittobia* sp. has attacked a few nests (Macfarlane and Pengelly, 1977). The *Melittobia* is probably recently adventive to New Zealand, but most of the other organisms almost certainly were introduced with the imported queen bumble bees.

Halictidae

Introduced alkali bees (*Nomia melanderi* Cockerell) belong to the Nomiinae. Both sexes approach honey bees in size, but can be distinguished from other bees by the presence of four variously coloured (green, yellow or reddish) transverse shiny abdominal bands. Pollen is carried in the same manner as in native Halictidae. Alkali bees are cultured in the north-western United States for lucerne pollination, and were introduced to New Zealand for the same purpose in 1971 (Donovan, 1975; 1979).

Life cycle

The life cycle of alkali bees is very similar to that of native Colletinae. Prepupae overwinter in

nests in the soil, pupation occurs in November and December, and both sexes emerge in late December and January. Following mating soon after emergence, females reneest in the soil from which they emerged or search for similar soil to colonise. Peak nesting occurs through January and February, and all adult activity ceases by mid to late March. In warm summers a small second generation may emerge in March but evidence of nesting has not been seen.

Nest sites

Alkali bees nest only in moist soils; i.e., soils with centibar readings of between about 25 and 41 (Johansen, Mayer and Eves, 1978). Naturally occurring soils with a suitable moisture level usually show surface deposits of sodium or calcium salts. Although most soils with suitable moisture are acceptable to alkali bees, those with less than 31 % clay, 49 % silt and 83 % sand have proven most suitable for rapid bee propagation in New Zealand (Donovan, 1979). Soils suitable for alkali bee nesting can be provided where wanted by the construction of "artificial" nest sites (Stephen, 1965; Donovan, 1979). Naturally occurring saline soils have been colonised near Blenheim, and Lake Ellesmere, Canterbury.

Flower relationships

Alkali bee females collect pollen from composite or lucerne flowers where abundant near nest sites (Donovan, in prep.). Alkali bees have not been seen visiting native flowers although pollen removed from the scopae of a female alkali bee at a coastal nest site was 1 % *Selliera* sp.

Distribution and abundance

The number of nests, and thus the number of female alkali bees, has increased from 70 in 1971 to about 14000 in 1980. Most nests are distributed among lucerne fields near Blenheim, but two nest sites have been established in Canterbury and one in Central Otago. Alkali bees are on the wing from December to March. Large populations will develop only in the very few localised suitable nest soils, or in the vicinity of lucerne seed fields where man constructs nest sites.

Parasites and diseases

Quarantine effectively ensured that only healthy alkali bees (as prepupae) were released in New Zealand (Donovan, 1975; 1979). Some cells have been invaded by soil-inhabiting fungi including yeasts, which may have caused larval death, but these organisms are not primarily bee enemies.

Megachilidae

Lucerne leafcutting bees (*Megachile rotundata* (F.)) (Megachilinae) are widely utilised in western North America for lucerne pollination (Stephen, 1962; Hobbs, 1973). They are about two-thirds the size of honey bees, with a black integument lightly covered with white to yellowish hairs. Females carry pollen in a scopa beneath the abdomen, and leaf pieces between the legs, two characteristics which distinguish this species from all other bees in New Zealand. After quarantine the first bees were liberated at Seddon near Blenheim in 1971 (Donovan, 1975).

Life cycle

Winter is passed as diapausing prepupae in cells in nests. In naturally occurring nests pupation begins in early spring and the first bees (males) appear in late October. First nesting by females commences by late November, but most do not begin nesting until about mid-December. By late February the spring or first generation bees begin dying, but many new bees emerge from their nests as a second generation. Nesting usually ceases by late March but if autumn weather is mild some nesting may continue into mid-April before all adults die.

Most bees are managed by man so that peak nesting and therefore pollinating activity coincides with lucerne bloom. Pupation of managed populations is delayed by holding prepupae in cells at 2-3°C until about 3 weeks before lucerne begins blooming. Cells are then incubated at 25°C, the first bees emerge 3 weeks later, and emergence is complete within a further 10 days. Peak emergence is timed for early to mid-January. Delayed emergence reduces the percentage of nests producing a second generation, which results in fewer bees flying in April.

Nest sites

Female bees require a tube about 4-6 mm in diameter closed at one end and at least 20 mm deep. Holes about 100 mm deep are preferred. Wild bees will nest in beetle holes in logs and branches, gaps under bark, pith cavities in twigs, sticks and straws, and empty mud nests of mason wasps (*Pison* spp.).

Managed bees nest in drilled boards, modified drinking straws, and grooved polystyrene and wooden boards which are placed in hives within shelters in or adjacent to lucerne seed fields.

Flower relationships

Wild leafcutting bees visit many flowers but those of pasture legumes and composites appear to be

preferred. Managed bees visit mostly lucerne flowers or the flowers of other legumes or weeds in or near flowering lucerne fields.

Distribution and abundance

By autumn 1980 the number of managed leafcutting bee cells totalled about 2.35 million. Since 1977 the number of cells has increased by about 1.7 times annually, a rate of increase which should be maintained. Most are on lucerne seed fields near Blenheim, but small numbers of cells have been and are being distributed to lucerne seed growers throughout the South Island and to a lesser extent the North Island. Within the next decade leafcutting bees will probably become widely used by lucerne seed growers at least in the South Island. Widespread use of large populations will inevitably increase the number and distribution of wild bees as some bees disperse from managed populations.

Parasites and diseases

Prepupae are parasitised by the chalcidoid *Melittobia hawaiiensis* Perkins, (Donovan, 1976a; 1976b) and the straw itch mite (*Pyemotes tritici* (La Greze-Fossat and Montagne)) (Donovan, in prep.). In 1971 several hundred leafcutting bee cells imported illegally were released directly in the field. In nests seized after many cells had been constructed, five cells were found to contain the exotic chalcidoid *Monodontomerus obscurus* Westwood, but there is no evidence that the parasite established (Donovan, 1976b). At Whataroa, Westland, a leafcutting bee nest in a hole partly occupied by a nest of *Hylaeus relegatus* was attacked by the parasitoid *Gasteruption* sp. As *H. relegatus* appeared to be the primary host, the attack on the leafcutting bee nest was probably incidental.

In 1974 bodies that resembled spore cysts of chalk brood fungi (*Ascosphaera* sp.) were found among leaves of leafcutting bee cells, but none have been seen since. Prepupae in the cells appeared unaffected (Donovan, in prep.).

DISCUSSION

Primary facets of the biology of each subfamily of bees are summarised in Table 1.

Nest sites

Requirements of ground nesting native bees, honey bees, bumble bees and alkali bees for nest sites differ so markedly that no possibility of competition exists. Although several species of ground nesting native bees have nested in man-made alkali bee nest sites, only areas too dry for alkali bees or areas not utilised by alkali bees for unknown

TABLE 1. *Summation of main biological features of native and introduced bees in New Zealand.*

Bee species	Number of species	Social organisation	Natural nest sites	Artificial nest sites	Primary flower relationships	Main foraging period	Distribution	Abundance	Parasites and diseases
NATIVE									
Colletidae									
Colletinae	30	Solitary	Bare soil, sand, clay	Road cuttings, ditch sides	Natives, many introduced		N.Z. wide	Seasonally very common	<i>Hyptiogaster</i> , <i>Betisia albei</i>
Euryglossinae	1	Solitary	Holes in wood - borer burrows	Unknown	<i>Leptospermum</i>	Late spring-early summer	Localised	Uncommon	Unknown
Hylaeinae	5	Solitary	Holes in wood < 6 mm across	Leafcutting bee nest holes	Natives, many introduced		N.Z. wide	Seasonally common	<i>Gasteruption</i> , <i>Melittobia</i> , other chalcidoidea
Halictidae									
Halictinae	4 or 5	Primitively eusocial?	Bare soil	Herbicide soil	Numerous native and introduced	September to May	N.Z. wide	Seasonally common	Unknown
INTRODUCED									
Apidae									
Apinae	1	Eusocial	Hollows in trees etc. 20-100 l	Honey bee hives	Numerous introduced and native	All year	N.Z. wide	Very common	Mites, protozoan, amoeba, bacillus, virus, <i>Ascospaera apis</i>
Bombinae									
	4	Primitively eusocial	Abandoned rodent nests	Bumble bee hives	Numerous introduced, few native	Spring, summer	N.Z. wide	Common	Protozoan, nematode, mites, <i>Melittobia</i>
Halictidae									
Nomiinae	1	Solitary	Moist alkaline soil	Alkali bee nest sites	Lucerne, composites	Summer only	Localised in South Island	Uncommon but increasing	Unknown
Megachilidae									
Megachilinae	1	Solitary	Holes in wood about 4-6 mm across	Leafcutting bee nest holes	Lucerne, composites	Summer-early autumn	Much of South Island, localised in North Island	Uncommon but increasing	<i>Melittobia</i> , <i>Pyemotes</i>

reasons, have been colonised. Euryglossinae and the smallest species of Hylaeinae occupy nest holes that are too small for leafcutting bees. However, the size ranges of holes occupied by large Hylaeinae and leafcutting bees overlap. Large Hylaeinae have been found occupying nest holes placed out for leafcutting bees and the survival of wild leafcutting bees suggests they may be using nest holes usually occupied by large Hylaeinae. Mason wasps and spiders also occupy some holes that are suitable nest sites for both Hylaeinae and leafcutting bees. Field-placement by man of trap nest holes for leafcutting bees may increase nesting opportunities for large Hylaeinae.

Flower relationships

The ranges of flowers visited by most bee species overlap widely. The marked specialisation for different flowers shown by many Colletidae and Bombinae indicates that competition among them is minimal. However, honey bees, because of their extremely wide flower visiting range, must compete with most other bee species. To a much lesser extent native Halictinae must provide similar competition because of their wide but more restricted flower visiting range. Because honey bees in commercial hives produce most of their surplus honey from introduced plants, competition between most (80%) bees in commercial hives and native bees must be small. However, commercial hives sited near native flowers and wild honey bee hives in areas of native vegetation would appear to be competing directly with native bees for pollen and nectar. Alkali and leafcutting bees exist in large numbers primarily near lucerne fields. Their small pollen and nectar requirements will be met by lucerne or weeds associated with lucerne, a source that will be competed for mainly by other introduced bees.

Main foraging period

Colletidae encounter and therefore face possible competition from introduced bees only during late spring and early summer, a period when pollen and nectar production by many flowers is maximum. The effect of competition from honey bees and bumble bees is probably minimal when food is abundant. Halictinae, however, may encounter competition from honey bees and bumble bees in early spring and to a lesser extent in autumn when the supply of pollen and nectar by flowers is not great.

Distribution and abundance

The ubiquity and high numbers of honey bees

means that native bees face potential foraging competition throughout New Zealand. Competition from bumble bees is probably minimal because of their generally low numbers compared to honey bees, and their preference for flowers other than those visited by native bees. Alkali and leafcutting bees are as yet too few to compete significantly with native bees, but leafcutting bees in particular could become more important within the next decade if their numbers increase as expected. These two species will, however, occur in high numbers mainly on lucerne seed fields where native bees are uncommon.

Parasites and diseases

No natural enemies or diseases known to attack honey bees or bumble bees have been recorded from native bees. Quarantining alkali and leafcutting bees precluded any possibility of introducing enemies of these bees. However, attacks by a parasite of Hylaeinae (and mason wasps), the chalcidoid *Melittobia hawaiiensis*, can cause high mortality in managed leafcutting bees (Donovan, in prep.). Several other species of hymenopterous parasites of native bees as well as some stored product insects that probably attack native Hylaeinae nests would appear to be potential enemies of leafcutting bees.

The small number of bumble bee nests attacked by *Melittobia* sp. indicates that the impact of this parasite is minimal. However, if man-made bumble bee hives become widely used, the incidence of *Melittobia* could increase as bumble bee nest density increases.

The pollen mould fungus *Bettisia alvei* that was recorded from a *Leioproctus* sp. pupa, is present in honey bee hives in Europe and the United States (Morse, 1978). It has apparently not previously been recorded from other bee species. More data are needed on the identity and distribution of the closely related genera *Bettisia* and *Ascosphaera* both in New Zealand and elsewhere before their status as possible inter-species transmissible bee enemies can be ascertained.

Other factors

Bees have here been considered in isolation, but many other insects, birds and even bats take nectar and pollen from flowers. The occurrence and importance of these flower visitors has recently been reviewed by Godley (1979) so will not be discussed here. However, early work by Thomson (1881 a, 1881b, 1927) and Heine (1938) showed that insects other than bees frequent a wide range of native flowers. Primack (1978) in a study of insect visitors to montane and alpine flowering plants found that

the flowers of most plants were visited by a wide range of unspecialised insect species. Native bees formed only a part of the pollinator assemblages although at times they could be tremendously abundant. From the flowers of *Discaria toumatou* Raoul, at least 23 species of insects were recorded, only one of which was a native bee (Primack, 1979). primack (1978) observed only two isolated competitive interactions among insects on native flowers. He concluded that competitive interactions of flower visitors on New Zealand montane and alpine plants are rare or very subtle.

Several of the seven native birds and the one bat species listed by Godley (1979) as flower visitors are now uncommon or rare. Presumably this reduction of numbers must have reduced the quantity of pollen and nectar removed by them from native flowers.

Activities of man have probably influenced native bee numbers more than any other factors. The destruction of huge areas of native flowering plants must have reduced the quantity of food available for native bees. On the other hand, the introduction of many flowers which native bees are successfully exploiting for both pollen and nectar may have compensated for the loss of native flowers to at least some degree. The relative competitive foraging abilities of native and introduced bees either individually or collectively are unknown. However, the storage by honey bees of pollen and nectar from flowers visited by honey bees and native bees, and at times when native bees outnumber honey bees, indicates that pollen and nectar are abundant. In general, the quantity of food seems ample to support both native and introduced bees, as well as numerous other flower visitors.

The main constraint to bee population levels seems to be the availability of nest sites. The colonising of suitable nesting soils by introduced grasses and other plants has almost certainly reduced nesting opportunities for some Colletinae and Halictinae. On the other hand, man's inadvertent creation of nest sites by various earthworkings such as roading, ditching and the barring of ground with herbicides, has partly balanced the loss due to introduced plants. Regeneration of *Leptospermum* spp. after milling of climax podocarp forest, coupled with the unintentional creation of nest sites, has probably increased the population of some Colletinae particularly in parts of Northland and the central North Island where *Leptospermum* regeneration is extensive.

Native bees have been discussed as a group, but it is the interactions of individual species with introduced bees which may be important to the

survival of native bee species. A consideration of interactions at the species level will require more detailed taxonomic, distributional and biological data than are available now. This review has shown that *most* contact among bee species occurs on flowers. Species survival could possibly be determined by the relative competitive foraging abilities of female bees either individually or collectively in times of pollen and/or nectar dearths. Studies of intra floral relationships of bees (and other insects) should lead to clarification of the survival status of individual bee species.

CONCLUSIONS

Wide differences in nest site requirements among almost all species indicate that there is very little or no competition between native and introduced species for this resource. Leafcutting bees may compete to some extent for nest holes with some Hylaeinae, but Hylaeinae in turn benefit from occupying man-made nest holes of leafcutting bees. Inter-species effects of parasites and diseases appear to be minimal and localised. Some degree of specialisation for different flowers by most bee species and the coincidence of peak numbers of most native bee species with abundant pollen and nectar production further reduces competition for these resources between native and introduced bees. Large environmental changes wrought by man have both reduced and enhanced population levels of many native bee species. These environmental changes probably outweigh any possible competitive effects of introduced bees. The ability of some native bee species to outnumber honey bees and bumble bees on many native and introduced flowers after about 140 years of contact indicates that these native bees are enjoying considerable competitive success. The indications are that they should continue to do so. The status of poorly known native bee species is less certain.

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