FOOD DEMAND FOR COLONY DEVELOPMENT, CROP PREFERENCE AND FOOD AVAILABILITY FOR *BOMBUS TERRESTRIS* (L.) (HYMENOPTERA: APIDAE)

A thesis

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I am tempted to give one more instance showing how plants and animals are bound together by a web of complex relations. I find from experiments that humble-bees (bumble bees) are almost indispensable to the fertilisation of the heartsease (wild pansy) and some kinds of clover. Humble-bees alone visit red clover, as other bees cannot reach the nectar. Hence, we may infer that, if the whole genus of humble-bees became extinct or very rare in England, the heartsease and red clover would become very rare, or wholly disappear. The number of humble-bees in any district depends in a great measure on the number of field-mice, which destroy their combs and nests. Now the number of mice is largely dependent, as everyone knows, on the number of cats; and Col. Newman says 'Near villages and small towns I have found the nest of humble-bees more numerous than elsewhere, which I attribute to the number of cats that destroy the mice.' Hence it is quite credible that the presence of feline animals in large numbers might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!

Charles Darwin 1882.

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ABSTRACT

Eight *Bombus terrestris* (L.) colonies were reared in laboratory observation hives in 1986 and foraged in cages. Pollen and sugar consumption were correlated and could be estimated from larval area and number of live workers. Pollen consumption peaked within two weeks of maximum larval area in 6-8 week old colonies and coincided with peak worker emergence. Sugar consumption peaked with the emergence of males and queens two weeks later. The optimum period for maximum pollination efficiency for a colony would be from one week prior to peak larval area to two weeks after.

There was a positive correlation between the total productivity of a colony ('Productivity Index', a biomass estimate from the number and size of empty cocoons) and the maxima of live worker numbers, larval area and rate of food consumption, and the total food consumption and biomass (but not sex ratio) of reproductives produced. Colonies with higher consumption made greater investment in reproductives, but larger colonies did not invest proportionally more into reproduction than smaller colonies. Larger colonies grew faster with more workers emerging per unit time than smaller colonies.

Food consumption and development of indoor colonies was compared with ten colonies maintained in the same observation hives but free foraging outdoors on flowering crops in 1987. Maximum weekly pollen consumption was 12.6 times less in free foraging colonies and sugar energy consumption was 43 times lower with no queens produced in colonies foraging outdoors. The pollen consumption/cm^2 at maximum larval area was 14 times lower in free foraging than indoor colonies so consumption (rate and total) for free foraging colonies could not be predicted from maximum larval area using indoor consumption data.

The order of *B. terrestris* nectar gatherers' and queens' crop preference over the whole season was: borage, *Borago officinalis* > fodder radish, *Raphanus sativus* > swede, *Brassica napus* > broccoli, *Brassica oleracea*. Flower preference was not correlated with flower density or production. *B. terrestris* males and honey bees preferred borage with broccoli as second choice. Honey bees were on average seven times more abundant on crops than *B. terrestris* workers and with a similar tongue length honey bees provided the greatest competition for food. On calm, warm days honey bee numbers on borage exceeded 2/m^2, nectar and pollen became depleted and *B. terrestris* switched to nectar gathering on fodder radish. The long corolla tube of fodder radish excluded nectar collection by honey bees with a short tongue, whereas *B. terrestris* workers bit holes in the corolla base and 'robbed' nectar. Honey bees and *B. terrestris* males removed nectar from previously perforated fodder radish flowers.

Borage secreted nectar throughout the season and had the most pollen and nectar per flower. Fodder radish had the highest flower density and pollen and nectar standing crop, producing nectar later in the season as weather improved. *B. terrestris* being less sensitive to poor weather, foraged for nectar and pollen each day before and after the peak in honey bee numbers.

B. terrestris workers collected pollen on borage by vibrational pollen harvesting ('buzz' pollination) from poricidal-like anthers. On crucifers, incidental dusting of pollen while nectar collecting occurred. Early in the season borage pollen was collected throughout the day, but later in the season with increasing honey bees on borage, *B. terrestris* pollen gatherers collected borage pollen early in the day and crucifer pollen during the rest of the day.

Sugar concentration of nectar returning in foragers was highly correlated with sugar concentration of the most preferred crop at that time. With higher temperature and decreased rainfall, more pollen and nectar became available, more pollen and nectar gatherers and honey bees foraged on the crops and workers returned to colonies with more food. The high density of honey bees on borage did not reduce the food intake returning to *B. terrestris* colonies.

LIST OF ABBREVIATIONS AND SYMBOLS

p or PR	=	probability
S.D.	=	standard deviation of sample
S.E. (M.)	=	standard error of mean
S.E.D.	=	standard error of difference
t test or t	=	Student's t test
df (DF)	=	degrees of freedom
F_S or VR or F ratio	=	variance ratio
F. prob. or F PR	=	variance ratio probability
n.s.	=	not significant ($p > 0.05$)
n	=	number of cases (observations)
Reps.	=	number of replicates
L.S.D.	=	least significant difference (Sokal and Rohlf 1969, p.235)
*	=	$p < 0.05$
**	=	$p < 0.01$
***	=	$p < 0.001$
r value or R	=	Pearson's correlation coefficient
z value	=	Fisher's transformation for correlation coefficients r
ANOVA	=	analysis of variance
temp.	=	temperature
R.H.	=	relative humidity
µm	=	micron (10^{-6} m)
nm	=	nanometre (10^{-9} m)
mg	=	milligram (10^{-3} g)
µl	=	microlitre (10^{-6} litres)
µE	=	micro Einstein
kj	=	kilojoule
% sugar	=	percentage total sugar content in solution
RSQ or R^2	=	R squared (% of variance accounted for by the regression coefficient)
INT	=	y intercept
LIN	=	linear function (slope)
INT S.E.	=	standard error of y intercept
LIN S.E.	=	standard error of slope
S.E. REG	=	standard error of regression equation
SS	=	sum of squares (sum of squared deviations from the mean)
SS %	=	percentage sum of squares
MS	=	mean square
MV	=	missing values
QUAD	=	quadratic function
CUB	=	cubic function
QUART	=	quartic function

COV EF	= covariance efficiency
% VAR	= percentage of variance
CUM %	= cumulative percentage
coef	= coefficient
ł	= ± one standard error of mean (figures)
y=1.3324*x^0.325	= y=1.3324 multiplied by $x^{0.325}$ (fig. 3.14)

Note: All levels of statistical significance have been recorded in the appropriate tables or in the appendix and are therefore not generally recorded in the text.

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DECLARATION

This thesis does not contain any information which has been accepted for the award of any other degree or diploma in any University and, to the best of my knowledge and belief, this thesis does not contain any information previously published or written by any other person, except when due reference is made in the text of the thesis.

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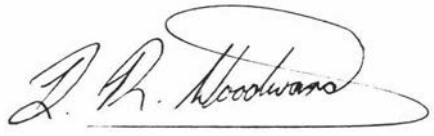

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APRIL 1990

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 Crop pollination by bumble bees

Introduction of red clover, *Trifolium pratense* L. and lucerne, *Medicago sativa* L. into New Zealand resulted in poor seed set of these crops, even following the introduction of honey bees, *Apis mellifera* L. in 1839 (Donovan and Macfarlane 1984).

Darwin (1858) drew attention to the efficacy of bumble bees (*Bombus* spp.) as suitable pollinators of red clover, and so importation was implemented. 'Acclimatisation societies', with little entomological knowledge, ignored warnings that unsuitable species could be introduced (see Belt 1878), and attempted importation unsuccessfully in 1870 (Montgomery 1962a). Successful establishment was finally achieved from shipments of queens from England in 1884.

Population increases in New Zealand were explosive following liberation, with bumble bee queens spreading up to 160km per year. Red clover yields increased dramatically (Hopkins 1914; Montgomery 1962a) with estimates of 336-560 kg/ha on the Canterbury Plains (Gurr 1961). Beekeepers became worried as supplies of honey diminished enormously, this being attributed to an overabundance of bumble bees (Thomson 1891).

However the anxiety was short-lived. After 1895 red clover seed yields declined to about one third of peak production years, following a decline in the bumble bee population (Hopkins 1914; Montgomery 1962a). The cause of the demise in abundance of bumble bees was not entirely clear but most likely, over exploitation of adventive spring forage, combined with poor weather conditions and diminishing suitable nest sites, reduced the population.

Farm organisations pressed for further release of bumble bees to improve seed yields, leading to more introductions in 1906. Gurr (1957b) found that four species had established in New Zealand: including *Bombus terrestris* (Linnaeus), *B. ruderatus* (Fabr.), *B. subterraneus* (L.) subsp. *latreillellus* (Kirby) and *B. hortorum* (L.). Other species introduced had apparently not established (Gurr 1961).

In hill country areas where *B. ruderatus* was common, red clover seed yield remained high, while on the plains where *B. terrestris* predominated, yields were much lower (Montgomery 1962a). *B. terrestris*, with its shorter proboscis, was unable to reach nectar secreted at the base of red clover flowers and resorted to 'robbing' flowers by perforating the corolla base with extended mandibles. This method rewarded the bee but

did not pollinate flowers resulting in this species being condemned by growers of clover seed as an unfortunate introduction (Gurr 1955). However, as Gurr (1955) pointed out, this nectar robbing behaviour was not resorted to by all nectar gathering workers and certainly not by pollen gatherers. Also hole-biting did not damage the ovary of flowers and long-tongued species were still capable of effecting pollination after robbing had occurred.

B.terrestris also has potential for pollination of other crops in New Zealand such as white clover, *Trifolium repens* L. (Palmer-Jones, Forster and Jeffery 1962), lucerne (Hadfield and Calder 1936; Gurr 1955, 1961, 1974; Palmer-Jones and Forster 1964, 1971; Macfarlane 1970; Donovan and Macfarlane 1984; Read, Donovan and Griffin 1989), apple varieties, *Malus sylvestris* Mill. (Palmer-Jones and Clinch 1966, 1967), chou moellier, *Brassica oleracea* L. (Forster, Clinch and Palmer-Jones 1972), greenhouse muskmelons, *Cucumis melo* L. (Fisher and Pomeroy 1989), tomatoes, *Lycopersicon esculentum* Mill. (Macfarlane pers. comm.), and kiwifruit, *Actinidia deliciosa* (A.Chev.) (Palmer-Jones and Clinch 1974; Pomeroy 1982; Donovan and Macfarlane 1984; Macfarlane and Ferguson 1984; Read *et al.* 1989).

Research emphasis changed in the early 1980s, when the export potential of kiwifruit (first introduced in 1910) was realised. Honey bees are the only pollinating agents currently managed for this purpose, but are not ideal pollinators of kiwifruit as the flowers lack nectar and honey bees prefer nectiferous blooms such as white clover (Palmer-Jones and Clinch 1974). Honey bees are also reluctant to forage in cold, wet, windy weather which often prevails for at least part of the late spring flowering period. The value of honey bees as pollinators is severely limited at temperatures below 15 C (Heinrich 1979a).

B. terrestris has a number of attributes which make it a particularly useful pollinator of kiwifruit and other crops: 1. The ability to forage for extended periods under conditions preventing flight by honey bees (Free and Butler 1959). Queens can forage at 2 C and in strong wind or drizzle while workers normally forage between 10-30 C (Barth 1985). 2. Flower visiting rate is twice that of honey bees (Free 1968). 3. Their large hairy bodies carry considerably more pollen than honey bees (Free and Williams 1972) frequently contacting stigmas of large flowers such as kiwifruit (Donovan and Macfarlane 1984). 4. Where the stigma may be well above the stamens, honey bees may not be effective pollinators of certain fruit trees. Bumble bees may be more effective as their large bodies bridge this gap (Free 1960). However, two factors have so far reduced their usage: 1. Natural populations are often too low for effective pollination with numbers fluctuating widely within and between seasons (Macfarlane 1974). 2. Bumble bees are, at present, not fully manageable i.e. colonies cannot yet be supplied on a large enough scale when and where required for pollinating target crops.

A relative dearth of potential enemies in New Zealand reduces the number of potential domestication problems faced by overseas bombiculturalists.

Attempts to increase bumble bee populations (locally and overseas) in the last 80 years have met with both success and failure. The main methods used are:-

1) Relocation of existing natural populations:-
   a) queens only (Clifford 1973)
   b) whole nests (i) collecting from natural sites
   (ii) trap-nesting in field hives: setting out domiciles with nest material to provide nests for naturally overwintering queens (Sladen 1912; Frison 1926; Fye and Medler 1954b; Free and Butler 1959; Medler 1962; Hobbs 1962a, 1967; Hobbs, Nummi and Virostek 1960, 1962; Donovan and Weir 1978; Pomeroy 1981a; Macfarlane, Griffin and Read 1983, 1984).
2) Environmental enhancement to increase wild populations near target crops by
   a) increasing food supply by growing a succession of flowers (Gurr 1957a; Holm 1966a; Free 1970a; Macfarlane *et al.* 1983).
   b) increasing nest sites (i) natural nest sites by leaving land fallow (Cumber 1953a; Free and Butler 1959; Holm 1966a), now very expensive on modern farms.
   (ii) providing artificial domiciles (Macfarlane *et al.* 1983).
3) Controlled rearing:
   (a) confining queens in glasshouses or screen cages with nesting boxes and flower bouquets (Lindhard 1912; Haas and Holm 1960).
   (b) confining queens in screen cages with nesting boxes placed over flowering crops (Montgomery 1962b).
   (c) total confinement: naturally or artificially overwintered queens are induced to nest in observation hives provided with food and, in some cases, nesting material (Sladen 1912; Plath 1923; Frison 1927; Hasselrot 1952; Free and Butler 1959; Dottlinger 1965; Holm 1966a and b; Plowright and Jay 1966; Sanduleac 1966; Roseler 1985 and others). Colony expansion may occur outdoors prior to transfer to the target crop.

The success of the outdoor expansion phase is likely to depend on the food supply in the field. Hence this project was initiated to determine the food requirements of growing colonies of *B. terrestris,* and to examine the food availability from and attractiveness to *B. terrestris* of certain candidate crops.

The main objectives of the present study were:

1) To determine pollen and nectar consumption of *B. terrestris* during colony development and to consider developmental factors affecting this consumption.
2) To evaluate a limited number of selected bee forage crops for *B. terrestris* colony development.
3) To determine the relative floral preference for these crops by *B. terrestris.*
4) To examine factors (biotic and abiotic) influencing food harvesting by *B. terrestris* on these crops.

1.2 Forage crops

The main forage crops utilised by *B. terrestris* during experimental trials were:

Boraginaceae

Borage, *Borago officinalis* L.

A herb or weed of European origin, borage is cultivated for honey and as an ornamental. The floral formula is five (petals, sepals, stamens, lobes). The flowers have sky blue petals alternating with hairy dark red to green sepals.

Flowers are actinomorphic and the inflorescence is clustered in a helicoid (scorpioid) cyme; when first open the flowers are pink but change to sky blue.

Poricidal-like (see Buchmann 1983), introrse (inward dehiscent), dual chambered, black anthers are clustered in a vertical ring (cone) around a single style/stigma which contrasts with the blue corolla. The flowers are protandrous.

Pointed deep purple lobes, half the length of the stamens, arise from their base. The lobes hold the stamens in position preventing separation. The stamens alternate with tongue-like fleshy lobes which arise from the base of each petal forming a ring around the stamens. Nectar is secreted by a receptacle at the base of the ovary and collects between, and is concealed by the base of the lobes and stamens (Pellett 1967).

The pendulous flowers of borage yield nectar freely. Owing to their inverted position, nectar is not easily washed out by rain. To obtain nectar the bee hangs under a flower inserting it's proboscis to the base of the lobes. In so doing, pollen may become sprinkled on the venter.

Nectar contains sucrose, glucose and fructose in equal proportions, or either with sucrose dominant, or fructose and glucose dominant. Lesser amounts of maltose, an oligosaccharide, may also be present (Percival 1961).

The pollen is off-white. Individual grains have constrictions in the centre characteristic of many plants of the Boraginaceae. Once established, the crop may maintain itself from self-sown seed.

Brassicaceae (Cruciferae)

Broccoli, *Brassica oleracea* L.var. italica; kale, *B. oleracea* L.var. acephala cv. Maris Kestrel; swede, *B. napus* L. var. napobrassica; fodder radish, *Raphanus sativus* L.cv. Neris; mustard, *B. alba* L.

Flowers are hermaphrodite, the floral formula is four (petals, sepals) with green sepals and yellow petals in the shape of a crucifix. There is an inner whorl of four longer stamens (fodder stamens) and an outer whorl of two shorter (pollinating) stamens. The superior ovary of two united carpels is surmounted by a style with a two-lobed stigma (Free 1970a). Long-tubed crucifers have polysepalous calyces. The petals are long-clawed and separate, but the very strong imbrication of the sepals forms and preserves the flower tube as well as protecting the nectar. Although the sepals part and are shed after anther dehiscence is completed, the flower shape is often maintained long enough to enable legitimate exploitation by long-tongued insects (Percival 1965).

In broccoli, the anthers dehisce simultaneously and instantaneously as the flower opens. In fodder radish, flowers produce all their pollen during a brief period so their potential for cross-pollination is limited (Percival 1965).

Crucifer pollen is yellow, and the grains are round to oval with characteristic markings (like a 'radioactive' symbol). Free (1970a) considered that distribution of pollen by wind was limited and that the most common flower visitors were honey bees.

Nectar of Brassicaceae contains predominantly glucose and fructose with a trace of sucrose (Percival 1965).

Papilionaceae (Leguminosae)

White lupin, *Lupinus albus* L.; yellow lupin, *L. arboreum* L. blue lupin, *L. angustifolius* L.; tick bean,*Vicia faba* L.; tree lucerne,*Chamaecytisus palmensis* (Christ) Bisby et K. Nicholls; white clover, *Trifolium repens* L.

The flower of this group is zygomorphic with a standard petal, two winged petals and two keel petals, all of which are partially joined at the base to form the corolla tube. The keel petals are partly fused to enclose the staminal column of ten stamens, nine in a ring and one free, with a single style. Nectar is secreted at the base of the corolla tube (Free 1970a). The calyx is fused around the base of the corolla tube. Legumes dehisce pollen instantaneously before the flower opens (Percival 1965).

Tick bean has an extended corolla tube and short tongued bumble bees e.g. *B. terrestris,* 'rob' the flowers by biting holes in the corolla base (Free 1962).

Tree lucerne or tagasaste has white flowers with concealed nectar and pollen and an explosive pollen presentation mechanism. Only bumble bees are effective in operating the flowers, and both bumble and honey bees rob the flowers of nectar through the calyx (Webb and Shand 1985).

Pollen of lupin and tree lucerne is brick red. Bumble bee queens, because of their size, often split the keel petals, permanently exposing the pollen and stigma, allowing other insects not strong enough to depress the keel to pollinate.

White clover has a 3mm long corolla tube allowing short tongued bees to reach nectar. When flowers are pollinated, they turn brown, become reflexed and cease production of nectar (Free 1970a).

1.3 Bumble bee life history

B. terrestris (L.), first described by Linnaeus (1758), includes at least ten subspecies (ssp.) (Rasmont 1983) of which *B. terrestris* ssp. *audax* most closely resembles that found in New Zealand.

Since its arrival in New Zealand, the life cycle of *B. terrestris* has evidently changed to suit the temperate climate in contrast to colony development in England (Brandenburgh 1961). Prys-Jones and Corbet (1987) explained how bumble bee species with long life cycles often extend the period of active colony development at lower latitudes in temperate regions. Cumber (1954), by studying worker numbers, wing wear, corbicular pollen, fat body content and ovary development, discovered that nest founding occurred during nine months of the year from May to January. Cumber observed queens with wing wear in most months of the year and queens were seen on the wing during mild sunny winter days. Workers were observed on the wing throughout the year with males present from December to April in the Wellington area. Cumber (1949a) discovered what he believed to be an overwintering nest of *B. terrestris* on 4 November 1948 in Nelson. However this may have originated from early spring nest founding. Cumber discounted occurrence of perennial nests as no evidence of more than one functional queen was found.

In England, the four species which occur in New Zealand, produce strictly seasonal colonies with a solitary phase (queen hibernation) in winter. The life cycle in New Zealand was illustrated by Macfarlane and Donovan (1976), and later modified by Donovan and Macfarlane (1984) to include a bivoltine cycle with the first generation from July to February and the second from January to March. Second generation colonies probably survive into the following spring during mild winters. In northern Africa *B. terrestris* breeds in winter and it is thought inseminated queens aestivate in summer (Sladen 1912). Hence, this species has a degree of adaptive plasticity, modifying the life cycle to suit the local climate.

After the death of workers and males, the colony is survived by the young fertilised queens. After mating and fat body development, these queens seek hibernation. Non-mated queens do not hibernate (Alford 1975). *B. terrestris* queens burrow 2-15cm into

soil in shaded sites at the base of trees, often covered with leaf litter (Sladen 1912; Alford 1975). Entry to hibernation is an endogenous queen caste characteristic, independent of temperature and light (Roseler 1985).

Queens usually have full honey stomachs (200mg) of concentrated honey before entering hibernation. The breakdown of fat during hibernation produces water which reduces desiccation. While temperature is unimportant in initiating hibernation, soil temperatures and sunshine govern emergence (Haas and Holm 1960; Holm 1965). From all accounts, early emergence is a feature of New Zealand *B. terrestris* queens. Occasionally in England, if cold weather is followed by a warm spell, some *B. terrestris* queens emerge in winter and even attempt to nest if flowers are available (Prys-Jones 1982). In New Zealand, *B. terrestris* queens are most common on the wing from July to October.

Emerging queens forage for nectar and search for nest sites as their ovaries develop. *B. terrestris*, as the name suggests, nests in the ground inhabiting dry subterranean cavities often in vacated rodent or rabbit burrows, among woodpiles, under houses, within compost heaps, or in bits of carpet or upholstery (Donovan and Macfarlane 1984). The queen does not forage for nest material, burrow or excavate a nest (Alford 1975), and nest cavity size often dictates maximum colony size. Nests may be up to 1m below the soil surface with tunnels over 2m in length (Cumber 1953a). Competition for limited numbers of nest sites during spring may result in foundress queens being superseded by invading queens after a fatal conflict. Sladen (1912) found up to 20 dead *B. terrestris* queens which had died as a result of conflict during usurpation of the original nest.

Four stages of nest development can be identified: an incipient stage; a growth stage; sexual production and maturity; and finally senescence or decline (Macfarlane and Donovan 1976).

The incipient stage involving nest initiation can occur at any time during a 3-4 month period in New Zealand. During this time the foundress queen secretes wax, makes a honey pot, forages for nectar and pollen and lays up to 16 eggs (Alford 1975) in a wax egg cup which she then incubates. Eggs hatch after 4-5 days (Cumber 1953b). The white 'C' shaped larvae, adapted to living in darkness, are hairless, legless and blind with a distinct head and biting/chewing mouthparts. Larvae are completely dependent on progressive feeding of regurgitated pollen and nectar from the queen. This is fed to larvae through a small hole which the queen makes with her mandibles in the enclosed wax 'cell' wall. On reaching the fourth (and final) instar, larvae spin a flimsy silken partition which separates them from others in the brood clump. Larvae develop most rapidly during the fourth instar and after about ten days in the larval stage a more substantial cocoon is spun with the meconium incorporated into the cocoon wall (Free

and Butler 1959). Larvae vary in size depending on the extent of feeding and position within the brood clump. This results in different sized adults.

The pupal stage lasts about 12 days (Cumber 1953b). The queen meanwhile removes wax from cocoons which she moulds into new egg cells on top of developing pupae. In field colonies in southern England the imago emerges 27-28 days after oviposition (Cumber 1953b). Development is temperature dependent with the egg to adult period being reduced to 21 days in laboratory conditions at a constant 30 C. The newly emerged silvery grey worker (known as a callow) feeds from nectar pots and colours up over it's first 1-2 days of life.

Colony growth occurs after the first workers emerge and the queen ceases foraging. A division of labour within workers exists, with larger workers usually foraging for food while smaller ones rear and incubate brood and defend the nest. Roseler (1967) found a seasonal increase in size of *B. terrestris* workers. The number of workers may double each week until nest maturity some 10-15 weeks after first egg laying (Macfarlane and Donovan 1976). Workers attending to the brood (house bees) may live for two months while foragers may live as little as 2-3 weeks (Alford 1978).

The foundress queen and workers attempt to maintain colony temperature at around 28-30 C, which is optimal for brood development. During cold weather the temperature may fall well below 30 C;this can stunt growth and may result in developmental defects in some species (Heinrich 1979a). Workers incubate by extending their abdomen over the brood. The major area of contact is the ventral abdominal surface which is devoid of hair. Bees shiver to generate heat by rapid contraction of indirect thoracic muscles. Heat is shunted from thorax to abdomen where it is conducted directly to the brood. Incubating bees can maintain brood at 25 C above ambient air temperature in the absence of nest insulation (Heinrich 1979a).

B. terrestris colonies construct a canopy of wax completely covering the brood. This stabilises temperature and regulates relative humidity at 60-70% (Alford 1975). Workers cool the nest by fanning with their wings or creating vents in the canopy (Free and Butler 1959; Alford 1975).

Sexual production and maturity is reached when the queen switches to laying non-fertilised eggs which develop into males. Fertilisation is controlled by a valve within the spermatheca. The switch to sexual production (males and queens) is not well understood and may be influenced by different factors in different species. Adequate food stores, worker:larva ratio, chemical cues, nest temperature stability and bee density may together or in isolation be important (Prys-Jones and Corbet 1987).

At a certain point, either before or after male production, new potential queens (gynes) are produced. Brian (1980) suggested that *B. terrestris* is a 'complex' species whereby the foundress queen, with the aid of pheromones, controls queen production by

preventing workers feeding the female larvae with sufficient frequency to enable them to develop into queens (distinctly larger than workers). Worker production can therefore occur at high worker:larval area ratios with ample food. Thus, 'complex' species can delay queen production, allowing adequate build-up of large worker populations and a long colony life cycle.

When the foundress switches to queen production she relaxes her pheromonal influence on worker-larval feeding, so that female larvae are fed more for longer and thus develop into queens. Pheromonal inhibition of worker-larval feeding is relaxed as the foundress queen ages (Roseler 1967, 1970). A weak foundress may broadcast her degree of aging, presumably by decreased pheromonal concentration, allowing new queens to be produced before she ceases to produce fertilised eggs (Pomeroy 1981b). The queen also produces a 'dominance' pheromone, which is detected by the antennal sensilla of workers through contact, and suppresses oogenesis by inhibiting the activity of the corpora allata via the nervous system, this inhibits egg laying by workers (Roseler 1970, 1975).

The production of sexuals usually occurs from late spring to early summer (October-December) in New Zealand. The sex ratio of new males to queens produced is strongly male biased (Owen, Rod and Plowright 1980; Plowright and Laverty 1984). While many colonies produce both sexes, other colonies may produce mainly one sex (Duchateau and Velthuis 1988). This may depend partly on queen vigour (health) but food availability, nest temperature and bee density may also be important (Prys-Jones and Corbet 1987).

Colony decline or senescence occurs 5-8 weeks after peak maturity (or sooner) due to death of old workers and evacuation of the nest by males and some queens (Macfarlane and Donovan 1976). Males usually leave the colony permanently after 2-3 days, collecting their own nectar and finding shelter at night (Free and Butler 1959). New queens take their mating flight about five days after emergence (Cumber 1953b). Young queens may return to the colony for 1-2 weeks during which time they feed from food stores and develop their fat bodies for hibernation (Alford 1978). New queens may also feed brood, produce wax, defend and forage for the colony, collecting nectar and pollen depending on colony demand (Free and Butler 1959). Some new queens contain developed eggs and may even lay in the parent nest if the foundress has died (Plath 1934).

Macfarlane and Donovan (1976) suggested that an 'average' nest in New Zealand produces about 900 adult bees during a season of which 200 are queens. As many as 430 workers may be present at any one time in a large nest. However, the founding and successful growth of colonies may be dependent upon a succession of available nectar and pollen sources.

1.4 Bee - flower ecology

The association of bumble bees with flowers mutually assures reproductive success of both (Kevan and Baker 1983). Bumble bees harvest nectar and pollen from flowers providing mainly carbohydrate and protein respectively. The dense layer of body hair covering the bumble bee plays a vital role in collection and transfer of pollen from the anther of one to the stigma of another flower of the same species, thus determining the relationship between flower and bee (Percival 1965).

This review considers four main areas of bumble bee - flower interactions:

1) Floral attractants: flower colour, scent and form
2) Floral rewards: pollen and anther dehiscence, nectar and nectar secretion
3) Foraging of bumble bees: learning behaviour, foraging strategy, pollen harvesting
4) Physical environment and bee adaptations: to light, wind etc.

1.4.1 Floral attractants

Colour

Bombus spp. have trichromatic colour vision and within the range of the insect visual spectrum (300-650nm), ultraviolet (UV), blue and yellow-green show peaks of sensitivity. The order of bee sensitivity is UV > blue > yellow, being negatively correlated with the daylight spectrum. Hence, where there is minimal daylight, the insect eye compensates by being most sensitive (Mazokhin-Porshnyakov 1962; Menzel and Erber 1978; Kevan and Baker 1983).

Flowers attractive to *Bombus* have corollas corresponding to colours to which the bees are most sensitive. Red flowers are generally unattractive to bees as they do not perceive red wavelengths, while white flowers, being more favoured by Diptera (Percival 1965) may be visited by *Bombus* often in failing light (Free and Butler 1959).

Series of spots or lines from the edge to the centre of flowers of contrasting colour, act as nectar guides (honey guides), directing the bee from the outer edge of the flower to the nectaries (Manning 1956a). Bees use these guides during initial visits, but as the location of the nectar source is learnt the guides become less important.

Nectar guides and nectar may reflect UV light (Thorp and Estes 1975). Reflective corolla patterns may change with age and following pollination, providing cues for visiting bees as to the age and presence of rewards.

Darwin (1876) noted that bumble bees visiting flowers of one species become accustomed to their colour, but will fly within a few centimetres of flowers of the same colour but of different species without alighting, so other cues may be important. When

visiting flowers of the same species but with different coloured corollas e.g. Pansy, bees use other cues such as scent to maintain flower constancy.

Scent

While colour attracts *Bombus* at a distance, scent acts to entice alighting of bees on flowers. Bee olfaction is similar to that of humans but is more sensitive to floral scents and pheromones. However, bumble bees can recognise some scents not detected by humans e.g. Vipers Bugloss, *Echium vulgare* (Free and Butler 1959; Corbet 1978).

Flower scents comprise volatile essential oils and are complex mixtures of compounds from many different chemical groups e.g. phenols, ketones, aldehydes (Percival 1965).

In diurnal blooming flowers, scents may not be as strong as in nocturnal flowers, where the roles of colour and scent are reversed; thus there is an association between flower colour and scent (Kevan and Baker 1983). Scent normally originates from the petals. However, other floral parts e.g. pollen and nectaries, may have an attractive odour. Scent guides on the petals have different peripheral scents compared to inner petal scent. This may be associated with nectar guides; the scent becoming more intense towards the centre of the flower (Percival 1965).

Bombus associate scent with food reward, and individual bees can be trained to accept one scent among an array of others. If the scent is removed the bee hesitates before alighting (Free and Butler 1959). Unvisited flowers have a stronger scent than visited flowers (Heinrich 1979a).

Flower form

Bumble bees particularly favour irregularly shaped zygomorphic flowers, compared to honey bees which prefer actinomorphic flowers. The larger the flower and the more broken the outline, the further away the bumble bee perceives the flower. Within limits, bumble bees recognise petal numbers, with more petals being preferred over less petals. Colour, shape and size are determined by sight at a distance (Free and Butler 1959). *Bombus* can recognise different shaped petals. Heinrich (1979a) explained, for *Clarkia* species which flower simultaneously in North America, how each species has different shaped petals, the greater the differences the less likely were the bumble bees to stray.

Flowers with deep corolla tubes are preferred over disc-shaped flowers. However, the degree of dark shading towards the centre of disc flowers affects attractiveness (Free and Butler 1959). *Bombus* species prefer flowers with a corolla tube the same or slightly shorter than the length of their proboscis (Brian 1957; Hobbs, Nummi and Virostek 1961; Teras 1976).

Bumble bee flowers often require forced entry e.g. lucerne, to encourage maximum contact with male and female flower parts and to allow entry of only intelligent pollinators that learn to manipulate the flower (Heinrich 1979a).

Darwin (1876) noted that bees can recognise the shape of the plant independent of whether it is flowering. This was also corroborated by Manning (1956b) when studying bumble bees foraging on Hound's-tongue, *Cynoglossum officinalis*.

1.4.2 Floral rewards

Pollen

Pollen provides the major source of nitrogenous food for bee larvae and is important for egg maturation of the queen. The amount of protein in nectar is small, (0.2%), therefore, without pollen, larvae would cease growing and the colony would decline (Howes 1948). Pollen constituents include protein, fat, carbohydrate and various minerals (Percival 1965). Pollen energy reserves may be in the form of starch or lipids, small pollen grains having lipids while large grains have starch stores. Many plant families, e.g. Compositae, exhibit phylogenetic constraint, i.e. pollen constituents are consistent throughout the family. Lipids include phytosterols which attract insects by scent and may provide hormone or pheromone producing capabilities (Kevan and Baker 1983).

Volatile lipids and amino acids may be important as phagostimulants (Hopkins, Javans and Boch 1969). Proline, an amino acid from pollen, is important in honey bee flight, nutrition and honey production (Kevan and Baker 1983). Pollen odour may be different or similar to the overall floral scent.

During the final stage of pollen wall development, lipoidal and other substances may accumulate on the exine surface. This material has been called pollenkitt by Knoll (1930) and imparts colour, odour, possible phagostimulants and varying degrees of stickiness due to the abundance of lipids present. This oily coat is water resistant.

Recognition of attractive pollen by bumble bees is either chemosensory or mechanical from setae or sensilla on appendages. Bumble bee workers assess pollen availability using age related morphological cues of the flower on *Anemonopsis macrophylla* (Pellmyr 1988). With a positive stimulant, grooming pollen into corbiculae is initiated. With a negative stimulant, the pollen is groomed off the body and discarded (Buchmann 1983). When pollen is fed to larvae the whole grain is ingested, the outer exine often remaining intact after passing through the gut. Nutrients are extracted, possibly by bursting osmotically, and the pollen grains are eliminated into the cocoon wall prior to pupation.

The amount of pollen produced per flower species and the longevity (viability) may vary considerably e.g. clovers - 12 days, apples - three months (Percival 1965). The colour, size and outer sculpturing are important features aiding in species identification (Hodges 1974).

Anther dehiscence

Anther dehiscence is the release (presentation) of pollen following breakdown of the anther wall either by a longitudinal split or the opening of a pore (poricidal dehiscence) (Goodwin 1987). The timing of anther dehiscence may influence the day to day variation in timing of pollen collection by foragers.

Pollen is released in two different ways: 1) from longitudinally dehiscent anthers such as in brassicas or 2) from poricidally dehiscent anthers. Although splitting longitudinally, borage anthers release pollen apically protecting the pollen until release, this species can therefore be considered as representative of group 2.

1) Longitudinal dehiscence: pollen from anthers is exposed after splitting occurs. In brassicas, this is simultaneous with the opening of the flower. The pollen functions as an attractant or arrestant being exposed and available for collection by generalist pollen feeders (polylectic) or specialists (mono- oligolectic), while the nectar remains concealed. Carotenoids in these flowers make the pollen yellow and the lipid pigments protect the pollen tube and generative nucleus from UV light (Buchmann 1983). The pollen often contains pollenkitt and is water resistant. The tacky pollen permits rapid and complete removal by honey bees without any moistening of regurgitated nectar. Pollen is released during a single foraging period (Percival 1965). Pollen is released at relative humidities up to 90-100% without any rain. Dehiscence normally increases with temperature and light levels (Percival 1965). With the pollen exposed to foragers, diurnal weather patterns influence pollen availability.

2) Poricidal dehiscence: anthers may be exposed but the pollen is normally concealed and available only to specialised bees having learnt to vibrate the anthers to release pollen. Pollen may be difficult to remove unless vibrated. The pollen grain is generally small (5-40μm diameter) with a dry surface, lacks pollenkitt and has a smooth exine with little sculpturing. Dry grains are necessary for expulsion from apical anther pores. Pollen is often white as the pollen remains hidden from UV radiation inside the anther locule and does not require carotenoid pigments for protection (Buchmann 1983). Anthesis in poricidally dehiscent flowers generally occurs at sunrise. Thus, pollen is available and the stigma receptive during early morning hours. Most flowers are pendulous (nodding) and flower over an extended period. Bees collecting from these flowers may be active

early in the morning (matinal) when anthesis occurs, then again later in afternoon toward dusk (crepuscular). Weather has less influence on poricidally dehiscent flowers, which release pollen even during light rain. Electrostatic forces between bee and pollen assist in pollen deposition onto the bee venter rather than being lost as a result of the pendulous nature of the flower (Erickson and Buchmann 1983).

Nectar

The nectary secretes nectar, which is a phloem sap derivative. Nectaries are normally located at the base of the ovaries and filaments. Nectar is a product of photosynthesis and therefore increases with light intensity (Free 1970a).

Nectar is a mixture of mainly sugars and, to a lesser extent, amino acids, proteins, lipids, antioxidants, alkaloids, vitamins and minerals (Kevan and Baker 1983). Percival (1961) classified nectars on the basis of the predominant sugars (sucrose, fructose, glucose). Three classes were considered: 1) sucrose dominant, 2) glucose and fructose dominant and 3) equal proportions of sucrose, glucose and fructose. Phylogenetic constraint exists whereby botanical families have comparable sugar ratios. Several more recently evolved families e.g. Umbelliferae, Brassicaceae and shallow unprotected flowers have two monosaccharides (glucose and fructose), whereas less evolved families e.g. Ranunculaceae and long-tubed flowers have nectar containing mainly sucrose. Sucrose is normally broken down to fructose and glucose by enzymatic reaction. However, nectar from more recent families is technically honey requiring no further enzymatic reaction. Bumble and honey bee flowers generally have nectars with sucrose predominating over fructose and glucose (Percival 1965).

Many of the minor constituents may act as gustatory stimulants or taste modifiers, while the concentration of amino acids in nectar is higher for flowers whose pollinators use nectar as their major protein source (Baker and Baker 1983).

Nectar secretion

The potential for nectar secretion is hereditary. Whether it is fulfilled depends on the plant's environment (climatic and edaphic (soil) factors). Nectar secretion depends on: the size of the flower; the size of the nectary; the age of the flower and plant; the amount of nectar removed and the sex of the flower, while differences in nectar secretion also occur between species, varieties, flower colours and degrees of polyploidy (Percival 1965).

Increased light intensity may stimulate or impede nectar secretion depending on the species. The effect of relative humidity on nectar depends on the flower corolla depth. In deep tubed flowers, the environmental effects on nectar secretion are dampened (Kevan and Baker 1983). Shallow flowers with unprotected nectar are affected by

diurnal changes in relative humidity, as well as rain and air movements. These factors may influence nectar concentration and hence the pollinating potential of the flower. Each plant species normally has upper and lower limits of temperature which limit secretion. Soil moisture does not normally limit nectar secretion in temperate regions except during drought. Plant nutrients may influence nectar by affecting the health of the plant.

Generally, flowers with concealed nectar e.g. Boraginaceae, have sugar concentrations between 16-55%. While honey bees may be at an energetic loss to collect nectar below 18%, bumble bees may forage at lower concentrations (Heinrich 1979a). The upper concentration is limited by viscosity and hence the ability of bees to withdraw the nectar (Kevan and Baker 1983).

1.4.3 Foraging of bumble bees

Learning behaviour

Bumble bees are eusocial and the colony survives throughout much of the flowering season. The life span of one worker may embrace the flowering period of a succession of species, hence the bee needs to be polytropic (wide pollen and nectar plant range) (Free 1970a).

Different plant species sharing a given habitat compete for pollinators and must maximise attractiveness. This has resulted in the evolution of floral attractants and rewards as well as development of sequential blooming times throughout the season, together with differences in the diurnal timing of anther dehiscence (Heinrich 1976; Barth 1985).

For a bee to maximise nett gain in food reward from an array of flower species, handling time per flower must be minimised. By remaining flower constant to a single species on any one foraging trip, bees minimise handling time and maximise food harvesting (Darwin 1876). However, this requires a degree of learning, firstly to identify the flower from a distance, secondly, to manipulate the flower, and thirdly, to extract the reward (Menzel and Erber 1978).

While the colours attractive to bees have been reviewed, bees learn and remember UV (400-420nm) most rapidly while blue-green (490-500nm) is learnt most slowly (Menzel and Erber 1978). The critical moment to remember colour is during the last phase of the approach flight i.e. the last three seconds, and will be reinforced if food is available (Barth 1985). Scent is more rapidly learnt than colour or shape with shapes and patterns learnt relatively slowly. Naive bees learn the location of nectar by trial and error and initial responses are often innate (Plowright and Laverty 1984), while exploitation of complex flowers must be learnt (Laverty 1980). Each bee must individually learn which

are the most rewarding flowers because bumble bees do not communicate the whereabouts of food rewards (Free and Butler 1959). Each forager develops a 'search image' i.e. an integration of the attributes of the rewarding flowers (Eickwort and Ginsberg 1980). Bumble bees begin their foraging career by sampling a number of different species and subsequently specialise on the most rewarding (Plowright and Laverty 1984).

Short and long term memory has been recorded in honey bees (Menzel and Erber 1978); long term memory being the result of favourable reward conditioning. A similar system seems likely in bumble bees as suggested by movement patterns between inflorescences (Pyke 1978b). While learning a rewarding food source has an adaptive significance, the ability to switch to an alternative food source may be equally important.

Foraging strategy

Bumble bees select the most concentrated nectar from flowers in the field (Free and Butler 1959; Percival 1965; Heinrich 1979a). *B. terrestris* has the following sugar preference: sucrose > fructose > glucose with a combination of the three sugars proving most attractive over other combinations (Pouvreau 1974). The energy is used for rearing larvae, feeding the queen, incubating the nest and foraging.

Bumble bees have a lower degree of flower constancy (Plowright and Laverty 1984) than the honey bee e.g. 95-98% of honey bees visit one species on a single foraging trip (Grant 1950; Free 1963). This depends partly on the floral diversity within the foraging area. Honey bees exhibit temporary fixation, ceasing to forage when the flower species is not presenting food rewards. By contrast, bumble bees are less constant with 55-56% of pollen loads of a single flower species and 32% of two species (Hasselrot 1960; Brian 1952; Free 1970a). Plowright and Laverty (1984) suggest that honey bees' higher flower constancy results from their ability to communicate. This enables them to pool information from scout bees and then to forage on the most rewarding crop, whereas bumble bees, lacking communication, have to individually conduct their own sampling to 'test' flower rewards.

In a field of mixed flowers, individual bumble bees specialise by 'majoring' on a single flowering species while occasionally sampling flowers with 'minor' rewards (Heinrich 1979b). This strategy enables individual foragers to monitor food rewards on less favourable flowers and, in cases where nectar levels shift among these flower species, foragers can switch their foraging onto flowers which are becoming more favourable as their major food source declines (Heinrich 1976, 1979b; Oster and Heinrich 1976). Flower constancy allows specialisation without dependence on a single flower species (Eickwort and Ginsberg 1980). The longer the forager remains on the 'major' food source, the less the 'minor' food crops are sampled (Oster and Heinrich

1976), hence resource availability also influences flower constancy (Free and Butler 1959).

Bumble bees exhibit optimal foraging i.e. they forage in ways that maximise their rate of nett energy intake (Pyke, Pulliam and Charnov 1977; Pyke 1978a, 1978b, 1979, 1980). Bumble bees have a high energy demand, in part because of their ability to thermo-regulate (Heinrich 1979a). Certain strategies are employed to maximise energy intake. For example, bees avoid visiting flowers which have been previously visited either by flying in the same direction when moving between flowers, or by scent marking with short-lived repellent pheromones (Eickwort and Ginsberg 1980). Also, post-pollination changes on flowers are recognised by foragers and assist in flower avoidance (Heinrich 1979a). Bumble bees probe more flowers on an inflorescence when the rewards are great and the distance between flowers is low (Waddington 1981). In rich flower patches, bees turn more and with sharper angles (leptokurtic) than they do on poorer patches. This activity keeps bees on the patch for a greater number of flower visits (Kevan and Baker 1983). Bumble bees forage on smaller patches of crops than honey bees (Free 1970a) and fly from patch to patch less as the distance increases (Hartling and Plowright 1979).

When flower density and food reward are high, bees may not remove all the accumulated nectar before moving to another flower. As flower density and food reward decline, bumble bees remove small nectar rewards as they become available (Witham 1977). Where flowers are packed together in inflorescences, bumble bees walk between flowers to conserve energy, rather than fly. On foxgloves, *Digitalis purpurea*, bumble bees work up the inflorescence, as flowers lower down have more nectar. However, nectar concentration may increase up the inflorescence, thereby controlling gustatory saturation (Hocking 1968; Heinrich 1979a).

Bumble bees establish flight paths, using landmarks to aid in site fidelity. They may return to the same rewarding patches of flowers on consecutive visits and days (Manning 1956b). This helps to maximise foraging returns. Bumble bees can even learn the position of individual plants, visiting them in sequence. However, site specificity declines as food resources become more dispersed (Manning 1956b; Heinrich 1975).

Optimal foraging does not always apply in the field as bumble bees are central place foragers (Prys-Jones and Corbet 1987) that transport food back to a fixed location. Prys-Jones (1982) found that the most rewarding plants were not always the optimal choices when transport cost was considered. Individuals of a colony show polyethism (behavioural foraging differences) (Plowright and Laverty 1984) due to size differences. Larger workers with longer tongues may exploit flowers with longer corollas, forage for

longer and return with larger stores of pollen and nectar, but smaller workers can exploit shallow corolla flowers closer to the nest (Waddington 1981).

Interspecific resource partitioning among bumble bees is on the basis of tongue length (Hobbs 1962a) and sugar requirements as evidenced by body size (Kevan and Baker 1983). This influences foraging efficiency and nectar ingestion rate (Harder 1983).

Pollen harvesting

The ratio of pollen to nectar gatherers depends on the species, the length of colony life cycle and colony demand (Free and Butler 1959; Prys-Jones and Corbet 1987). Bumble bees may collect pollen or nectar or both, however because energy is required for pollen collection, pollen and nectar gathering often occur simultaneously. The range of plants visited for pollen may be quite different from those visited for nectar (Liu, Macfarlane and Pengelly 1975). Bumble bees may be polytropic (Free 1970a) with regard to nectar collection but may be oligolectic (collect pollen from a few closely related plants) with regard to pollen gathering (Percival 1965; Eickwort and Ginsberg 1980).

Pollen collection in bees is dependent upon colony demand, the attractiveness of and ability to locate pollen sources, seasonal and diurnal synchronisation of activity with anthesis, morphological adaptation to plants and the degree of intra- and interspecific competition (Eickwort and Ginsberg 1980). The main collection methods of pollen by bees depend on both the flower and the pollinator. For bees generally, collection methods fall into three classes; 1) milking - drawing mouthparts from base of anther to apex, 2) biting - puncturing anther with proboscis and 3) gleaning - collecting residual pollen. Milking and gleaning occur in *Bombus* (Thorp and Estes 1975). The major pollen collection methods of *B. terrestris* appear to be: 1) deliberate scrambling over anthers or catkins (Prys-Jones and Corbet 1987), 2) incidental dusting while collecting nectar (Free 1970a), and 3) vibrational pollen harvesting (buzz pollination) (Michener 1962; Buchmann and Hurley 1978).

Vibrational harvesting is an adaptation for efficient removal of pollen by bumble bees from poricidally dehiscent anthers. It is not an attribute of honey bees (Buchmann 1983). Bumble bees alight on the corolla, curl around the anthers and grasp the stamens with wings held stationary. Rapid contractions of large indirect flight muscles transmit strong vibrations through the thoracic skeleton and legs. Body parts contacting the anthers directly (mandibles, legs, thorax) transmit this high frequency oscillation to the flower and anthers. Vibration of the anther locule causes rapid expulsion of pollen through the anther apex within a fraction of a second (Buchmann and Hurley 1978). The procedure results in an audible buzzing noise. Pollen is attracted to the bee venter by electrostatic forces. These forces are slowly discharged during pollen gathering (Erickson and Buchmann 1983).

Body hairs covering the bee are important in pollen collection. They are often branched or feathery (Alford 1975) with a large number of hooks and teeth on each hair (Barth 1985) to which pollen grains adhere often aided by the presence of pollenkitt. Bumble bees brush the pollen from the body with the midlegs and metatarsal brushes of the hind legs and pack it onto the corbiculae (see Sladen 1912).

Early in the season, pollen reserves in *Bombus* colonies become exhausted overnight (Plowright and Pendrel 1977). Pollen gathering rate may be depressed by intraspecific competition. During pollen shortages, bumble bees extend their range of foraging species, often visiting unusual plants e.g. *Chenopodium* sp. (Plowright, Pendrel and McLaren 1978).

1.4.4 Physical environment and bee adaptations

Weather influences food availability and floral rewards and this in turn affects food harvesting by bees. Weather may also directly influence bumble bee foraging. While honey bee foraging is limited below 15 C (Heinrich 1979a) and ceases below 10 C (Burrill and Dietz 1981), bumble bee queens may forage at 2 C in strong wind and rain due to their ability to thermo-regulate (Heinrich 1972, 1975, 1979a). The dense pile covering bumble bees, together with a counter-current heat exchange between thorax and abdomen, maintain thoracic temperatures of 35 C by shivering, thus allowing flight at low temperatures. Muscles also generate heat without shivering by a biochemical cycle called substrate cycling (Prys-Jones and Corbet 1987). Bumble bees may also regulate their thoracic temperature by flying at different heights to remain in air within a certain temperature range (Heinrich 1979a) or by basking (Prys-Jones and Corbet 1987). Worker bumble bees fly mainly between 10-30 C (Barth 1985) although maximum activity is between 15-25 C. Above 35 C, bumble bees cannot dissipate heat through the ventral abdomen rapidly enough to prevent overheating, and cease foraging.

Light and cloudiness may influence foraging. At low light intensity, bumble bee foraging declines while in Arctic regions, where it is light in summer for 24 hours and the season is short, bumble bees continue foraging. Initiation of foraging in the morning is related to a threshold of light intensity. This does not affect the completion of foraging in the evening where foragers may remain on crops overnight if light levels drop suddenly (Alford 1975).

Rain has less effect on foraging at the start of the season because the urgency to collect food is much greater (Free and Butler 1959). Rain hampers foraging and reduces anther dehiscence and nectar concentration. Bees may shelter in flowers or at the base of plants during light rain, while Arctic bumble bees continue to forage (Kevan and Baker 1983).

Wind may shorten the life of bumble bees (Brian 1952). However, they are stronger fliers than honey bees, the latter ceasing to forage in winds above 24kph (Kevan and Baker 1983). Wind strongly influences foraging direction in bumble bees through the aerodynamics of upwind flight, the visibility of pendulous inflorescences and the downwind movement of odour plumes. This results in upwind foraging and prevents revisiting with pollen carry over determining gene flow (Woodell 1978).

CHAPTER 2

DEVELOPMENT AND FOOD CONSUMPTION OF COLONIES CONFINED INDOORS

2.0 Introduction

B.terrestris can develop large colonies in temperate regions (Donovan and Macfarlane 1984; Prys-Jones and Corbet 1987) and is relatively common in New Zealand, making it among the most suitable bumble bee species for pollination research. It is important to know more of colony food requirements so that adequate supplies of forage crops can be provided.

Previous work considered larval development (e.g. Plowright and Jay 1977; Plowright and Pendrel 1977; Pendrel and Plowright 1981), but little emphasis has been given to food consumption. In contrast intraspecific colony interactions, particularly caste determination and reproductive dominance have been given considerable attention (Pomeroy 1981b; Pomeroy and Plowright 1982; Wilde and Beetsma 1982; Plowright and Laverty 1984; van der Blom 1986; Tod 1986). Food consumption of bumble bee colonies was considered indirectly by Pomeroy (1977) when studying larval ejection in *B. ruderatus*. He found a relation between pupal cocoon diameter and estimated larval pollen intake, represented by pollen grain coats in the meconium. From the pupal cocoon diameter a Productivity Index (P.I.) was developed where an assessment of foraging effort required to rear a cohort of bees could be established from cocoon counts of dead colonies. For *B. ruderatus,* using the cocoon diameter formula, queens were given a weighting factor of 3.3 times the pollen investment of workers and males. This was later modified by Tod (1986) to 3.5 for *B.terrestris* queens, taking into account the larger cocoon diameter for queens of this species.

Pouvreau (1974) investigated sugar solution consumption of *Bombus* spp. with different sugars. The uptake of sugar solution depended upon temperature, fasting, sugar composition and concentration. Sugar solution uptake peaked at 40% concentration and was high between 30-50%. The most preferred sugar was sucrose.

Heinrich (1979a) suggested a pollen to bee conversion ratio of one gram of pollen producing one gram of adult bee biomass. He recognised the additional consumption by sexuals (males and/or queens) after emergence, but made no measure of this.

A number of questions deserved attention. For a given size do different colonies consume similar amounts of pollen and nectar? Do colonies with a higher consumption produce more sexuals? Do all colonies grow at the same rate? What stage

in colony development has the greatest food requirement and for how long does this extend? Does the maximum food requirement coincide with the greatest number of foragers? What is the most suitable time in the colony cycle for transfer into orchards to improve pollination? Can brood bionomic parameters e.g. larval area, be used to predict consumption?

The aim of the trial reported in this chapter was to determine the pollen and sugar (solution) consumption during the stages of colony development from pre-oviposition to completion of sexual production under laboratory conditions and to examine how the pattern of colony development influences consumption, final colony size, and sexual production.

2.1 Methods

2.1.1 Colony rearing

B. terrestris colonies were kept in the laboratory to minimise external variables which cause differences in field colony development and consumption e.g. temperature. Indoor rearing enabled food consumption, brood bionomic parameters and timing of sexual production to be easily recorded.

Thirty-three queens were captured off tree lucerne, flowering on Keeble farm 3km south of Massey University on 26 August 1986. The queens were introduced into flight cages (0.5 x 0.5 x 1.2m high) for one hour before each was placed into rearing ('starter') boxes, (N.Z. patent number 216-115, fig.2.1). An absorbent wick in a small jar allowed each queen to feed on a sugar solution. The solution was 50:50 v/v sugar/water, giving a 52-55% sugar concentration measured on a hand held Atago refractometer.

After worker emergence, the eight most advanced (non-male producing) colonies were shifted, during weeks 5-7, to the base of large conical observation hives (Pomeroy and Plowright 1980) for detailed monitoring (fig. 2.2). A layer of absorbent paper and a layer of wire mesh were put under the brood. The rearing box was supported on sand. The wire stopped any brood adhering to the base of the hive and absorbent paper prevented dampness and mould from accumulated faeces.

Each hive had a thermistor probe connected to its own thermostat and pilot-light, built into a central control panel. Each probe was set to switch the heating cable off at 30 C.

Mercury thermometers were inserted into each hive. All eight hives maintained constant temperature throughout the trial (30.5±1.2 C). The laboratory was heated with a portable fan heater (18±6 C).

Figure 2.1. Rearing boxes used for nest initiation of *B. terrestris*: The bottom row of boxes was used for food consumption trials of 1986. The top row of boxes was for general laboratory rearing. Pollen was supplied in numbered vials, suspended with a matchstick, from an acetate cover in the defecating chamber. Sugar solution was provided via sugar pottles and absorbent wicks beneath the defecating chamber. The brood chamber was heated to 30 C from below by a metal plate.

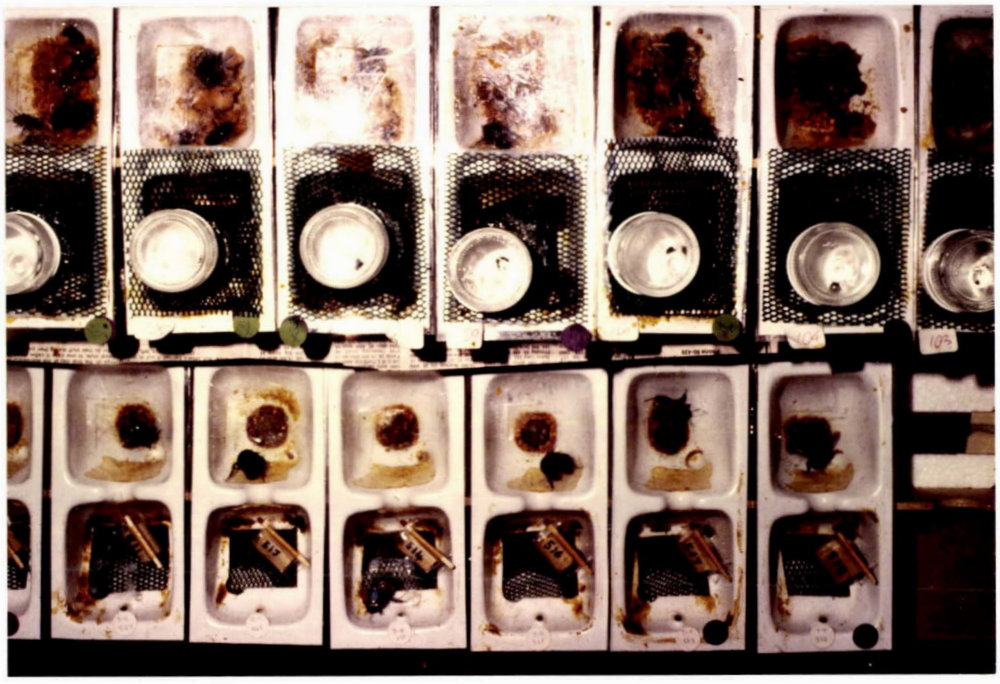
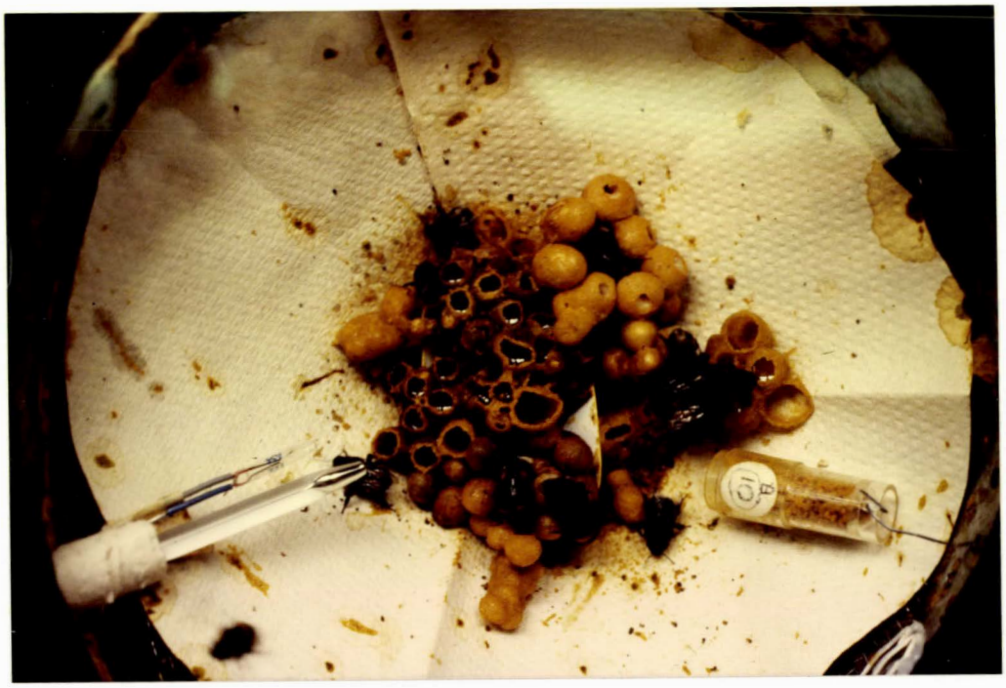


Figure 2.2. Conical observation hives used for colony food consumption trial in1986: Hives were maintained at 30.5±1.2 C by a thermostat (probe and thermostat bottom left). Pollen was supplied in plastic vials (bottom right) 3 times/week. Sugar solution was provided from pottles in flight cages. The foundress queen is (middle right) feeding from peripheral nectar pots. The brood contains fourth instar larvae (top right), pupae and young larvae (bottom right), workers are also present.



Each hive had a 15mm diameter exit hole connected to a 30mm diameter tunnel of plastic mesh (32% shade cloth), sufficiently wide to allow incoming and outgoing foragers to pass one another. Exit holes were covered by 6mm wide queen excluders (diamond shaped aluminium mesh glued in position) to confine queens to the hive. Each tunnel enabled workers to travel 0.5-2m to a flight cage.

Larval brood area was recorded weekly. A divider was inserted through a slot in a plastic lid and temporarily replacing the glass lid. Dividers were lowered onto the brood to measure the dimensions. This method avoided any parallax error that would have arisen had measurements been made from the height of the glass lid, but it was not entirely satisfactory as some smaller workers escaped through the narrow slit.

Artificial reduction of worker numbers was initiated three weeks after each colony was introduced into larger observation hives to simulate natural worker attrition of field foragers. Workers were culled weekly, with the first cull randomly removing 50% of those present. Each week thereafter from the total estimated number of newly emerged workers, 50% were removed at random. This method was used rather than the alternative of removing a fixed number of workers each week to ensure there was no bias against colonies growing at a slower rate. Removal rate was thus proportional to colony growth. As it was discovered that the second and subsequent removals involved approximately a 10% counting shortfall (due to workers hidden beneath the brood), the subsequent counts were increased by 10%.

Culling workers avoided overcrowding the colony and encouraged each worker to perform both hive and foraging duties. This reduced the risk of queen debilitation arising from inactive workers interacting with the queen, resulting in premature sexual production (Tod 1986). As males do not normally return to their parent colony, those found in the flight cages were removed. This avoided inflated sugar consumption from non-returning males.

Brood development and sexual production were recorded until the trial terminated at completion of the colony cycle i.e. when no further sexuals emerged.

Productivity indices were calculated for each colony in two ways:- first by counting and sexing total numbers of dead and live bees during and at the conclusion of the trial, including the number of unhatched pupae; second by counting the number of silken cocoons remaining on terminating the trial. The latter method, used in field trials, can be less accurate if white shouldered house moth, *Endrosis sarcitrella* (L.) decimate colony remains, as occurred to a small degree in this trial. Queen cocoons can be differentiated by size from worker and male cocoons, but male and worker cocoons cannot be differentiated.

Two colonies were destroyed when trials were concluded and for these colonies the first method (bees emerging) of calculating P.I. was used. Both methods were

comparable so P.I. values were calculated from numbers of live bees emerging for this experiment.

The productivity index is calculated by:

P.I.=total males and workers emerging + (F x total queens emerging)

OR

P.I.=total male and worker cocoons + (F x total queen cocoons)

F = queen weighting factor (3.5) representing the greater pollen investment required for rearing queens compared to workers and males (Pomeroy 1977; Tod 1986).

2.1.2 Measurement of sugar solution consumption

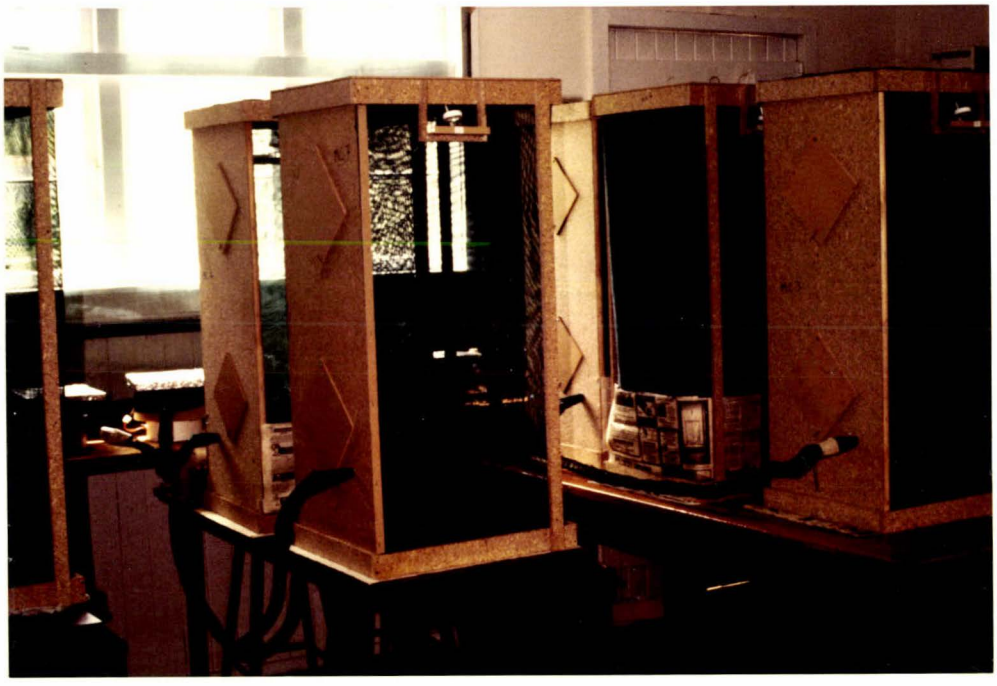
Each jar and wick from rearing boxes was numbered and weighed initially to the nearest 0.01g. Every seven days the jars, wicks and sugar solution were re-weighed to determine consumption and replaced with a clean set. Six control jars were introduced into empty rearing boxes to determine the quantity lost by evaporation. Results are presented in grams of sugar solution.

In flight cages, workers imbibed sugar solution from absorbent wicks in jars situated on a shelf 120mm below the cage roof (fig. 2.3). With wicks pressed against the outside 'Netlon' cage mesh, workers could feed while remaining within the cage. This allowed sugar jars and wicks to be conveniently weighed and replaced without the bees escaping. As there was always syrup visible in the honey-pots in the hives, it can be assumed that the 1-3 syrup wicks were sufficient for colony needs.

2.1.3 Measurement of pollen consumption

Fresh frozen pollen was introduced into the outer chamber of each rearing box in plastic vials (20 x 12mm diameter) every 2-3 days. Pollen pellets were pressed into each numbered vial with a wooden rod. Each vial was attached by masking tape to a matchstick and suspended through a slit in the acetate cover with the opening facing towards and about 12mm away from the brood chamber entrance. Trays beneath the mesh floor of the outer chamber collected uneaten pollen spillage from the vials. Vials were weighed prior to introduction, and on removal any spilled pollen was included in the final weight. All vials were oven dried at 60 C for 21 hours minimum then removed to a desiccator containing silica gel to prevent moisture weight gain during cooling. Finally each pollen vial was weighed on an electronic balance to 0.001g to determine dry weight of pollen remaining.

Figure 2.3. Flight cages connected to observation hives: Workers were encouraged to 'forage' for sugar solution placed outside the cage on a shelf 120mm below the cage roof. Workers lapped sugar solution through the 'Netlon' cage mesh from an absorbent wick.



As bumble bees would not accept dried pollen, initial fresh weight was converted to dry weight values and dry weight consumption for each 2-3 day period calculated. Conversions of fresh weight to dry weight pollen were calculated from mean percentage water loss of oven-dried control vials. These controls were replaced every time new pollen vials were introduced.

To determine time for complete water loss from oven dried pollen and possible differences between crushed and uncrushed pollen, fresh frozen pollen was crushed into three vials while uncrushed samples were placed on three, 20mm diameter inverted plastics lids. The six samples were oven dried at 60 C, removed at regular intervals over 48 hrs and weighed. Results indicated no further water loss after 21 hrs and no significant difference between crushed and uncrushed pollen.

For colonies in hives, fresh frozen pollen was crushed into 42 x 12mm diameter plastic vials connected to 150mm of 'S' shaped wire. Up to six numbered, pre-weighed vials were positioned adjacent to the brood three times/week. Upon removal, any uneaten pollen was oven-dried, and re-weighed.

2.1.4 Food consumption by sexuals

Ten male and ten queen pupae were separated from the brood of an indoor reared nest and placed in separate rearing boxes at approximately 30 C. After queens and males hatched they were supplied with fresh pollen every two days in 20 x 12mm diameter plastic vials placed into the brood chamber. Sugar solution was supplied, as with previous trials, from an absorbent wick in a glass jar. Post-emergence sugar and pollen consumption were recorded for queens and males during the first six days of adult life. Pigmentation developed within 24 hrs of emergence.

Another trial examined sugar consumption of males and queens while placed in separate flight cages. Twenty-five one-week-old males and 20, one-week-old queens were placed separately into two flight cages. Both the queens and males were fed sugar solution from jars with wicks placed on a shelf outside the cage as in previous trials. Fresh frozen pollen crushed into plastic vials was placed into empty starter boxes inside the base of each cage. Pollen was replaced every two days and sugar solution once a week. Pollen and sugar consumption/bee/day were calculated.

A third trial examined sugar consumption of both queens and males during mating. Twenty-five one-week-old queens and 25 one-week-old males were introduced into a flight cage. Bees were fed sugar and pollen as above. Mating began almost immediately. A plastic container 150 x 150 x 100mm deep was filled with approximately 450g of sphagnum peat moss, to which 350ml of water was added initially with a further 100ml added every 2-3 days to maintain moisture. Peat moss was removed and checked

at the termination of the two week trial for presence of a hibernaculum. Room temperature (20 C) was maintained as for previous trials. From total consumption of pollen and sugar, mean consumption/bee/day was calculated.

2.2 Results

2.2.1 Colony development

Of 33 confined queens, 17 (52%) oviposited in the rearing box. Of the remaining 16, five (15%) died, and the rest (33%) were removed after one month's confinement. Mean (±S.E.) time from confinement to oviposition for 17 queens was 10.6(±1.8) days, but 41% oviposited within seven days and 70% within two weeks. The last queen laid after 24 days. Later starting queens appeared to have lower fecundity and rarely produced colonies with workers only. Queens laying within two weeks of confinement consistently produced workers in the first brood.

Considerable variation in final colony size, measured by productivity indices, occurred with the eight indoor reared colonies for which detailed records were kept. Chronology of colony events are illustrated in figures 2.4a,b and 2.5a,b (and appendix I figures A2.1a,b-A2.6a,b).

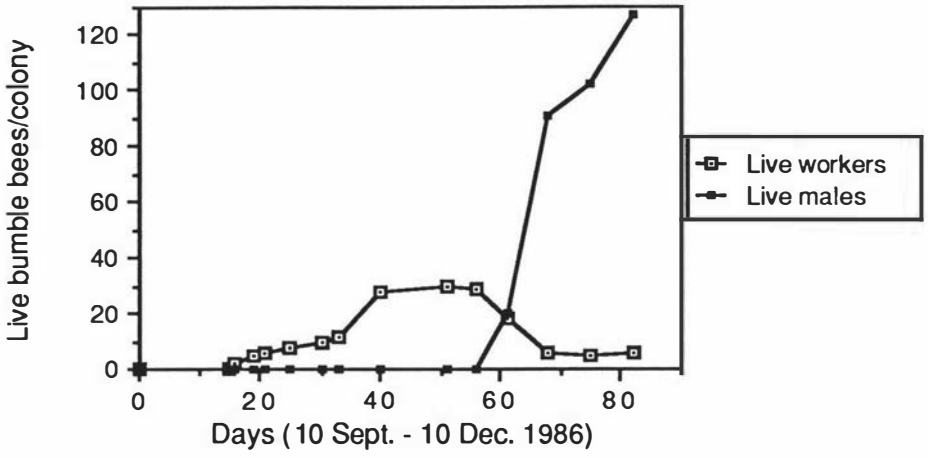
Developmental parameters (table 2.1a) were examined to determine factors affecting P.I. The P.I. was correlated with maximum live workers (fig. 2.6) and maximum larval area (fig. 2.7). P.I. was not correlated with the timing of first male emergence or first sexual emergence (males or queens), (table 2.2a).

Colonies with greater consumption produced more offspring (see later). However, it was also important to determine whether these high food consuming colonies invested a greater percentage of their total food into sexuals. Proportional investment ratios were calculated from P.I. and total sexual investment (males + (3.5 x queens)). As final colony size was not correlated to proportional investment, larger colonies did not invest proportionally more in reproduction (table 2.2c and 2.2d). All investment ratios were between 0.4-0.67.

To determine whether larger colonies grew faster, the number of new workers emerging every ten days for the first 40 days after first worker emergence was averaged for each colony. The four largest colonies with P.I. from 349-465 had an average of 13-19 workers emerging every ten days (table 2.2c) while the four smallest colonies had 5.5-9.5 workers emerging. Final colony size was correlated to growth rate during the colony growth period (table 2.2d). Larger colonies had more workers emerging per unit time.

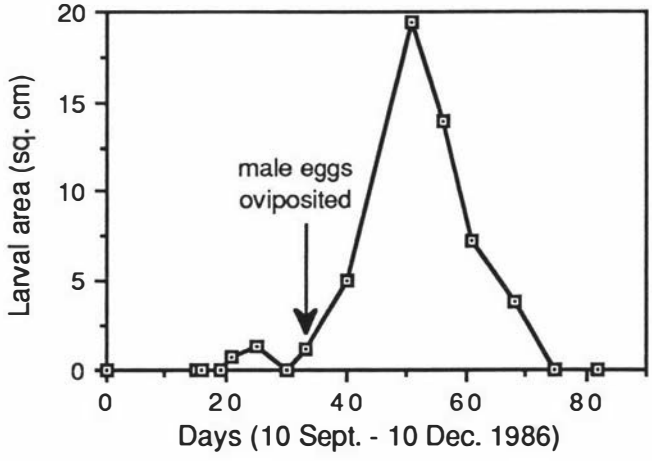
Figure 2.4. **Bumble bees for indoor hive 2**

(a)



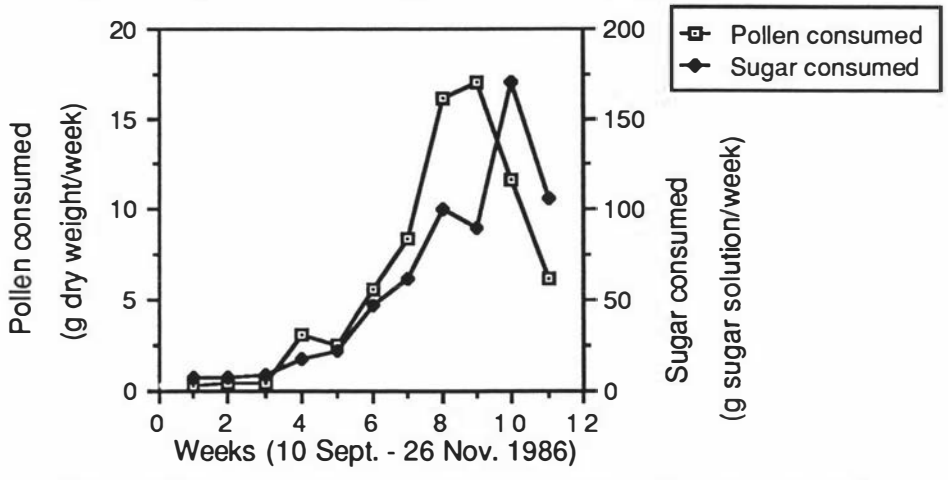
Larval area for indoor hive 2

(b)



Weekly pollen and sugar consumption for hive 2

(c)



Cumulative pollen and sugar consumption for hive 2

(d)

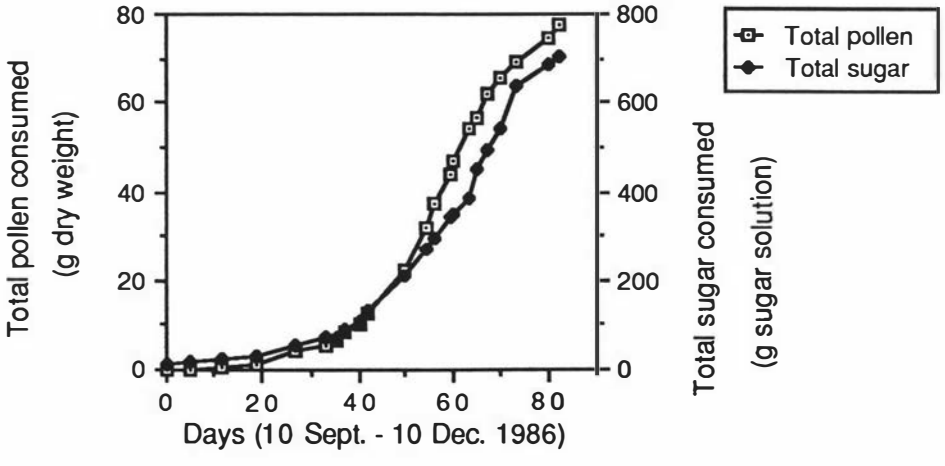
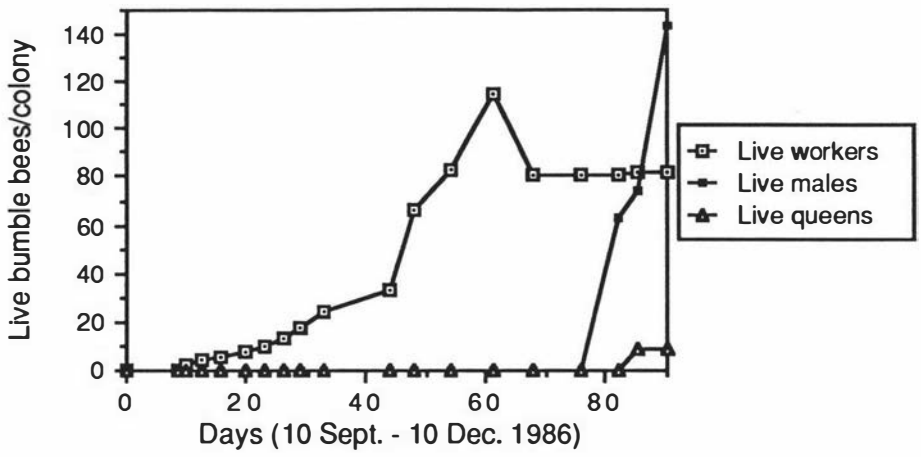
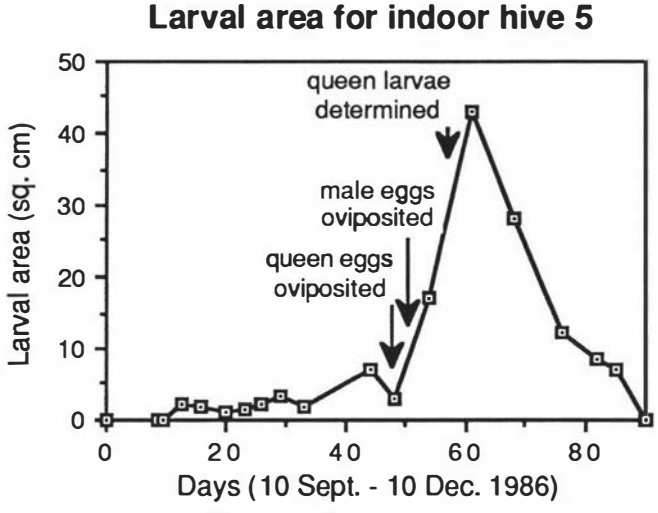


Figure 2.5.

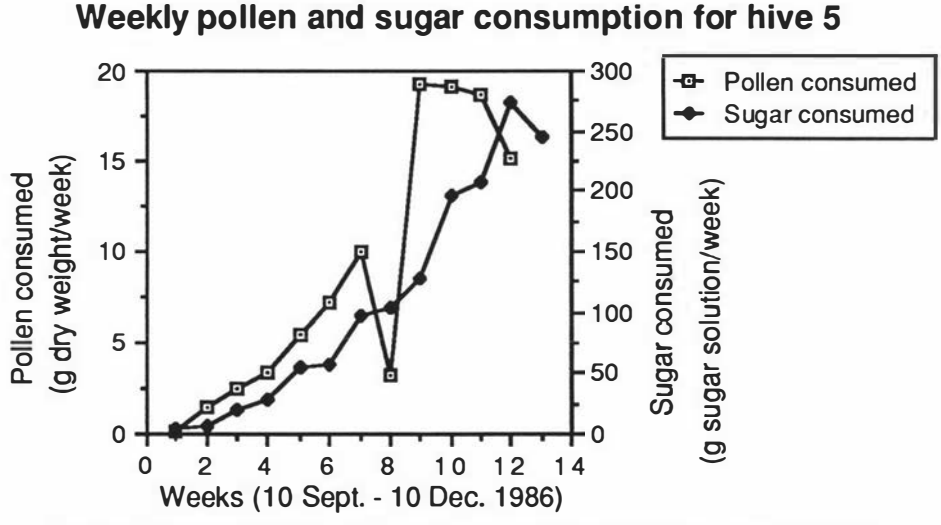
(a)



(b)



(c)



(d)

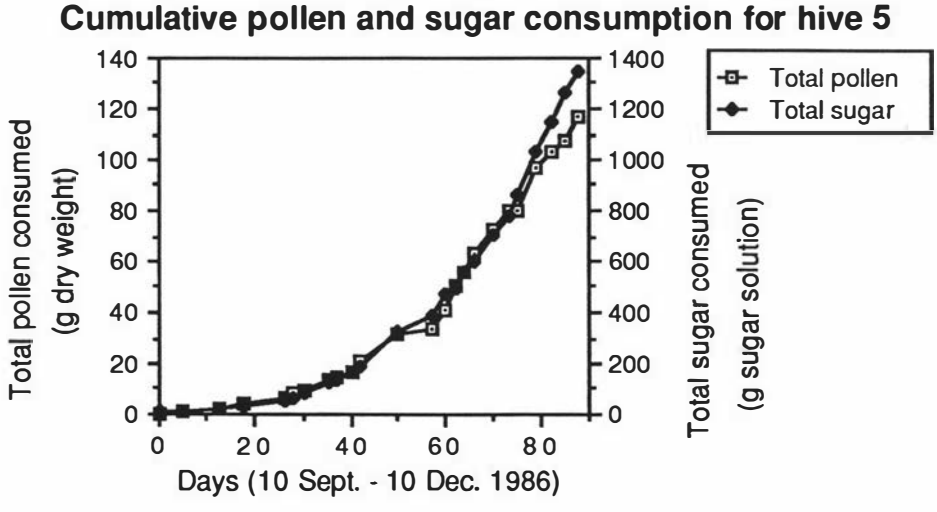


Figure 2.6.

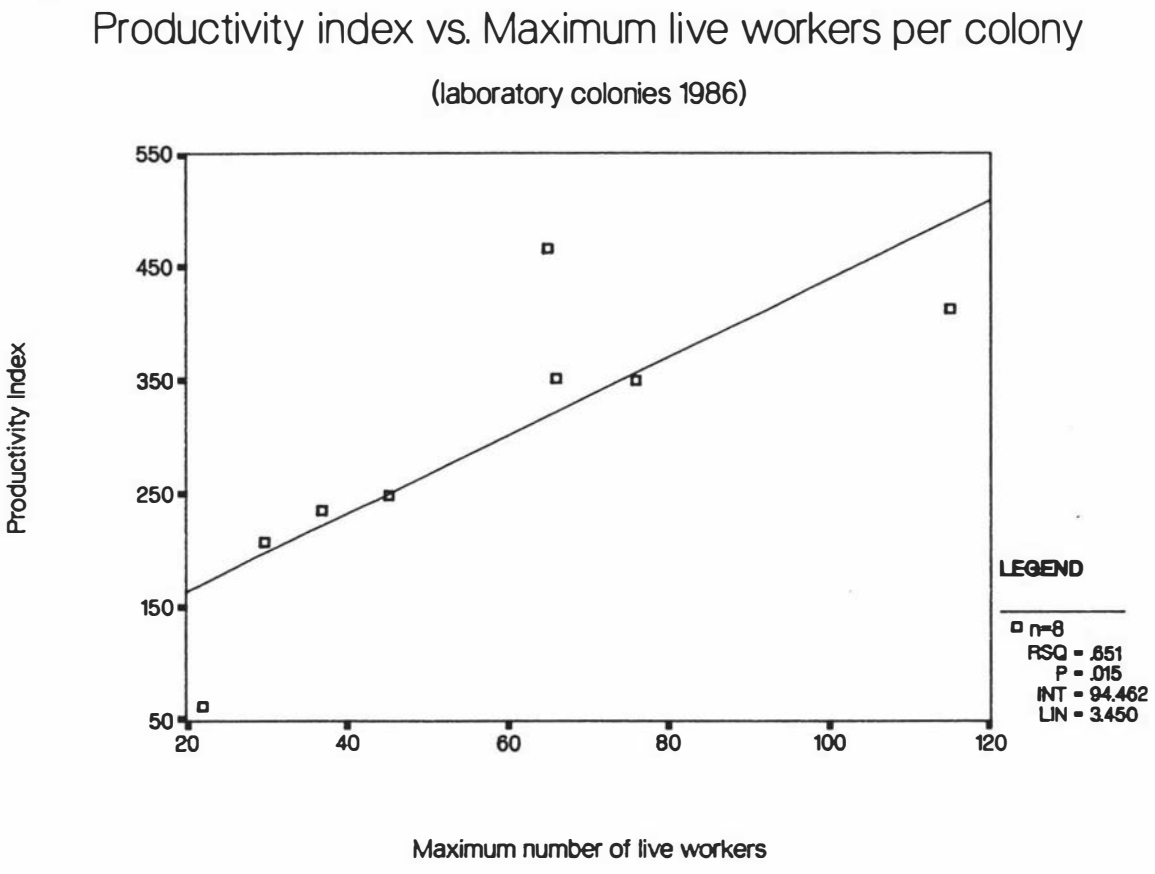


Figure 2.7. Productivity index vs. Maximum larval area

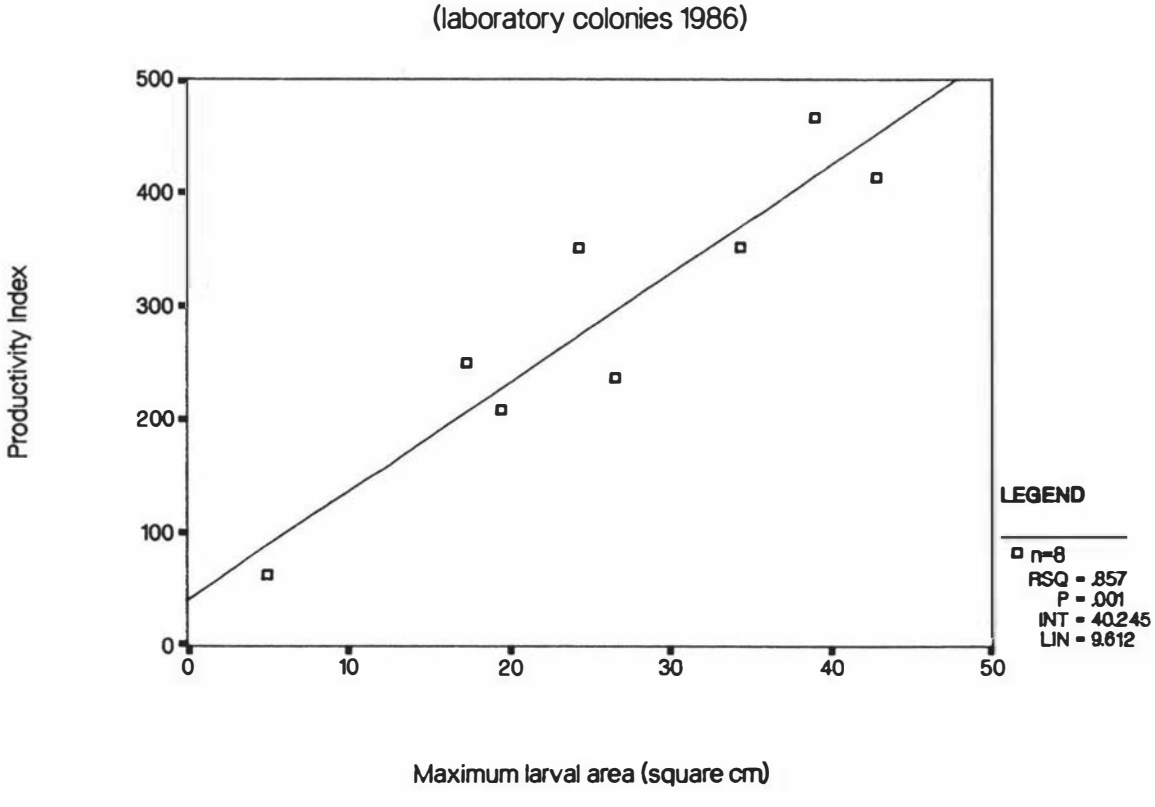


Table 2.1a. Developmental parameters for 8 *B. terrestris* colonies reared in indoor observation hives (August - December 1986).

Developmental parameters	Colonies: Non-queen producing 7	2	1	8	Queen producing 6	3	4	5
Total workers emerged	37	71	105	128	70	148	139	200
Total males emerged	25	127	124	313	48	5	122	143
Total queens emerged	0	0	0	0	28	44	16	9
Biomass, sexuals emerged	25	127	124	313	76	49	138	152
(males + (3.5 x queens))	-	-	-	-	146	159	178	175
Productivity Index (P.I.) bee counts	62	207	248	465	235	349	351	412
P.I. cocoon counts	-	218	217	441	-	330	343	372
Maximum live workers/colony	22	30	45	65	37	76	66	115
Maximum larval area (cm^2)	5.1	19.4	17.3	39.0	26.6	24.3	34.3	42.8
Max.ratio larval area: workers, prior to max. larval area.	1:20	1:6	1:4	1:10	1:10	1:3	1:4	1:22
Time (days) workers	22	21	19	21	23	20	18	22
from queen males	64	61	57	73	84	83	75	89
oviposition to queens	-	-	-	-	73	67	77	94
emergence of: last queen	-	-	-	-	89	81	84	98

Table 2.1b. Consumption parameters for 8 *B. terrestris* colonies.

Consumption parameters	Colonies: Non-queen producing 7	2	1	8	Queen producing 6	3	4	5
Max. P.D.W.C (g/week)	8.0	17.0	16.3	38.5	13.8	26.6	22.0	19.3
Max. S.S.C. (g/week)	57.9	170.7	200.4	289.2	111.3	196.1	200.0	274.0
P.D.W.C./cm^2/day at max.larval area (g/day)	0.13	0.08	0.12	0.10	0.05	0.14	0.21	0.06
(days to occur after first oviposition)	45	45	52	56	53	61	45	64
Total P.D.W.C. up to max. larval area (g)	10.9	24.6	50.7	51.6	19.9	59.7	50.7	45.9
Total S.S.C. up to max. larval area (g)	96.3	231.8	422.8	368.3	209.0	377.0	407.2	498.0
Total P.D.W.C. at termination (g)	29.8	77.4	77.7	188.1	66.2	98.3	106.7	117.3
Total S.S.C. at termination (g)	288.5	703.8	918.5	1660.7	712.0	1088.0	1164.3	1429.9
Half full honey pots at termination	33	51	90	62	40	50	60	15

P.D.W.C.= Pollen dry weight consumption S.S.C.= Sugar solution consumption.

Table 2.2. Pearson correlation coefficient of Productivity Index (P.I.) and workers/colony compared with (a) brood bionomic parameters and (b) P.I. compared with colony consumption parameters and (c) and (d) P.I. compared with growth and investment parameters, for 8 *B. terrestris* indoor reared colonies.

Table 2.2(a).

Brood bionomic parameters		r value	Probability	Significance
Productivity index compared with:				
Max. live workers		0.807	0.008	**
Max. larval area		0.926	0.000	***
Days from oviposition to first emergence of:	male	0.546	0.081	n.s.
	male or queen	0.594	0.060	n.s.
Workers per colony compared with:	total males and queens	0.387	0.172	n.s.
	total males + (3.5 x queens)	0.566	0.072	n.s.

Table 2.2(b).

Colony consumption parameters	r value	Probability	Significance
Productivity Index compared with:			
Max. pollen consumed/week (g)	0.858	0.003	**
Max. sugar consumed/week (g)	0.929	0.000	***
Total pollen consumed up to peak larval area (g)	0.809	0.007	**
Total sugar consumed up to peak larval area (g)	0.819	0.006	**
Total pollen consumed/colony (g)	0.923	0.000	***
Total sugar consumed/colony (g)	0.986	0.000	***

n.s. = not significant (p>0.05)

* = p<0.05
** = p<0.01
*** = p<0.001

$r_{0.05(1)[6]}=0.621$
$r_{0.01(1)[6]}=0.789$
$r_{0.001(1)[6]}=0.905$

Table 2.2(c).

Growth and investment parameters	Colony 8	5	4	3	1	6	2	7
Productivity Index	465	412	351	349	248	235	207	62
Proportional investment males + (3.5 x queens) P.I.	0.67	0.42	0.51	0.46	0.50	0.62	0.61	0.40
Mean growth rate new workers emerging * 10 days	14.3	15.0	13.0	19.0	9.5	6.5	6.8	5.5

* taken every 10 days for first 40 days after first worker emergence, then mean calculated.

Table 2.2(d).

Colony parameter	r value	Probability	Significance
Productivity Index compared with:			
Proportional investment	0.280	0.251	n.s.
Growth rate	0.815	0.007	**

Table 2.3. Pollen and sugar consumption/week for ovipositing and non-ovipositing field captured queens confined to starter boxes.

Week	(Mean±S.E.) Ovipositing queen	Non-ovipositing queen	Number df	of reps.	Student's t test T value	Two tailed prob.	Significance
Pollen consumed (g)							
1	0.20±0.08	0.15±0.01	13	13,12	0.75	0.466	n.s.
2	0.12±0.03	0.10±0.03	23	13,12	0.55	0.587	n.s.
3	0.17±0.03	0.06±0.01	14	13,12	3.39	0.004	**
4	0.39±0.12	0.03±0.00	12	13,12	2.94	0.012	*
Sugar consumed (g)							
1	4.8 ±0.4	3.9 ±0.3	23	13,12	2.00	0.057	n.s.
2	5.3 ±0.3	2.6 ±0.3	23	13,12	6.69	0.000	***
3	6.2 ±0.4	2.7 ±0.3	23	13,12	6.63	0.000	***
4	6.1 ±0.4	2.9 ±0.3	23	13,12	7.21	0.000	***

$t_{0.05[12]}=2.18$ $t_{0.05[22]}=2.07$
$t_{0.05[13]}=2.16$ $t_{0.01[14]}=2.98$
$t_{0.05[14]}=2.15$ $t_{0.001[23]}=3.77$

The number of workers emerging was not correlated with the total number (males + queens) or biomass (males + (3.5 x queens)) of sexuals per colony (table 2.2a).

Timing of male emergence in the colony cycle affected the number of workers produced as any fertilised eggs laid after the switch to male eggs developed into queens. Brood bionomic parameters at the approximate time in the colony cycle when the foundress queen first switched to laying male eggs i.e. 21-23 days prior to first male emergence (van der Blom 1986) were compared and the eight colonies ranked according to P.I. The time from colony initiation to the switch to male egg laying showed no pattern, although the sample size was small. Larval area, worker number and worker:larval area ratios, pollen and sugar consumption total or weekly rates were not related to the time of switch to male emergence (appendix II table A2.1).

To estimate the time at which queen determination of fertilised female larvae occurred, two assumptions from Roseler's (1975) work were considered. The first assumption is that queen-presumptive larvae took three days longer as larvae and four days longer as pupae to develop compared to workers; the second, that queen-presumptive larvae were determined during the first 2-3 days of larval life. Queens were assumed to have come from eggs laid 27-29 days before their emergence, and to have been queen-determined 5-8 days after oviposition. Brood bionomic parameters during this queen-determining period were recorded and the four colonies producing queens were ranked according to P.I. (appendix table A2.2). Colonies with higher P.I. with more workers, had greater larval area, and greater food (pollen and sugar) consumption during the time of queen-larvae determination, but this resulted in fewer rather than more queens produced and more males.

From the four colonies producing queens the two colonies (3 and 6) producing the higher number of queens had lower P.I. and in both cases queens were produced well before males emerged (appendix fig. A2.2a and A2.4a). In the colonies where only small numbers of queens (9 and 16) were produced, queens emerged after males and probably from eggs laid just prior to the switch to male production by the foundress queen (fig. 2.5a,b and appendix fig. A2.3a,b). In colonies where queens emerged prior to males the larval area consisted mainly of queen larvae compared to colonies where queens emerged after males where the larval area was mainly male larvae. There was little indication that colonies producing more queens had more workers, greater larval area or higher consumption, although the sample size was small (tables 2.1a, 2.1b). However colony three, which produced a total of 44 queens, had the highest total pollen consumption at the time of peak larval area.

2.2.2 Sugar solution and pollen consumption

2.2.2.1 Whole colonies

Comparison of pollen and sugar consumption between non-ovipositing and ovipositing queens showed no significant differences during the first week in confinement (table 2.3). In the second week, oviposition resulted in significantly higher sugar consumption, and during the third and fourth weeks both sugar and pollen consumption were significantly greater in ovipositing queens. Pollen consumption of non-ovipositing queens dropped significantly in the third and fourth weeks of confinement compared to the first week (table 2.4).

Weekly consumption for eight individual colonies is illustrated in figures 2.4c and 2.5c (and appendix figs. A2.1c-A2.6c). In all eight colonies pollen consumption peaked before maximum sugar consumption. In six of the eight colonies, larval area (cm^2) was significantly correlated with pollen consumption (g/week) up to peak larval area (table 2.5). In four colonies peak weekly pollen consumption coincided with peak larval area. In the remaining four colonies, peak pollen consumption occurred two weeks after peak larval area coinciding with emergence of sexuals. Newly emerged sexuals contributed to the delay in peak colony pollen consumption (see later).

Peak weekly sugar consumption occurred late in colony development coinciding with peak emergence of sexuals, especially males. In all eight colonies the number of live workers present was highly correlated with weekly sugar consumption up to peak larval area (table 2.5).

The virtual exponential increase in colony pollen and sugar consumption from pre-worker emergence to sexual production is shown from the cumulative pollen and sugar consumption (figs. 2.4d and 2.5d and appendix fig. A2.1d-A2.6d). Pollen consumption was closely correlated with sugar consumption (no statistical analysis presented as graphs illustrate correlation) in all eight colonies. The peak in pollen consumption coincided with maximum numbers of workers emerging in each colony, so the foraging force peaked as the maxima for pollen demand from larvae was reached. Total weekly sugar consumption continued to rise even as colony worker numbers declined mostly as a result of consumption by sexuals. At the end of the colony cycle, between 15 and 90 honeypots with a mean of 50, were still half full with concentrated honey.

P.I. was correlated with the maximum weekly rate of food consumption (figs. 2.8 and 2.9) and also, the cumulative total food consumption at peak larval area and final colony size (table 2.2b; figs. 2.10 and 2.11).

Maximum food consumption rate was, in turn, correlated with the biomass of sexuals produced (males + (3.5 x queens)) (figs. 2.12 and 2.13), peak larval area (fig. 2.14) and

Table 2.4. Comparison of pollen consumption (g) of non-ovipositing queens between week 1 and weeks 2-4 confined to starter boxes.

Week	Week	df	Number of reps.	Student's t test T value	Two tailed prob.	Signif-icance
2	1	16	12, 12	1.57	0.136	n.s.
3	1	22	12, 12	5.01	0.000	***
4	1	12	12, 12	8.10	0.000	***

$t_{0.05[16]}=2.12$
$t_{0.001[22]}=3.79$
$t_{0.001[12]}=4.32$

Table 2.5. Pearson correlation coefficients for: (a) larval area (cm^2) vs. pollen consumption/week (g), (b) number of live workers vs. sugar consumption/ week (g). Analysis from first worker emergence to peak larval area for 8 colonies.

		Colony 1	2	3	4	5	6	7	8
Larval area vs. pollen consumed	r value	0.864	0.785	0.901	0.960	0.801	0.662	0.650	0.782
	No. cases	9	10	8	10	11	7	6	9
	Probabil.	0.001	0.004	0.001	0.000	0.002	0.052	0.081	0.006
	Signif.	**	**	**	***	**	n.s.	n.s.	**
Live workers vs. sugar consumed	r value	0.856	0.918	0.946	0.972	0.865	0.964	0.920	0.884
	No. cases	8	7	8	8	10	7	7	9
	Probabil.	0.003	0.002	0.000	0.000	0.001	0.000	0.002	0.001
	Signif.	**	**	***	***	**	***	**	**

$r_{0.05(1)[4]}=0.729$ $r_{0.001(1)[4]}=0.963$
$r_{0.05(1)[9]}=0.521$ $r_{0.001(1)[9]}=0.820$

Figure 2.8.

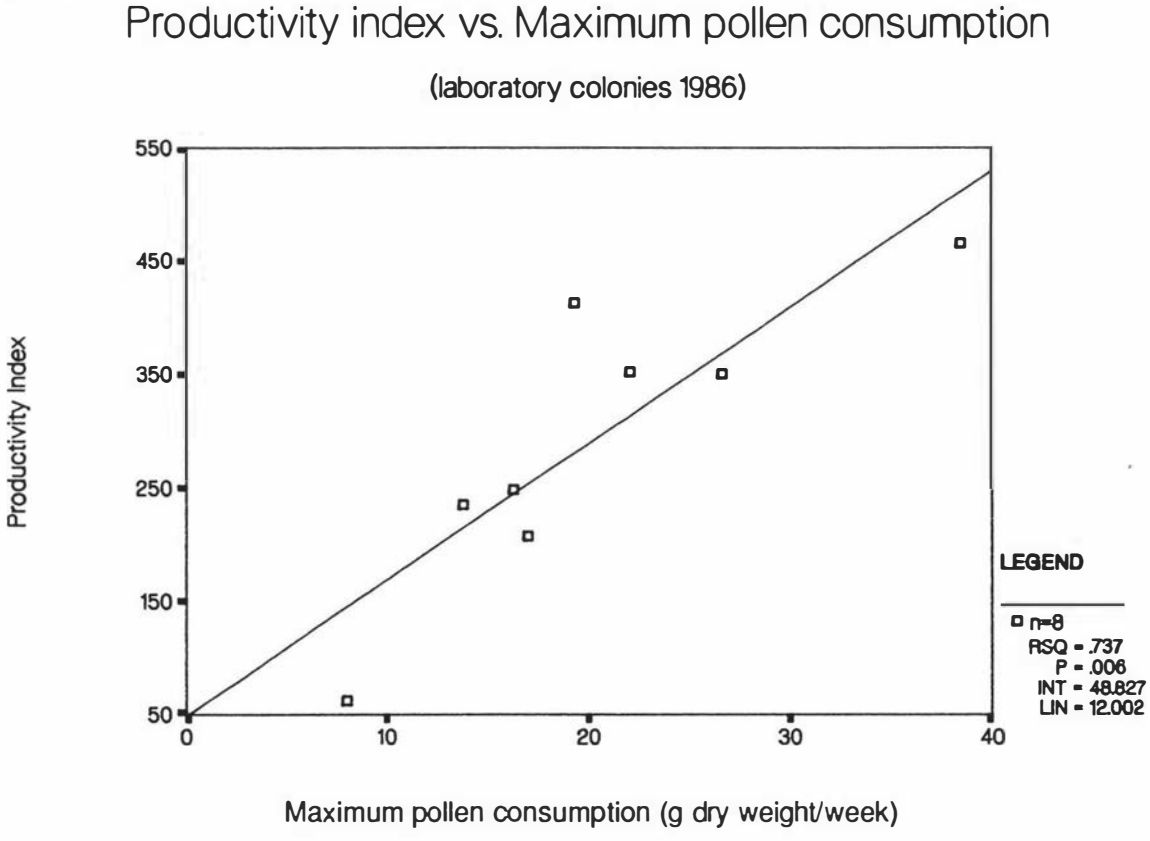


Figure 2.9.

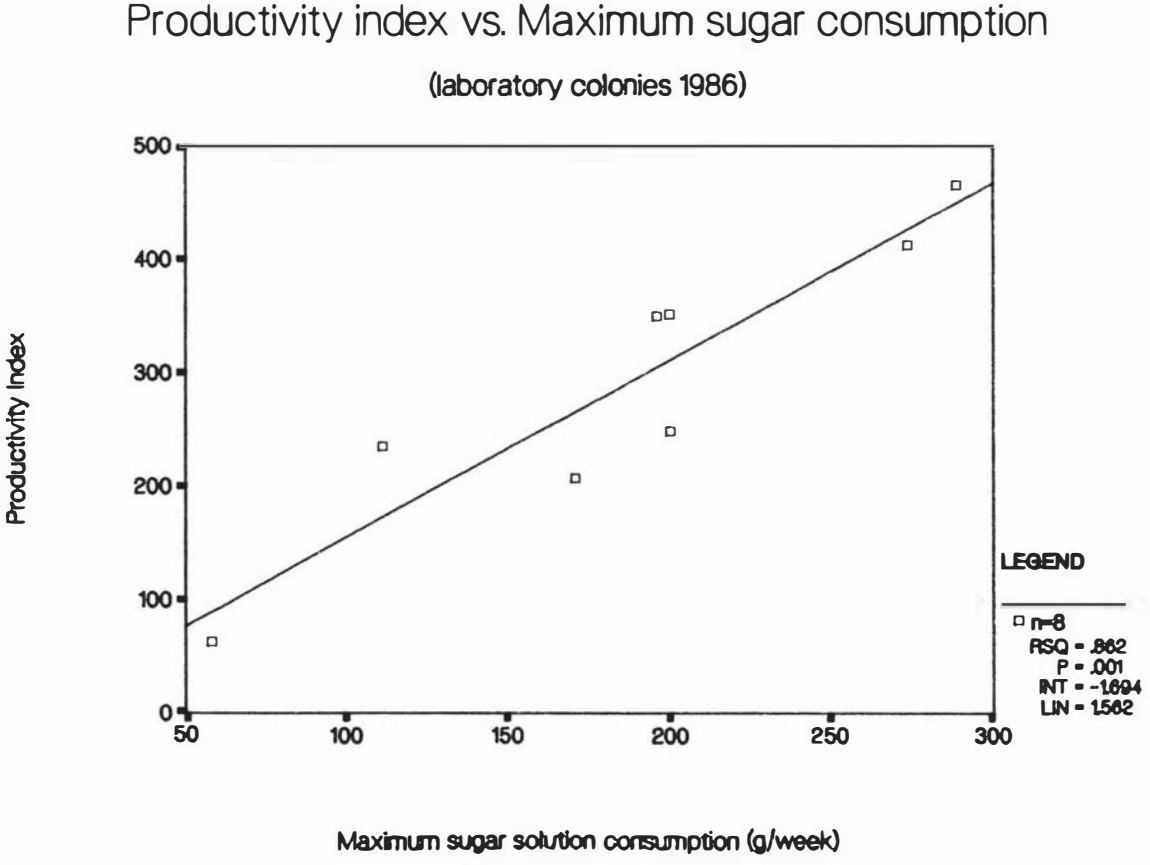


Figure 2.10.

Total pollen consumption per colony vs. Productivity index

(laboratory colonies 1986)

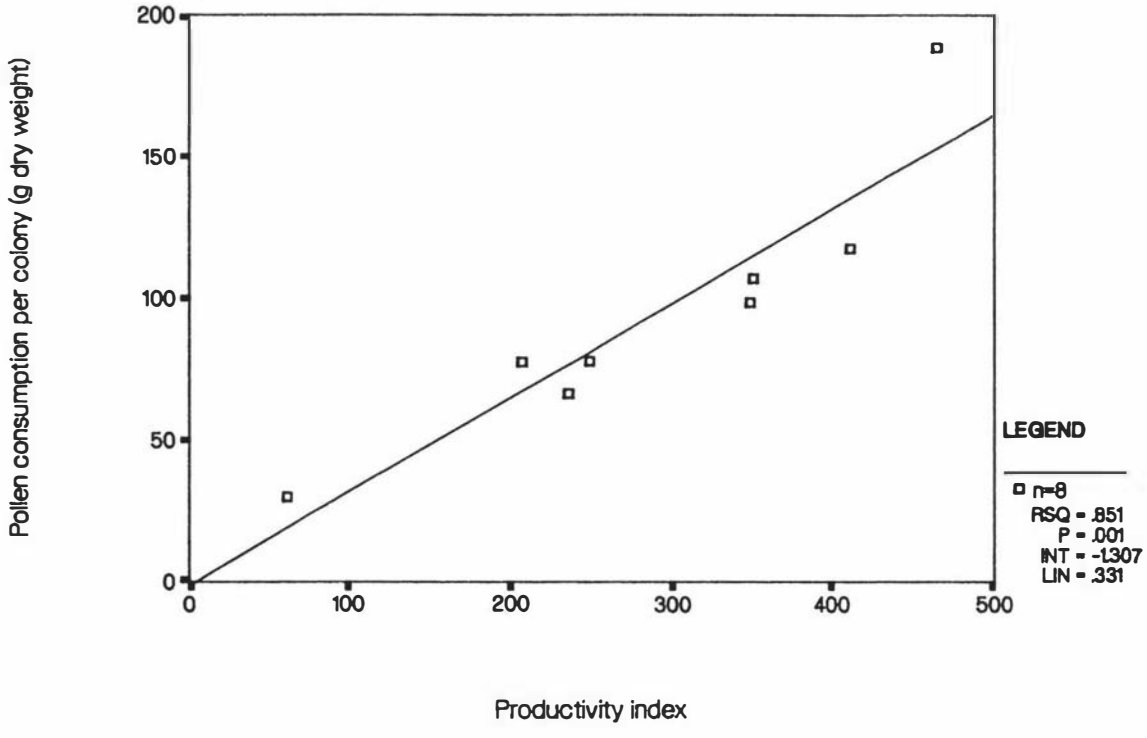


Figure 2.11.

Total sugar consumption per colony vs. Productivity index

(laboratory colonies 1986)

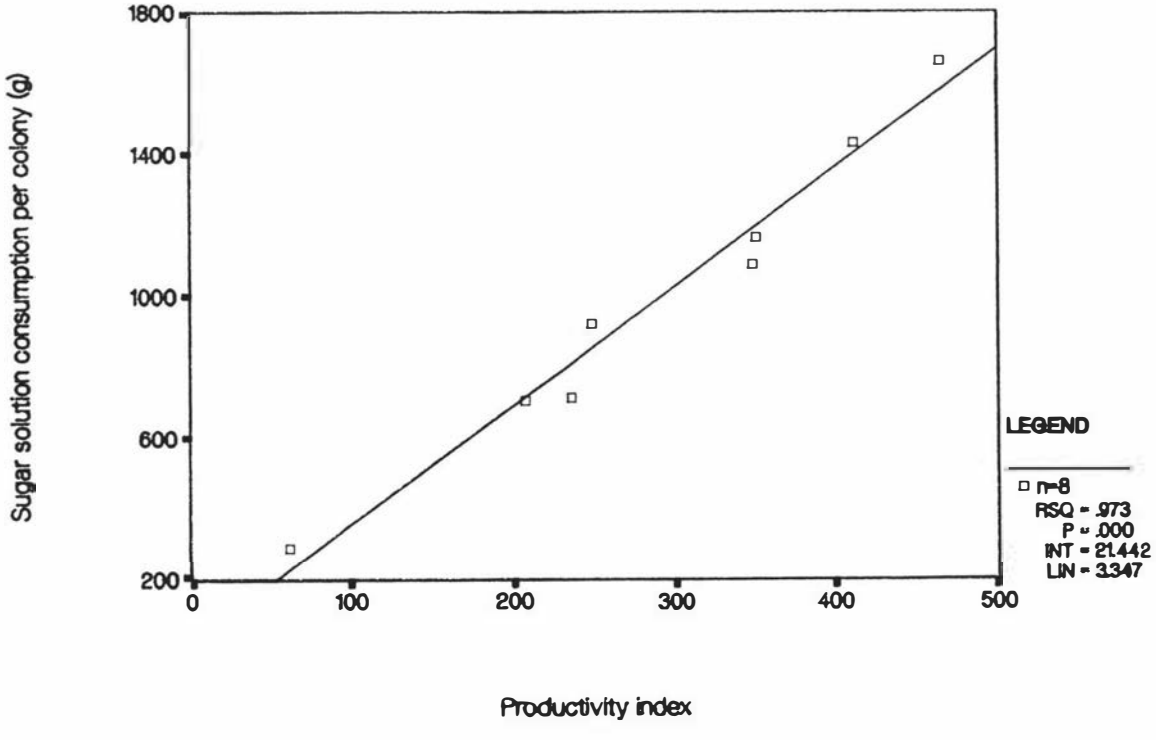


Figure 2.12.

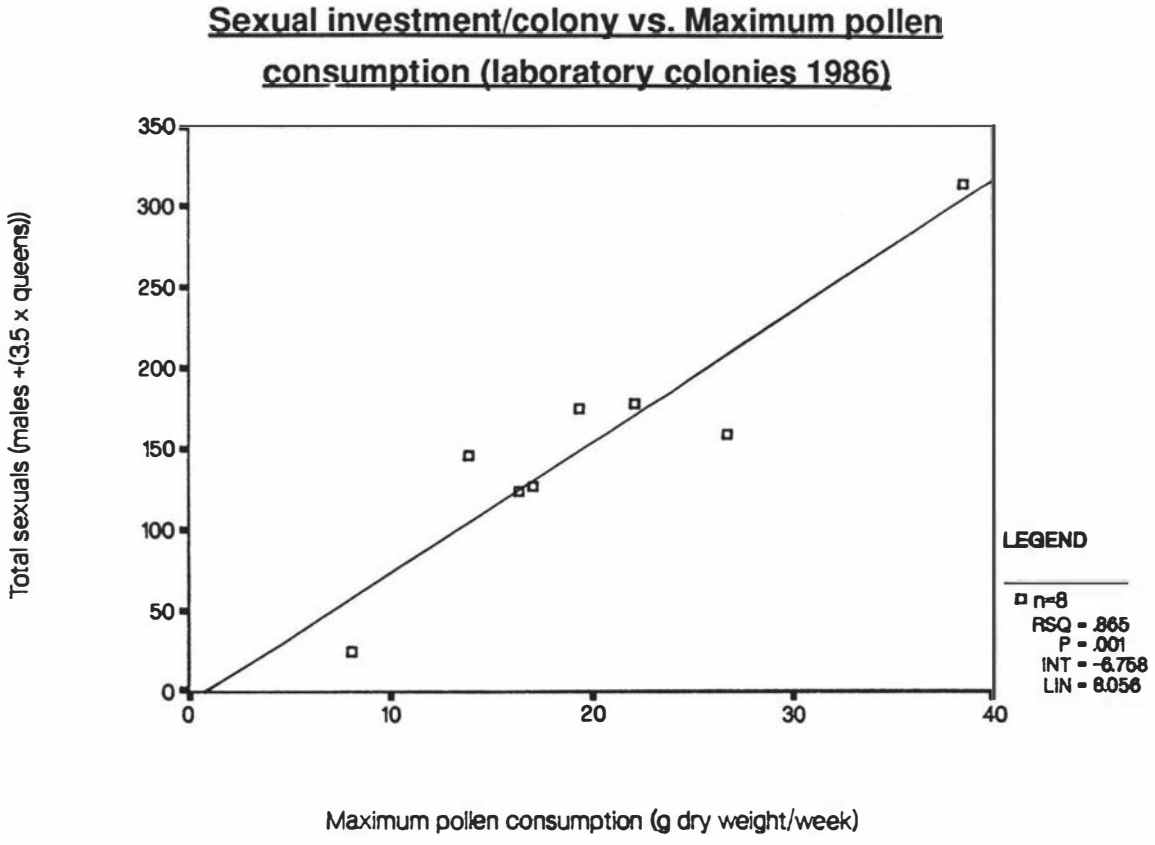


Figure 2.13.

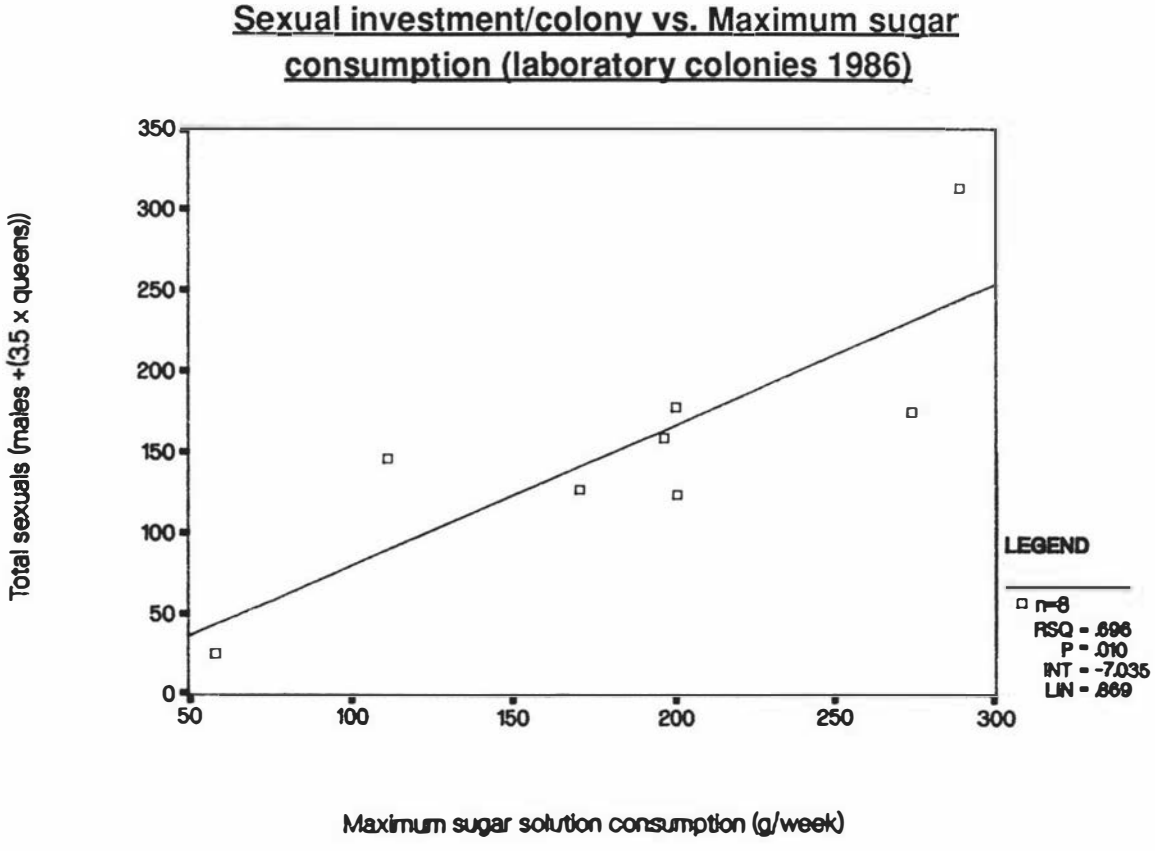


Figure 2.14.

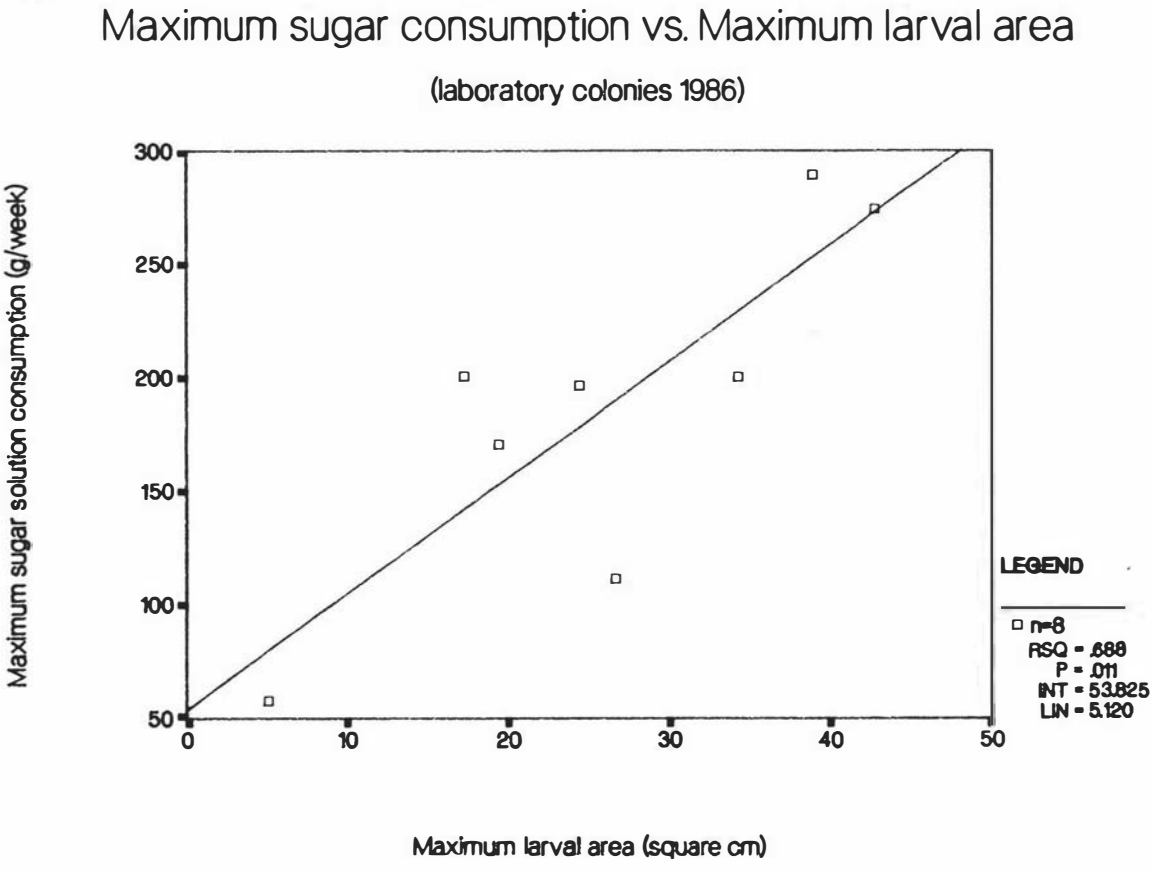
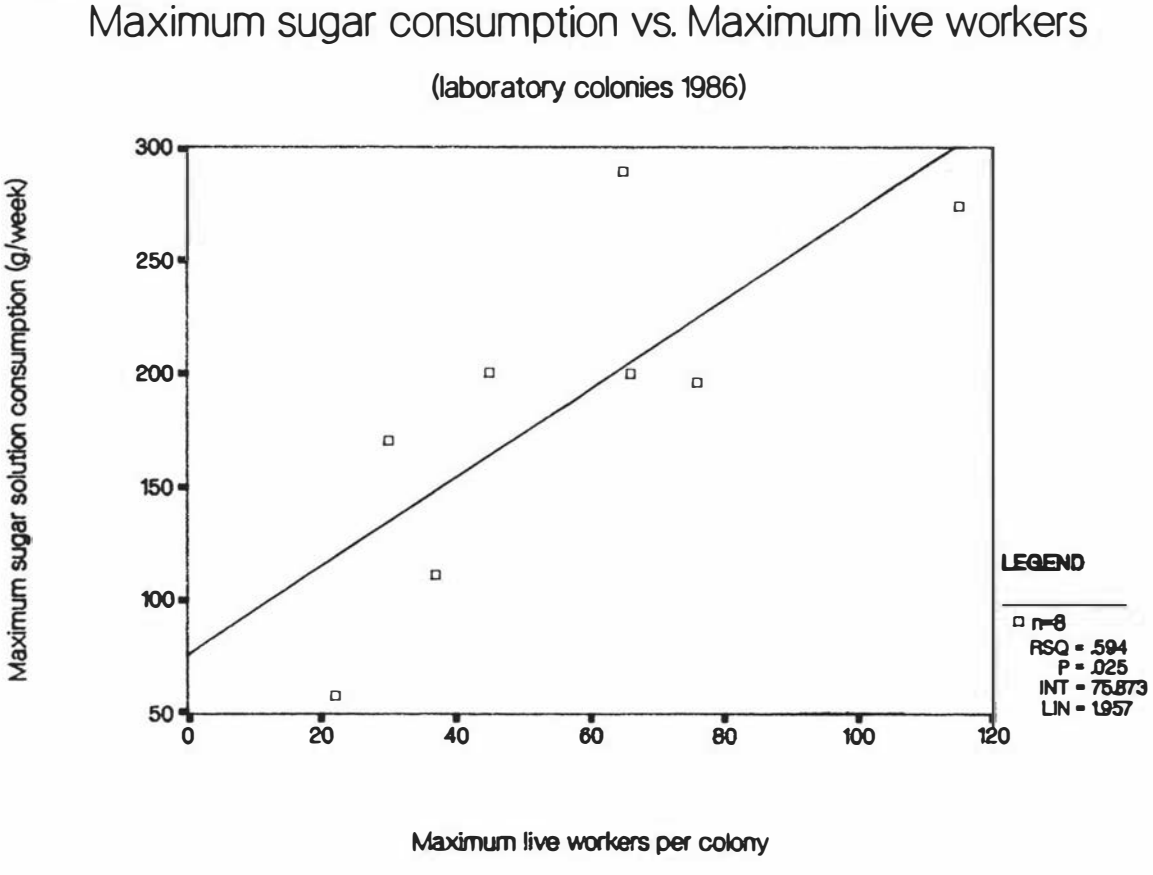


Figure 2.15.



live worker numbers (fig. 2.15), although pollen consumption and worker numbers were not significantly correlated (table 2.6).

Total colony food consumption was correlated with maximum larval area, total workers emerging, sexual biomass emerging and peak consumption rates (table 2.7).

2.2.2.2 Sexuals

Adult males consumed nearly twice the sugar 4-6 days after emergence than during the first three days. However, males consumed pollen during the first three days after emergence but not during days 4-6 (table 2.8). Newly emerged queens consumed 18 times more pollen on the first three days compared to days 4-6, but there was no difference in sugar consumption. Queens consumed 2.3 times more sugar than males during the total 6 day post emergence period and 6.3 times more pollen (table 2.9).

Queen sugar consumption per day for 25 queens in a flight cage was only 0.1g higher than in rearing boxes (table 2.10), while pollen consumption was the same. However the data were determined using different methods and the first method, using individual rearing boxes, was likely to be more accurate because each bee was independent. Male sugar consumption was similar under both trial conditions. Pollen consumption for males in cages was negligible. As the variance ratio (F_S) for sugar and pollen consumption by males and queens in rearing boxes was not significant, the overall mean consumption of pollen and sugar solution for queens and males was calculated. This enabled comparisons to be made with consumption for queens and males during mating in the flight cage. The combined mean consumption for queens and males in rearing boxes was the same as in flight cages and thus mating did not appear to significantly increase consumption. One mated queen entered hibernation near the end of the trial by burrowing into the moistened peat moss.

2.3 Discussion

The period of greatest colony pollen consumption occurred during and up to 1-2 weeks after peak larval area (5-8 weeks after first worker emergence). Peak sugar consumption coincided with peak emergence of sexuals. Adult males and queens made a significant contribution to colony consumption especially 1-3 day old queens. Emergence of sexuals extended the peak food consumption in 50% of the colonies by prolonging demand for up to two weeks after larval area peaked. This additional pollen and nectar demand suggests the optimum time for achieving maximum pollination efficiency from colonies would be from one week prior to peak larval area to two weeks after peak larval

Table 2.6. Pearson correlation coefficient of peak pollen and sugar consumption/week with peak larval area, peak live workers and biomass of sexuals (males + (3.5 x queens)), (n=8).

		Peak larval area (cm^2)	Peak live workers	Biomass of sexuals
Peak pollen consumed (g/week)	r value	0.665	0.473	0.930
	Probabil.	0.036	0.118	0.000
	Signif.	*	n.s.	***
Peak sugar consumed (g/week)	r value	0.830	0.771	0.834
	Probabil.	0.005	0.013	0.005
	Signif.	**	*	**

Table 2.7. Pearson correlation coefficient of total pollen dry weight and sugar solution consumption with brood bionomic parameters for 8 colonies.

Brood bionomic parameters	Total pollen consumed/ colony (g) r value	Probab.	Signif.	Total sugar consumed/ colony (g) r value	Probab.	Signif.
Days from oviposition to male emergence	0.308	0.229	n.s.	0.451	0.131	n.s.
Peak live workers present	0.588	0.068	n.s.	0.791	0.010	*
Peak larval area (cm^2)	0.817	0.007	**	0.905	0.001	**
Total workers emerged	0.639	0.044	*	0.838	0.005	**
Total sexuals emerged (males + (3.5 x queens))	0.974	0.000	***	0.912	0.001	**
Peak pollen consumed/week (g)	0.947	0.000	***	0.863	0.003	**
Peak sugar consumed/week (g)	0.897	0.001	**	0.960	0.000	***
Total pollen consumed/ colony (g)	-	-	-	0.950	0.000	***

$r_{0.05(1)[6]}=0.621$
$r_{0.01(1)[6]}=0.789$
$r_{0.001(1)[6]}=0.905$

Table 2.8. Comparison of pollen and sugar consumption between day 1-3 and day 4-6 by post-emergent queens and males confined to starter boxes for 6 days (totals for 3 day periods).

	Total consumption from Days 1-3 (Mean±S.E.)	Days 4-6	df	Number of reps.	Student's t test T value	Two tailed prob.	Signif-icance
Queens							
Sugar consumed(g)	1.51±0.40	1.75±0.17	9	8,8	0.55	0.592	n.s.
Pollen consumed(g)	0.18±0.03	0.01±0.01	8	8,8	5.89	0.000	***
Males							
Sugar consumed(g)	0.50±0.07	0.90±0.08	22	12,12	3.84	0.001	**
Pollen consumed(g)	0.03±0.01	0.00±0.00	14	12,12	2.63	0.020	*

$t_{0.05[9]}=2.26$ $t_{0.01[22]}=2.82$
$t_{0.05[14]}=2.15$ $t_{0.001[8]}=5.04$

Table 2.9. Comparison of pollen and sugar consumption between post-emergent queens and males.

	Comparison of males with queens	df	Number of reps.	Student's t test T value	Two tailed prob.	Signif-icance
Sugar consumed(g)	Day 1-3	7	12,8	2.51	0.038	*
Sugar consumed(g)	Day 4-6	18	12,8	5.12	0.000	***
Pollen consumed(g)	Day 1-3	8	12,8	5.37	0.001	**
Pollen consumed(g)	Day 4-6	18	12,8	2.06	0.055	n.s.

$t_{0.05[7]}=2.37$ $t_{0.01[8]}=5.04$
$t_{0.05[18]}=2.10$ $t_{0.001[18]}=3.92$

Table 2.10. Comparison between male and queen consumption in starter boxes, flight cages and during mating.

	Sugar consumed /day/bee (g)	Reps.	Pollen consumed /day/bee (g)	Reps.
Males:				
Starter boxes[#] (Mean±S.E.)	0.30±0.03	12	0.00±0.00	12
Flight cages (Mean)	0.31 -	1	0.00 -	1
Queens:				
Starter boxes[#]	0.58±0.06	8	0.00±0.00	8
Flight cages	0.71 -	1	0.00 -	1
Males and queens:				
Starter boxes[#&]	0.41±0.04	20	0.00±0.00	20
Mating in flight cage	0.40 -	1	0.00 -	1

[#] mean consumption/day from day 4-6

[&] variances of pollen consumed and sugar consumed for queens and males from starter boxes were not significantly different.

$F_{s[7,11]}=3.29$ n.s. (male/queen sugar consumed) $F_{0.05(2)[7,11]}=3.76$

$F_{s[7,11]}=0.00$ n.s. (male/queen pollen consumed) $F_{0.01(2)[7,11]}=5.86$

area or up to ten days after sexuals first emerge i.e. when consumption is highest and the number of emerging workers peaks.

Pomeroy (1979) found that *B. ruderatus* queens consumed 0.3 g of (presumably) fresh pollen during the first three days after emergence. Males, whose body weight was half that of queens, consumed half as much (0.15g). This compares with 0.18g of dry weight pollen (or 0.22g fresh pollen) consumed over the first three days by *B. terrestris* queens in the present study. However, male consumption was found to be only 0.03g, one sixth that of queens. The small *B. terrestris* male consumption may reflect the proportional difference in body weight between queens and males for this species compared to *B. ruderatus*.

Friden (1966) recorded sugar solution consumption of queens (50% sucrose in water) every 72 hours for 11 species of *Bombus* confined in outdoor nest boxes (natural temperature and humidity). He found consumption increased during nest establishment with 60% of queens (all species) consuming 3ml per 72 hours and in some cases as high as 6ml. This compares with 1.7-2.1ml in 72 hours (4.8-6.2g/week) for ovipositing *B. terrestris* queens for this study. The higher sugar consumption for Friden's queens may be due to the lower temperatures.

Sexuals that emerged as the colony declined were subject to dwindling food supplies from a decreasing forager force. Young queens requiring more pollen for consumption may forage for a colony with low stores or feed on the remaining pollen and honey stores built up during times of food abundance from a well provisioned colony. All indoor reared colonies stored viscous honey in waxen honey pots,and this benefited the survival of sexuals. In this trial bees could not accumulate pollen as nest stores because it was provided in separate containers and workers consumed it directly rather than transferring the pollen to their 'own' pots. Normally pollen is carried on worker corbiculae after collection from flowers and deposited into pollen pots directly. However in this trial pollen was not 'foraged' for, whereas sugar solution was carried from the flight cage in bee honey stomachs and regurgitated into nectar pots.

The total consumption of sugar and pollen was linearly related to the colony's productivity (P.I.). The amount of food needed to produce a particular sized colony can be calculated from the equation:

$$\text{Dry pollen (g)} = 0.33\ (\text{P.I.}) - 1.307$$

$$\text{Sugar solution (g)} = 3.35\ (\text{P.I.}) + 21.4$$

(P.I.= worker equivalents)

As the data do not exceed a P.I. of 460 it cannot be assumed that the relationship continues linearly for larger colonies.

Monitoring total larval area and total live workers per colony could provide accurate predictions or. the anticipated final P.I. of the colony. By setting a minimum P.I. threshold e.g. 200, it would be possible to determine which colonies would be expected to reach this minimum size simply by recording larval area, total live workers or, alternatively, weekly pollen or sugar solution consumption. These four predictors are not difficult to measure and could be recorded over any one week during colony development. Any colony switching to sexual production before the minimum larval area, worker number or consumption were reached could be discarded. Using all four predictors would be most accurate. However, with just larval area and worker numbers, maximum sugar consumption can be estimated and these three variables used to predict P.I. Sugar and pollen consumption can also be used to predict the total sexual biomass produced (males + (3.5 x queens)), where 3.5 represents the greater pollen investment required for queen rearing compared to workers and males (Pomeroy 1981a; Tod 1986). It was not possible to make predictions of final colony size from very small indoor colonies prior to removal into the field.

As expected, colonies with the highest consumption invested the most in reproduction, but there was no indication that larger colonies invested a greater proportion of food into sexuals than smaller colonies. It was not possible to predict absolute numbers of males and/or queens produced, the ratio between the two or the timing of sexual production. Pomeroy (1979) found a strong correlation between the reproductive success of colonies and the estimated number of workers produced for *B. ruderatus*. He also found a correlation between P.I. and the time of male emergence for this species, although, in this case, males always emerged before queens.

In all colony rearing, the length of the worker production phase is the critical period for developing colonies suitable for pollination, rather than whether males emerge before queens. However, the latter information may provide insight into the health of the foundress queen.

For the eight colonies large inter-colony variation in growth rate occurred under identical rearing conditions and ample food. Larger colonies appeared to have more workers emerging per unit time than smaller colonies. Higher worker numbers did not necessarily result in more sexuals however. While variability in colony growth is well known (Owen *et al.* 1980; Plowright and Laverty 1984), it s cause is less understood. These differences may be due to variation in fecundity (egg laying ability) of the foundress queen. Thus the low P.I. for colony 7 compared to colonies 5 and 8 could be due to a more fecund foundress queen in the latter two colonies. Colony 7 had a lower growth rate (workers produced/unit time) and produced sexuals earlier. Although colony decline for *B. ruderatus* is not due to egg shortage, but rather to death of the foraging

force and consequent loss of food and feeding of the brood (Pomeroy 1977). The initial limiting factor for larval area and worker numbers may be foundress fecundity.

Food availability, larval area and worker numbers were not responsible for male production. This contradicts Roseler's (1967) findings and recent results by Tod (1986) but is in agreement with Owen and Plowright (1982), Pomeroy and Plowright (1982), van der Blom (1986) and others. As van der Blom points out, a mechanism by which only workers induce the queen to produce males could be disadvantageous ultimately for workers because it would be detrimental to the production of queens. The presence of ovipositional sites may have been a factor in the switch to production of sexuals, as this switch in the colony occurred so that peak larval area (of sexuals) coincided with peak emergence of workers. Brian (1951) indicated that foundress queens oviposited on the side of the pupal case when pupae were no older than three days to ensure that worker emergence coincided with developing larval food requirements. With the exception of colonies 3 and 6, where queens emerged before males, larval area was low when the queen switched to producing males. There was little evidence to suggest foundress queens 'switched' to laying male eggs, then later 'switched' to laying female eggs.

While Plowright and Jay (1966, 1977) suggest queen production in colonies is trophogenically controlled by workers, it seems likely that the trophic status of the colony as a whole was not the prime cause of queen production for these indoor reared colonies although individual queen larvae were fed more than worker larvae. Queen production was not apparently related to other brood bionomic factors. Trophogenic factors in *B. terrestris* were found by Roseler (1975) to be important only in caste differentiation in the absence of the foundress queen. Queen production in colonies 4 and 5 of the present study seemed to be initiated by the switch to male production possibly aided by abundant colony food and an aging foundress queen with declining pheromonal dominance over the worker-larval feeding regime. Although future queen eggs were probably laid before the switch to male production the critical time for caste differentiation is known to be in the first three days of larval life (Roseler 1975) and by this stage worker detection of male eggs and/or larvae seems probable.

However in colonies 3 and 6, where queens were produced considerably earlier than expected, a different cause for the switch to queen production seems likely. With an abundant food supply, a foundress queen with diminishing pheromonal dominance may have failed to inhibit the frequency of feeding by workers of female larvae, hence a much greater proportion of larvae became queens. This early production of queens may then have delayed male production by the foundress. These two different reproductive strategies i.e. early and late queen production, were recorded by Duchateau and Velthuis (1988).

Control of foundress queen fecundity, sexual production and the degree of dominance over the worker caste may depend on the health of queens, which in turn, may depend on pre-hibernation feeding (Holm 1972). Improving trophic conditions before and after hibernation may produce healthier queens, and this could be reflected in larger colony size.

A two-week maximum confinement period of field captured queens would be most suitable for indoor colony establishment. The few eggs laid after this period did not develop into large colonies and removal of such queens could be compensated for by introducing fresh queens. Increased food consumption by laying queens probably reflected development of brood and the need for the queen to promote glandular secretion and food regurgitation to larvae. Priming (providing a bed of pollen) of egg cups was not observed. Non-ovipositing queens lost interest in food, and this could be used to indicate the need for queen replacement.

2.4 Summary

1) For a given colony size (P.I.) colonies consumed similar amounts of pollen and sugar. Colony food consumption could be estimated from larval area and live worker number.
2) Colonies with higher consumption had a higher sexual investment (males + (3.5 x queens)) but larger colonies did not invest proportionally more into reproduction than smaller colonies.
3) The greatest pollen and sugar requirement from colonies was during peak larval area when worker emergence peaked and up to two weeks afterwards when emergence of sexuals peaked.
4) The optimum period for maximum pollination efficiency from colonies would be from one week prior to peak larval area to two weeks after the peak.
5) Male emergence was not correlated with worker number or brood bionomic parameters.

CHAPTER 3

PRELIMINARY STUDY OF FORAGING ON FIELD CROPS

3.0 Introduction

Fye and Medler (1954a) considered the most suitable areas for maintaining bumble bee populations were those with a good succession of spring flowers. European literature lists numerous forage plants visited by the polylectic *B. terrestris* (e.g. D'Albore and D'Ambrosia 1981), but in many cases the relative importance of such forage plants in providing food for *B. terrestris* has not been determined. Comparison with local flora is relevant for deciding when additional forage is required and what species might be most suitable.

Abundance of feral *B. terrestris* queens is influenced by seasonal availability of food supply (Gurr 1957a). Average nest size in New Zealand is at least twice that of Europe. Donovan and Weir (1978) concluded that nest sites, rather than food supply, are limiting. However, no mention was made by these authors of the number of nests in a given area, nor was any measurement made on occupancy of natural rodent nests. Trophic conditions however affect the relative abundance of different bumble bee species. Gurr (1957a) explained that at Grassmere (South Island), where tree lucerne predominated, *B. terrestris* built up rapidly on this spring food source.

Tree lucerne is an important bumble bee fodder crop (Gurr 1961) and an abundant source of nectar aiding survival of foraging queens in late winter and early spring (Macfarlane and Beresford 1982). *B. terrestris* is well adapted to foraging on tree lucerne. This legume was introduced to New Zealand from the Canary Islands (Webb and Shand 1985) where it was pollinated by the endemic *B. canariensis* Perez a close relative of *B. terrestris* (Erlandsson 1979). The value of tree lucerne as a fodder and bee forage crop has recently been re-emphasised (Davies and Macfarlane 1979; Logan 1982; Snook 1982). After nest founding, a small percentage of foragers collect pollen from tree lucerne until flowering is finished (Macfarlane and Beresford 1982). Unfortunately, bee forage in rural areas is often scarce after tree lucerne finishes flowering.

During September to November in New Zealand, widespread dearth of flowering prevails. In the northern hemisphere this early summer shortage is referred to as the 'June gap' by beekeepers (Percival 1965). In damper areas of New Zealand during early spring, willows, *Salix* spp., gorse, *Ulex europaeus*, and broom, *Cytisus scoparius*, provide a food source; elsewhere garden shrubs and fruit blossom are foraged upon. Gurr (1961) considered cruciferous flowers may be important while Macfarlane and

Beresford (1982) indicated *B. terrestris* pollinated brassicas after moving off tree lucerne. During this sparse flowering period considerable competition for forage from honey bees occurs (Cumber 1953a), foraging mainly on willows, dandelions, *Taraxacum officinalis*, and brassicas. By late November white clover and yellow lupin provide suitable bee forage; the latter species providing pollen only.

A number of criteria should be considered in deciding the most suitable forage crop for *B. terrestris* to provide food for colonies during this spring dearth of flowering.

1. availability of seed
2. cost of establishment
3. ease of cultivation
4. time from sowing to flowering
5. seasonal flowering time, flower duration, flower density
6. flower morphology
7. degree of competition from other foragers
8. preference by *B. terrestris* workers compared to other crops
9. food availability relative to weather conditions
10. amount of pollen and/or nectar in flowers
11. amount of pollen and energy content of nectar returned to hive from foragers on the crop

Criteria 1-3 were not formally studied in this thesis. During the first (1986) season, criteria 4-8 were considered for crops flowering from September to November; the second season considered criteria 5-11.

The main objective of the 1986 season was to determine the relative preference of *B. terrestris* for six field crops. Other foragers were also recorded together with weather and crop phenology data. In this experiment the areas of each crop differed, making comparisons between crops difficult to interpret. Thus only minimal statistical analysis has been employed, but instead, the data were used to provide a basis for a more satisfactory experimental design (implemented in the 1987 season) to determine the suitability of four selected crops as bee forage. The suitability of *B. terrestris* for nectar removal from the four selected crops was also considered.

A correlation exists between tongue (proboscis) length or head shape of bumble bees and the corolla tube length of flowers visited (Brian 1957; Hobbs *et al.* 1961; Teras 1976). Tongue length was recorded in this trial while corolla tube length is considered in chapter 4.

Harder (1982) considered the functional proboscis length in bumble bees was the length of the glossa only. Later Harder (1983) found that for *Adrena calini*, with a short 3.5mm tongue, this included the prementum and glossa, while for *B. pennsylvanicus*, with a long 18mm tongue, only the glossa was functional. Prys-Jones and Corbet

(1987) considered the functional proboscis length for bumble bees was the glossa and prementum. This length was henceforth recorded for these trials. Nectar robbing from fodder radish was also examined.

3.1 Methods

Six crops were direct drilled, together with 'Nitrophoska'(NPK % 12:10:10) fertiliser at 150 kg/ha and 'Phorate' (active ingredient:thimet) insecticide at 5 kg/ha, into herbicide (glyphosate) treated ryegrass,*Lolium perenne*, pasture. The six crops: borage, broccoli, kale cv. Maris Kestrel, fodder radish cv. Neris, tick bean and white lupin were sown on 26 March 1986 on Keeble farm 3km south of Massey University. Seeding rates and areas sown are shown in table 3.1 and the layout of plots in figure 3.1.

'Fusilade' (active ingredient: fluazifop-butyl) herbicide at 2 litres/ha was sprayed on legumes and 'Carbetamex' (active ingredient:carbetamide) herbicide at a rate of 5 kg/ha was sprayed on crucifers and borage on 16 May to control ryegrass. During the study period tree lucerne, yellow lupin, blue lupin, mustard and crack willow, *Salix alba*, flowered within the vicinity of the trial area.

The percentage of each crop flowering was recorded by visually estimating numbers of individual plants flowering in relation to total numbers of plants present each week. Flower density was determined at peak flowering of each crop by counting the number of flowers/m^2.

At the time of recording bumble bee numbers, daily temperature maxima and minima were recorded in the shade 1m above ground level. Wind speed was determined with a hand-held anemometer AM500 at a height of 1.5m. Daily climatological recordings 1km from the site were consulted for more complete weather data.

Between 29 August and 29 September, 202 laboratory reared colonies of *B. terrestris* were introduced onto Keeble farm,and by 1-4 December, 32 colonies were removed for kiwifruit pollination.

Once a week between 22 September and 14 November, bee activity was monitored on the six crops by holding a 2m stick and walking a 100m transect of each plot between 10am and 4pm. Species and caste of each bumble bee encountered were recorded together with presence or absence of pollen loads. Only total numbers of honey bees were recorded due to the large numbers present. Daily totals of *B. terrestris* workers, males, queens and honey bees were compared for the four most preferred crops using a one-way ANOVA. Treatment means were compared using Tukey's test at 0.05 level. No other valid analyses could be implemented.

A honey bee hive with a pollen trap was introduced onto the trial site to determine honey bee pollen preference due to difficulties in field assessment of pollen loads. The

Figure 3.1. Keeble farm 'colony expansion' area.

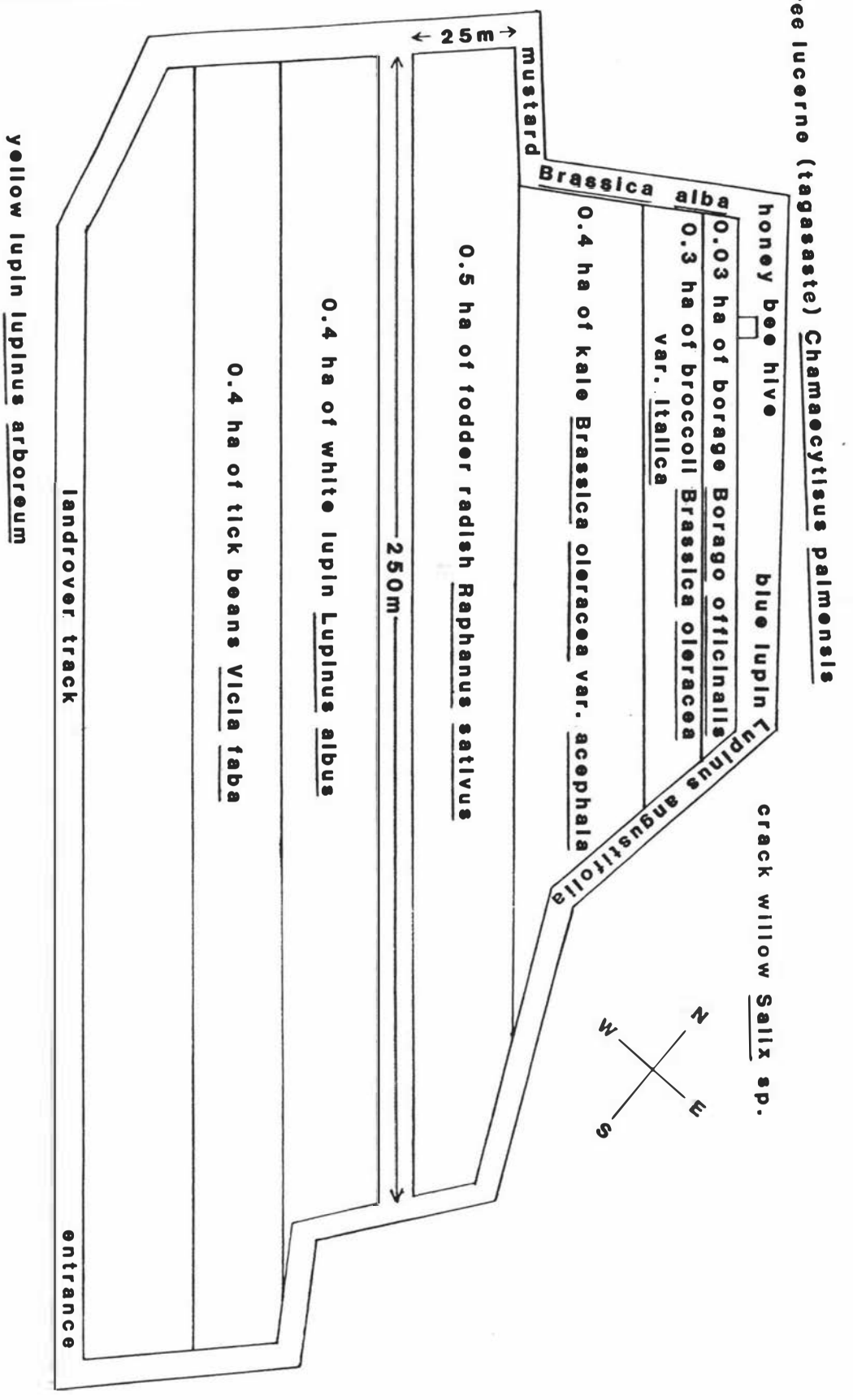


Table 3.1. Sowing rates and areas of crops on Keeble farm 1986.

Crop	Sowing rate(kg/ha)	Area planted (ha)
borage, *Borago officinalis*	20	0.03
kale, *Brassica oleracea* var. *acephala*	5	0.40
broccoli, *Brassica oleracea* var. *italica*	5	0.30
fodder radish, *Raphanus sativus*	10	0.50
tick bean, *Vicia faba*	120	0.40
white lupin, *Lupinus albus*	120	0.40

Table 3.2a. Relative distribution of *B. terrestris* and honey bees from 200m^2 transect on 6 forage crops (totals from 8 observations).

CROPS	Total *B. terrestris* workers	*B. terrestris* workers with corbicular pollen loads	*B. terrestris* males and queens		Total honey bees
			Males	Queens	
borage	113	24(21%)	29	8	971
kale	142	2(1.4%)	23	49	347
broccoli	103	4(4%)	78	17	377
fodder radish	118	7(6%)	16	6	314
tick bean	8	1(12%)	1	6	8
white lupin	3	0(0%)	0	0	0

Table 3.2b. Ratio of *B. terrestris* to honey bees and ratio of bumble bees to flower density.

CROPS	Bumble bee: honey bee ratio	Flowers /m^2# at peak flower density mean±SE	n	Mean bees/m^2 over 8 weeks	Bees /m^2* at peak flowering	Bees/10,000 flowers at peak flowering
borage	1:8.59	140±23,	5	0.071	0.02	1.43
kale	1:2.44	42±17,	10	0.089	0.04	2.86
broccoli	1:3.66	212±62,	10	0.064	0.13	6.13
fodder radish	1:2.44	379±52,	10	0.074	0.18	1.95
tick bean	1:1.00	-	-	0.005	-	-
white lupin	1:<1.00	-	-	0.002	-	-

peak flower density of each crop recorded on different days
* bee density recording varied between 10am-4pm

Table 3.3. Percentage of *B. terrestris* (mean±SE) pollen gathering workers (pollen on corbiculae) and nectar gathering workers (no pollen) trapped returning after 1 and 7 hours foraging (November 1986).

Pollen colour	After 1 hour				After 7 hours
	14 Nov.	19 Nov.	20 Nov.	21 Nov.	19 Nov.
brick red	10.2± 6.3	17.9±8.1	3.3±3.3	15.3±6.1	5.1±3.7
yellow	17.9±10.6	9.7±5.7	5.4±3.2	4.6±2.2	2.5±2.5
brown	3.9± 2.8	2.8±2.8	0.5±0.5	4.3±2.7	0.0±0.0
other	0.0± 0.0	2.5±2.5	0.3±0.3	0.0±0.0	0.0±0.0
nectar foragers	68.0±19.3	67.1±13.1	90.5±5.2	70.8±6.4	92.5±6.1
Number of colonies trapped	5	4	6	6	6

trap allowed collection of pollen loads from corbiculae of returning foragers between 7 November and 15 December. Pollen was removed from the trap every 1-5 days and stored in plastic containers at -18 C. Different coloured pollens were sorted from each mixed pollen sample and weighed to determine the percentage of each pollen. To identify species of pollen, each pollen colour (type) was compared with known pollen samples from crops and surrounding floral sources. For microscopic examination,pollen grains were smeared onto microscope slides, several drops of dichloromethane were carefully run over the slide to degrease the grains, then drawn off with absorbent tissue. This treatment removed oil from the pollen coat. The slide was placed on a warming plate at 45 C,and glycerine jelly containing Basic Fuchsin (1%) stain and phenol was melted over the pollen. Pollen grains were viewed under a compound microscope at 400x magnification. Pollen colour was compared with colour charts from Hodges (1974) and pollen grain structure from Hodges (1974), Sawyer (1981), and pollens from anthers of surrounding known species.

The proportions of pollen species returned to cardboard domiciles by bumble bees were determined using 5-6 bumble bee 'traps' introduced on four occasions between 14 and 21 November. To insert each trap, the inside liner of each domicile was removed and replaced by a cardboard box trap (fig. 3.2a,b,c). The trap had an acetate 'window' and a one-way entrance. Returning foragers entered through an external entrance and plastic tube into trapping boxes but could not exit. Traps were set for one or seven hours; the number of returning foragers and type of pollen loads on the corbiculae being recorded as traps were cleared.

Different sized *B. terrestris* workers (n=25) were squeezed to remove any nectar, killed, and weighed to the nearest milligram (electronic Mettler balance AE160). Then the tongue (prementum and glossa) was removed, flattened on the stage of a binocular microscope (Nikon SMZ-1), and viewed through a calibrated eyepiece micrometer at 14x magnification. *B. terrestris* queens (n=9), males (n=10) and honey bee workers (n=10) were also measured. Data were analysed with a one-way ANOVA and treatment means compared with Tukey's test.

One hundred fodder radish flowers, 25 from each of four field plots (52 m^2) were picked on 30 October 1987 and examined under a binocular microscope at 20x magnification. Each flower was examined at the base of the calyx for evidence of perforation by *B. terrestris* workers. The trial was repeated with 100 fodder radish flowers grown inside a wooden 4 x 2 x 1.75m high cage covered in 32% shade cloth (chapter 5) to exclude foragers. In another trial seven *B. terrestris* workers were separately introduced into a wooden box,12 x 8 x 6 cm high,after weighing each bee to the nearest milligram. The box was transferred into the cage, and the trapdoor opened allowing the bees to forage on the crop provided. Workers were observed for one hour

Figure 3.2a. Bumble bee 'trap' (side view).

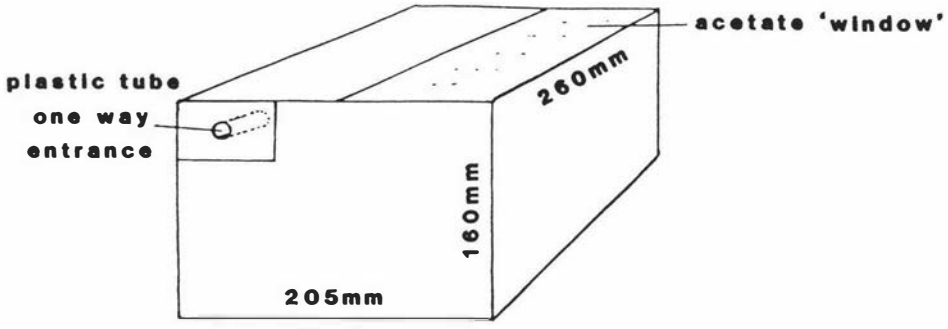


Figure 3.2b. Cardboard domicile with 'Netlon' inner liner containing brood in rearing (starter) box (transverse section).

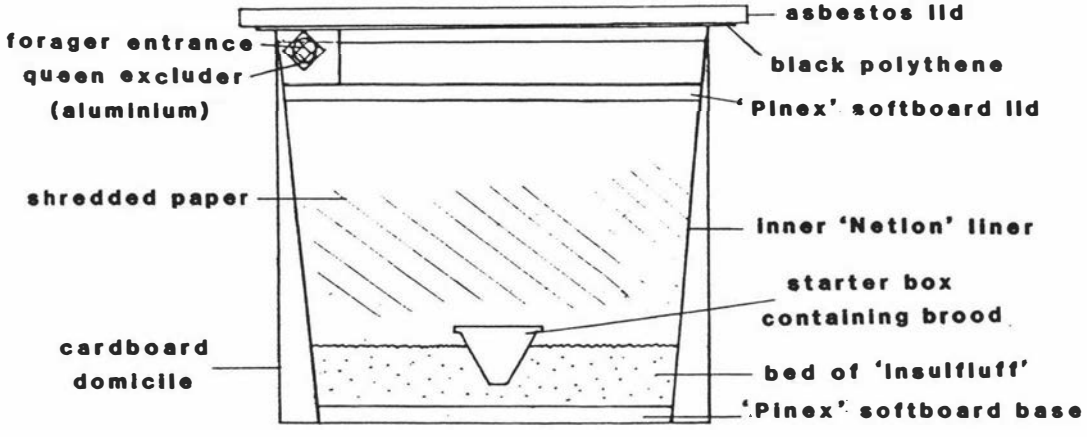
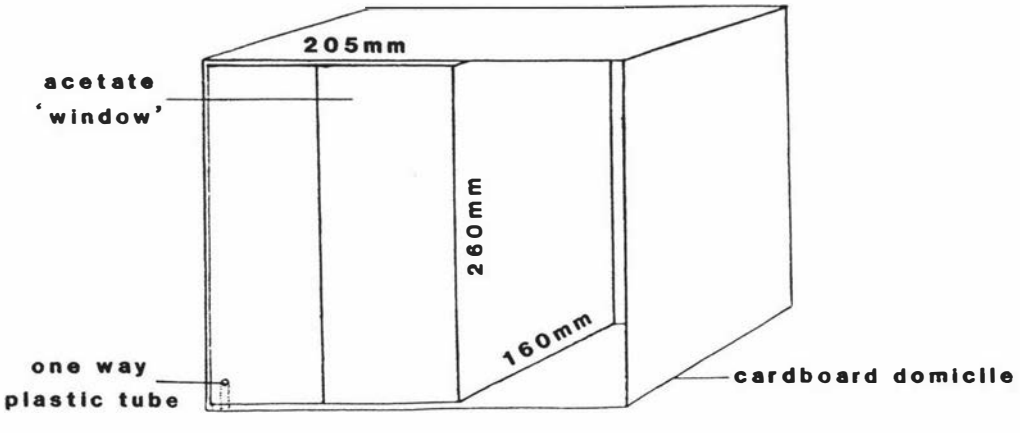


Figure 3.2c. Bumble bee trap inserted inside cardboard domicile with inner liner removed (aerial view).



to determine whether they would forage 'legitimately' or 'rob' the flowers. Flower nectar volume was recorded with a 5µl micropipette.

3.2 Results

Numbers of *B. terrestris* recorded from tick bean and white lupin were very low, but the majority of tick bean corollas had holes bitten in the base. In one plant 27 out of 30 flowers were perforated by queens or workers. *B. terrestris* thus acted as a 'primary robber'. On 22 September, two *B. ruderatus* queens were noted on tick beans at midday. This was the only sighting of long-tongued bumble bees during the trial.

Flowering of broccoli, kale, fodder radish and borage peaked between 10 October and 20 November 1986 (figs. 3.3a and 3.4), while white lupin and tick beans flowered earlier (fig. 3.3b). The total number of *B. terrestris* workers foraging on all six crops (fig. 3.5) increased from 1 October to 4 November then declined. Greater numbers of workers and male emergence coincided with the period of greatest percentage of plants flowering for broccoli, kale, fodder radish and borage.

The percentage of *B. terrestris* foragers on borage bearing pollen (21%) was at least twice that of foragers on other flowers (0-12%)(table 3.2a). Of the workers on borage, 16 had white pollen, four had brick-red pollen and four had yellow pollen. None of these bumble bee pollens was directly identified. No borage pollen was identified from honey bees as borage flowering finished before trapping started. Bees collecting pollen from crucifers yielded yellow pollen loads while from yellow lupin and tree lucerne a brick-red pollen was collected.

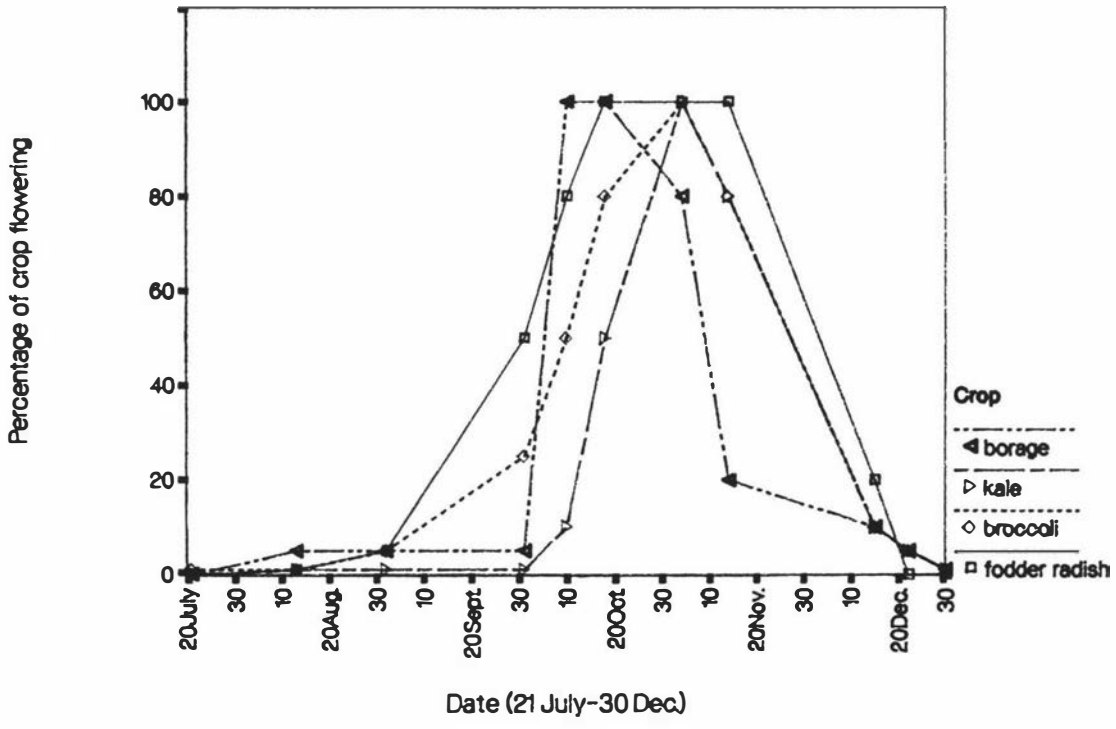
The distribution of workers changed on different crops during the recording period from 20 September to 15 November (fig. 3.6), but this was not directly related to percentage flowering of crops. Kale was, on average, the most attractive crop to *B. terrestris* workers during the eight weeks of observations and the highest worker density of 0.3 bumble bees/m^2 was recorded on kale on 18 October. However, when flower density was considered, broccoli appeared the most attractive (table 3.2b). As peak flower density for each crop occurred on different dates and bee density was recorded at different times, direct comparisons were difficult to interpret. ANOVA of numbers of workers on the four most preferred crops during the period was not significant.

Male *B. terrestris* were most abundant on broccoli (table 3.2a, fig. 3.7), but queen *B. terrestris* were more abundant on kale (table 3.2a, fig. 3.8). ANOVAs of males and queens on the four preferred crops showed no significant differences. Most *B. terrestris* queens were of feral origin whereas workers and males may have originated from feral or indoor rearing. This was because introduced colonies had queen excluders which were removed in mid November.

Figure 3.3. Percentage flowering of 4 crops

(July-December 1986)

(a)



Percentage flowering of 2 crops

(June-November 1986)

(b)

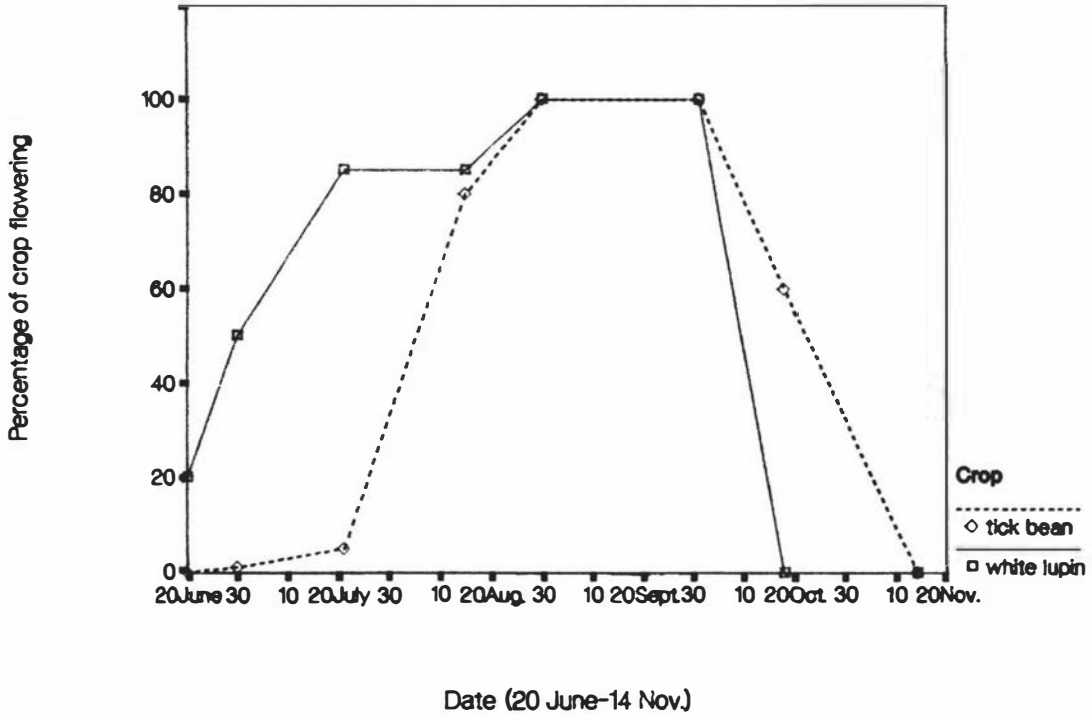
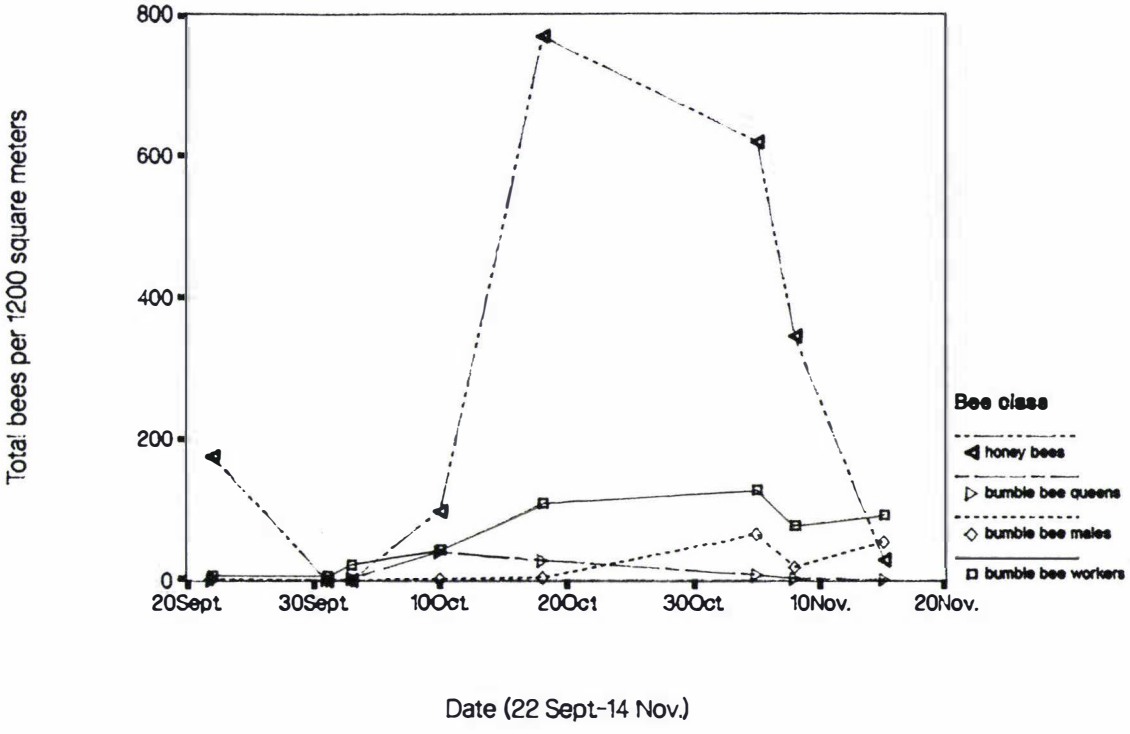


Figure 3.4. Flowering of 4 crops on Keeble farm on 30 October 1986: Foreground: borage (blue), broccoli (patchy yellow), kale (dense yellow), fodder radish (white). Middle: white lupin and tick bean (green) have already finished flowering.

Figure 3.5. Total bees foraging on 6 crops

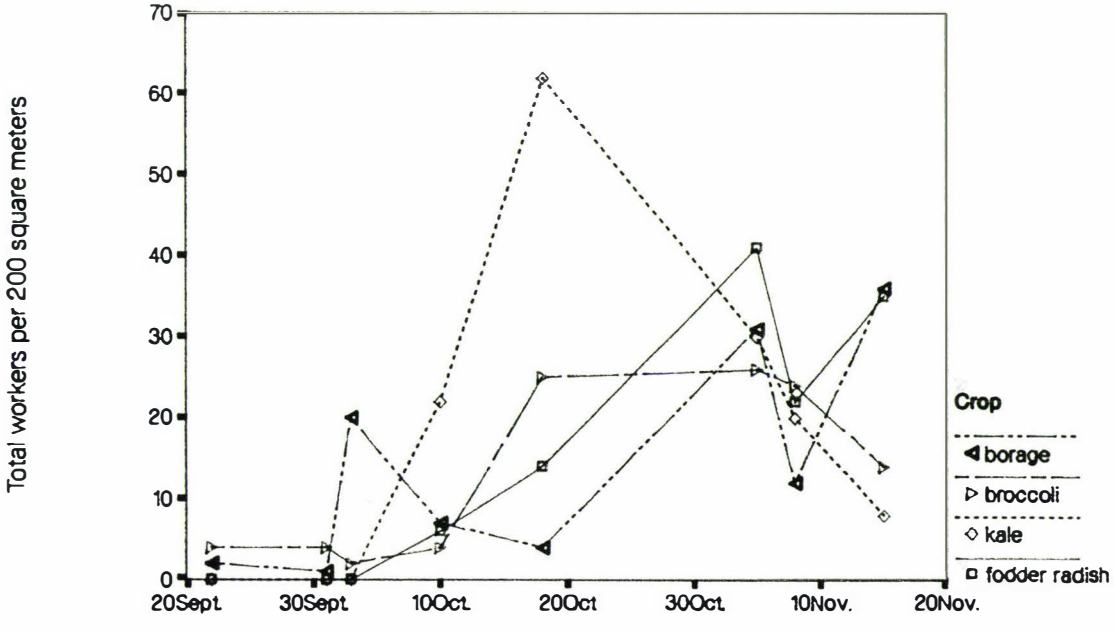
(September-November 1986)



Date (22 Sept-14 Nov.)

Figure 3.6. Bumble bee workers foraging on 4 crops

(September-November 1986)



Date (22 Sept-14 Nov.)

Figure 3.7. Bumble bee males foraging on 4 crops

(October-November 1986)

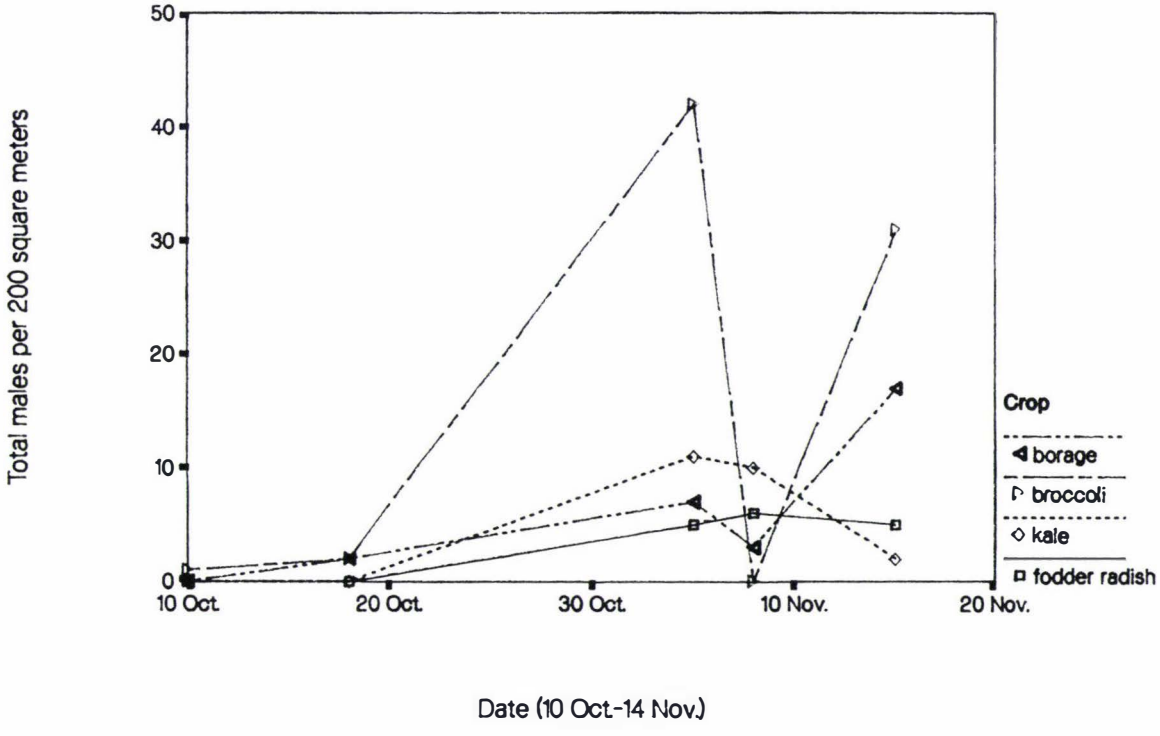
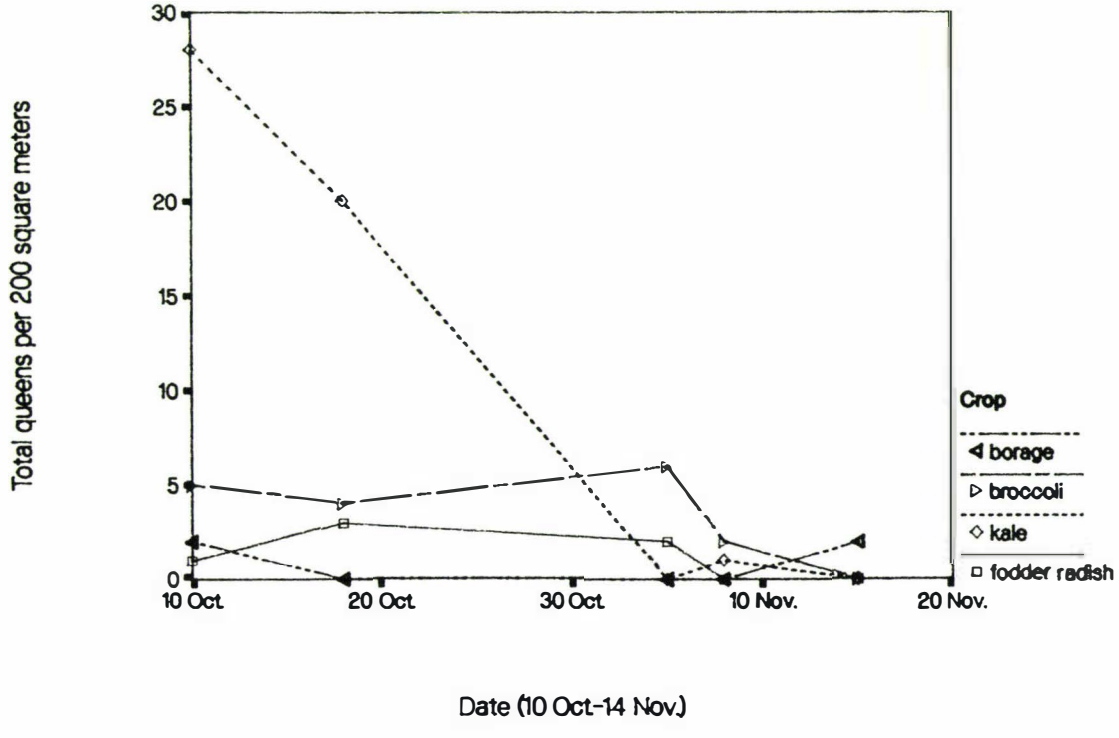


Figure 3.8. Bumble bee queens foraging on 4 crops

(October-November 1986)



The density of honey bees on the four main crops was between 2.4-8.6 times greater than bumble bees (table 3.2b). Honey bees showed a higher relative preference for borage (fig. 3.9), but ANOVA of honey bees on the four most preferred crops over the whole recording period showed no significant differences.

Observations of pollen gathering from kale indicated that, like *B. terrestris* workers, honey bees entered the flower legitimately. However when both species were collecting nectar, they 'robbed' the flower by probing between the polysepalous calyces. Robbing can only occur as the flower ages, and the strongly imbricated sepals relax allowing the protected nectar to be exploited.

On 17 October at 10am, 101 *B. terrestris* workers were noted foraging on borage along the 200m^2 transect. Forty of these workers carried white pollen and 40 had brick-red pollen on their corbiculae. The white pollen may have been borage while brick-red pollen was possibly blue lupin being the only lupin species flowering at that time (tree lucerne had finished flowering). No honey bees were recorded foraging at this time. As other crops were not examined that day this record was not included in the tabulation for crop comparisons. These observations suggest that nectar secretion and/or pollen dehiscence may occur under conditions favourable to *B. terrestris* but is unsuitable for honey bee foraging. The temperature at 10am on 17 October was 14 C with a wind velocity of 0.4 ms^{-1} (westerly).

On the four days bumble bee traps were operated between 14 and 21 November, the majority of workers collected nectar (table 3.3). Pollen collectors foraged mainly on yellow lupin (brick-red pollen) and the three crucifers (yellow pollen). Brown pollen was also collected by honey bees and identified as white clover.

During 30 minutes of observations of yellow lupin along the nearby riverbed, 15 workers and two queen *B. terrestris* were seen collecting pollen, probably attracted to the nectarless flower by the strong scent and colour.

Honey bee workers collected a mean of 71% yellow lupin pollen (table 3.4, fig. 3.10). Yellow pollen from crucifers was the second most favoured (mean 10.9%), while white pollen collected after the borage had finished flowering was probably Californian or Scotch thistle, *Cirsium* spp., and purple pollen was probably Nodding thistle, *Carduus nutans*, but the latter two pollens could not be identified for certain. The amount of pollen harvested per day peaked between 19 and 21 November. This was probably determined by larval demand as daily climatological records indicated no marked changes in weather.

B. terrestris workers foraged independently of wind speed (fig. 3.11), whereas honey bee numbers decreased at wind speeds above 2 ms^{-1} (fig. 3.12). The effect of temperature on foraging was inconclusive for both species.

Figure 3.9. Honey bees foraging on 4 crops

(October-November 1986)

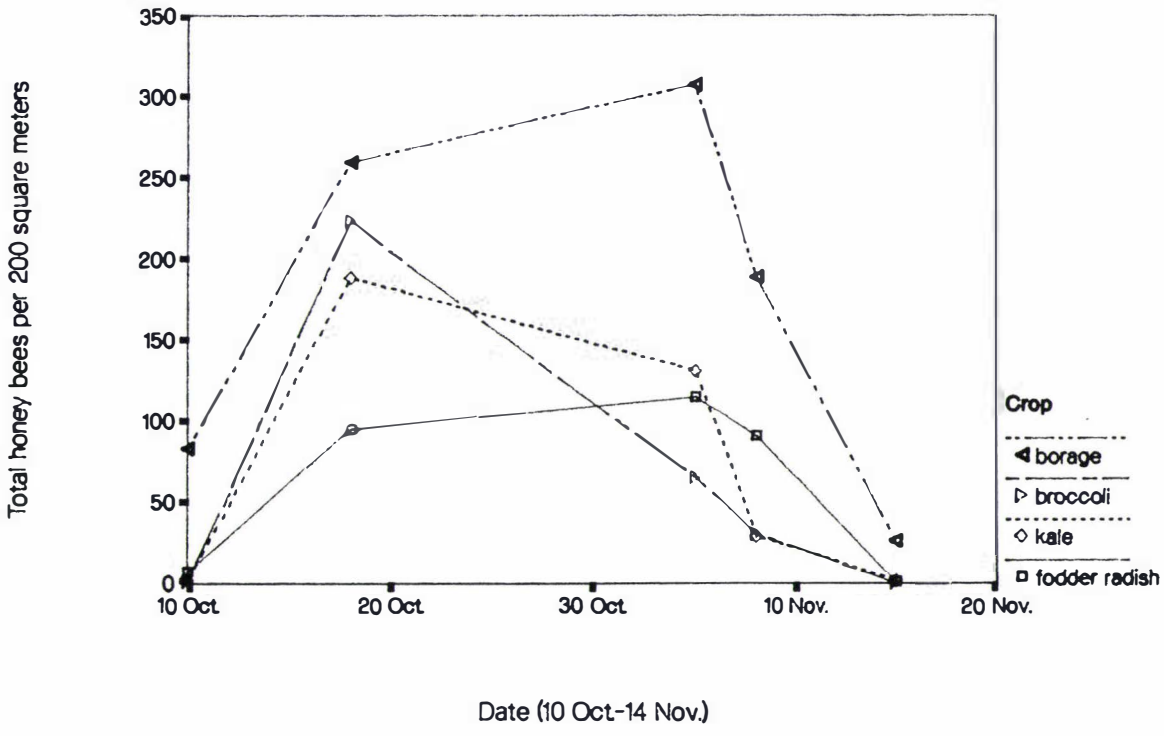


Figure 3.10. Contents of honey bee pollen trap inserted at the base of hive (Nov. - Dec. 1986): Brick red pollen isyellowlupin. Yellow pollen originated from crucifers. Brown pollen is white clover. Pollen was collected over 2-3 day periods.

Table 3.4. Percentages of different coloured pollens collected from honey bee pollen trap on Keeble farm (November-December 1986).

Date Nov/Dec	Duration* days	Pollen colour: brick red	yellow	brown	white	other	Fresh weight of pollen collected: total(g)	per 24 hours(g)
Nov7-9	2	63.7	27.3	9.0	trace	-	36.2	17.0
14-16	2	85.2	6.7	8.1	trace	purple	87.8	39.0
16-17	1	90.9	5.5	3.6	trace	purple	31.0	37.2
17-19	2	82.7	7.9	8.8	0.6	purple	92.5	48.3
19-20	1	80.5	13.3	6.0	0.2	purple	71.8	59.4
20-21	1	85.0	8.8	5.7	0.5	purple	64.2	64.2
24-27	3	60.2	12.2	10.6	17.0	purple	17.2	5.7
27-31	4	60.4	9.5	22.8	7.3	purple	125.0	31.2
31-5Dec	5	57.9	8.9	32.4	0.8	purple	133.3	26.7
12-15	3	43.9	8.4	25.7lb 22.0db	-	-	92.0	33.0

lb=light brown db=dark brown *=traps cleared at different times of day.

Figure 3.11.

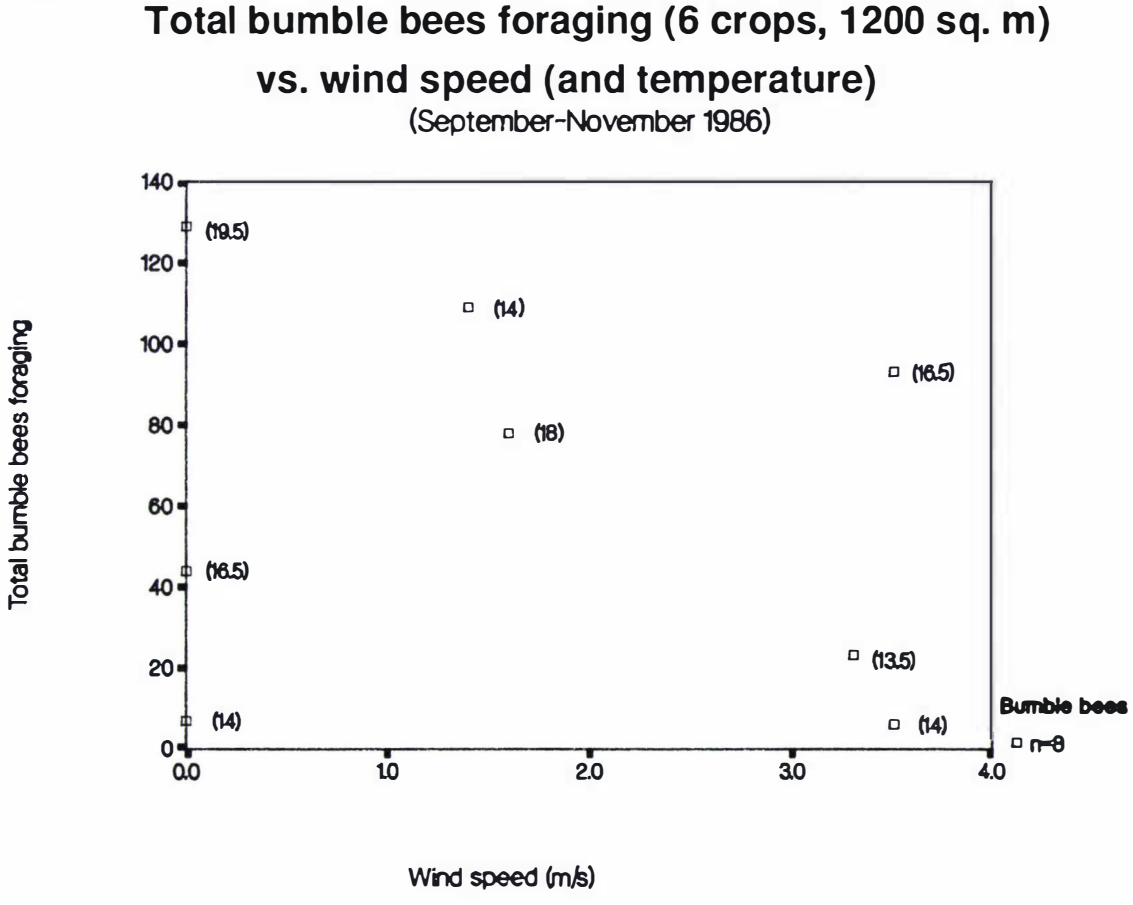
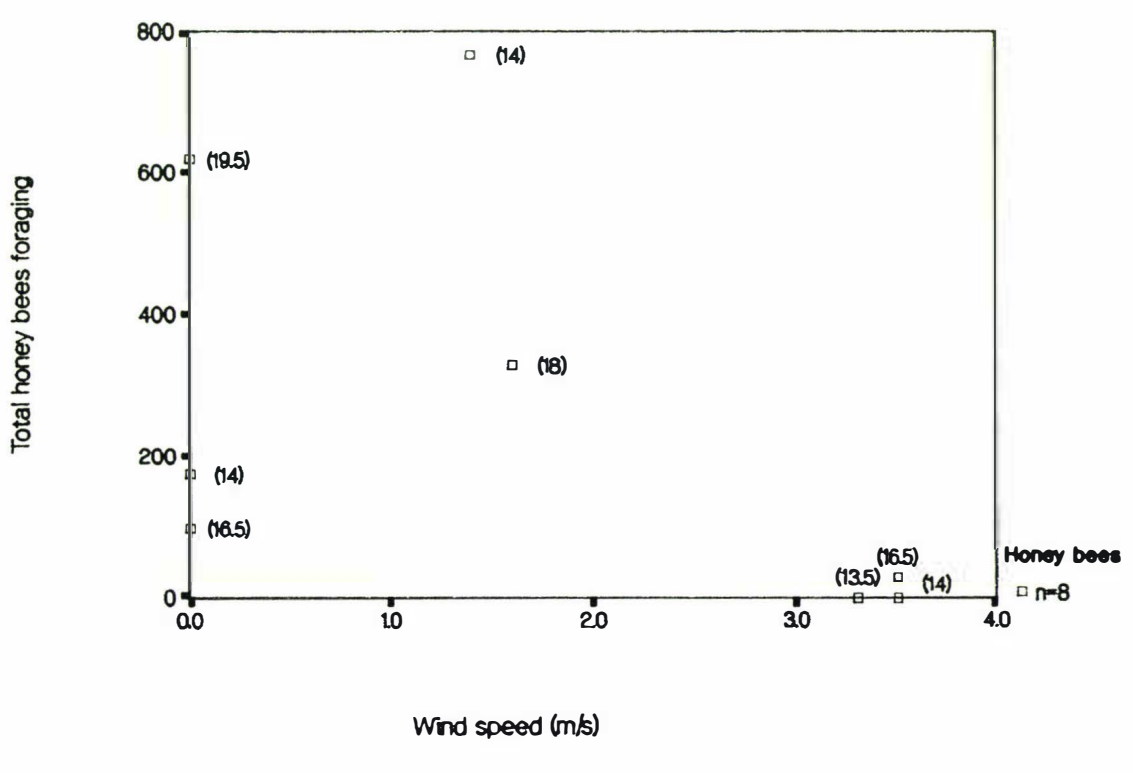


Figure 3.12.



Mean tongue length (prementum and glossa) of honey bees and *B. terrestris* workers was equal, (fig. 3.13). However, greater variation in tongue length in bumble bee workers, would enable nectar collection from a wider range of flower corolla depths . Males had longer tongues (6.9mm) than workers and shorter tongues than queens (11.2mm), (one-way ANOVA; F_S=59.14; df=3;53; p<0.001). Honey bee tongues were not significantly different from male bumble bees. Tongue length was correlated with body weight for all bumble and honey.bees taken together with a high regression coefficient (r = 0.95, fig. 3.14); this was a logarithmic relationship.

B. terrestris workers chewed holes at the base of the calyx of exposed fodder radish flowers where the calyces had not yet split. Holes were bitten with mandibles, then nectar was 'robbed' by probing with the proboscis.

Of the 100 flowers examined from field plots, 67 were chewed at the base of the calyx. Black thrips were recorded on the flowers, but their piercing mouthparts would not have caused such large holes in the calyx. The 100 flowers examined from the cage trial all lacked holes.

On 19 November at 18.5 C, only two out of seven workers began foraging in the cage trial. One worker visited 28 flowers legitimately. The second worker visited 45 flowers legitimately, 'robbed' one flower by probing between the base of the separating calyx, and bit holes in another two flowers at the base of the calyx before probing for nectar. The two bees had a mean flower handling time of 16.1 seconds but made a mean weight loss of -15mg. The mean nectar volume per flower was 0.03µl.

3.3 Discussion

Statistical comparisons between bee numbers on the four most visited crops were not significant. If kale had shown higher numbers, it would, in any case, have been difficult to draw any conclusions as to preference because of the different crop areas.

Kale, broccoli, fodder radish, and borage flowered during the flower dearth period (September to November), and these crops flowered for at least 6-8 weeks. Kale had the longest pre-reproductive period (time from sowing to flowering). Flower density for these four crops was in the order: fodder radish> broccoli > borage > kale. In an attempt to reduce cost of establishment (borage was imported from Holland), lower sowing rates of borage could be tried to see if any loss in flower density occurred. Little was known about borage cultivation; while broccoli was sensitive to many herbicides. White lupin and tick bean flowered too early for *B. terrestris* with only sparse flowering.

Competition from honey bees was high (as expected), especially on borage. Low numbers of long-tongued species suggested the crops were not suitable for these species.

Figure 3.13. Tongue length for honey bee and B. terrestris

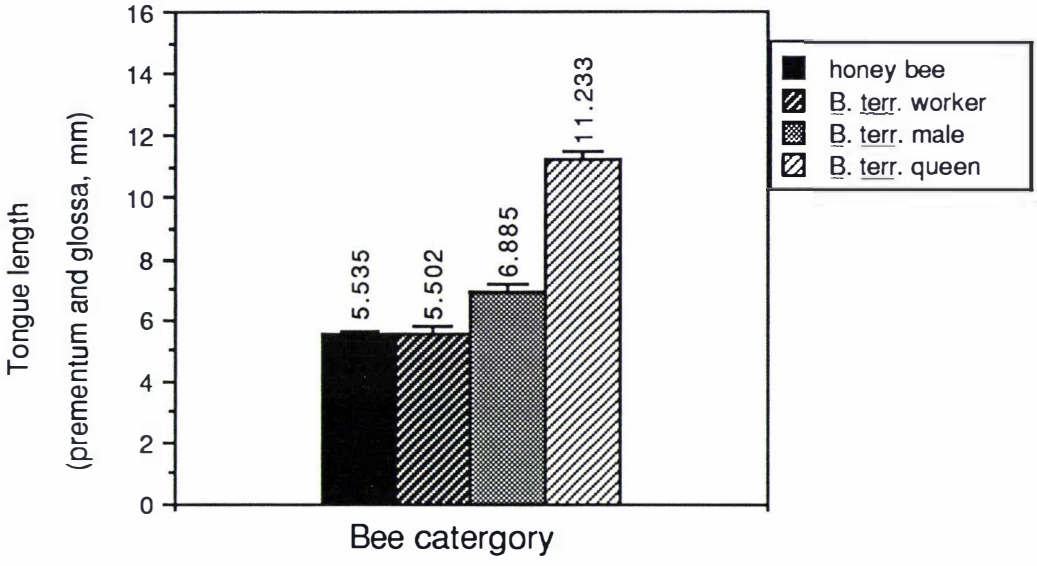
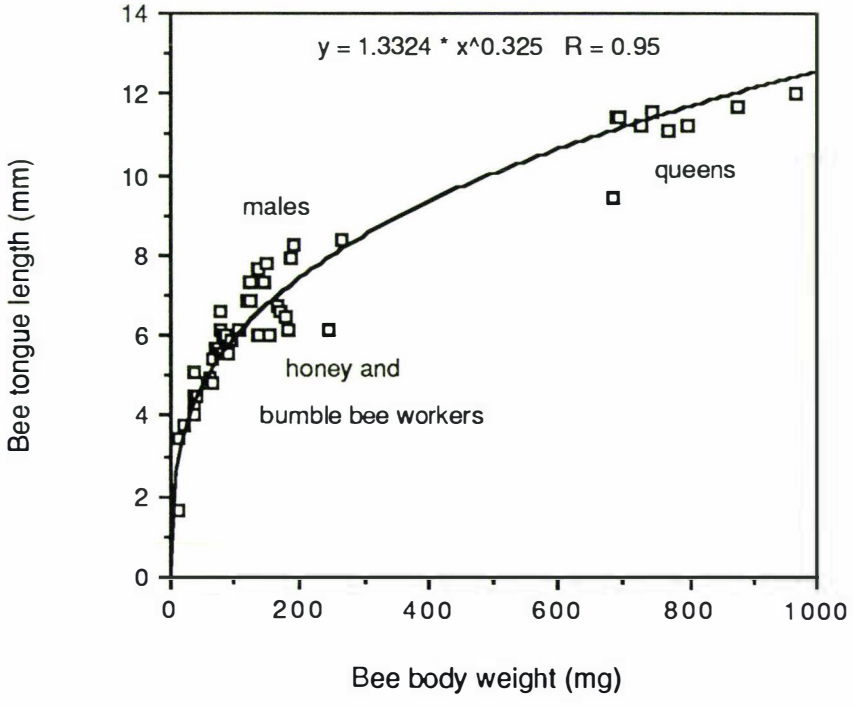


Figure 3.14. Bee tongue length vs. body weight

(B. terrestris workers, males, queens; honey bees)



Feral colonies possibly were also placed under constraint by the large introduced population.

Numbers of workers and queens were highest on kale indicating that corolla depth was not a deterrent to exploitation of nectar by workers with slightly shorter tongues than queens. This exploitation would be dependent on flower age, and hence the time when polysepalous calyces split allowing nectar 'robbing'.

Counting of bees posed certain difficulties. Transects damaged crops, and counts were probably less accurate in tall crops such as kale. Free (1970a) used the same method but recognised that foragers tended to decrease from edge to centre of the crop. Thus, counts at the edge may not give a true indication of bee populations as a whole. Data so obtained are however suitable for comparative studies. Rather than demarcating small zones randomly throughout large areas of crop, randomly arranging small plots of different crops over a given area was considered easier for recording. This was implemented during 1987.

High worker numbers recorded on borage on 17 October suggested more detailed diurnal evaluation of foraging behaviour, together with evaluation of weather conditions and food availability was necessary. Flower density assessment was time consuming, and a more appropriate method using flower stems, flowers/stem and flower production was developed. Flower density required recording every 1-2 weeks.

A method of differentiating between feral and laboratory reared bees was deemed necessary to assess intraspecific competition (see chapter 5).

Pollen trapping from *B. terrestris* workers is difficult to perform because of variation in body size and the ability of workers to tuck corbiculae behind their swollen abdomen to squeeze through holes without losing pollen loads (Pomeroy pers. comm.). A more suitable trapping system to that of figure 3.2 was developed allowing workers to exit but restraining them on re-entry. This allowed pollen assessment with samples easily removed for microscopic examination.

Pollen trapping removes between 20-40% of mixed pollen from incoming honey bee foragers' corbiculae according to Clinch (1981). However Goodwin (1987) found the percentage changed diurnally from 0.75-25% in kiwifruit orchards. This system does not determine percentage of nectar gatherers returning to the hive.

Coincidence of male emergence with peak flower abundance was recorded by Bowers (1986) working with *B. flavifrons* in subalpine meadows in Utah. Bowers found the occurrence of sexuals (males and queens) in meadows was correlated with forager and flower abundance; males and queens appeared earlier in meadows with a high forager and flower density. To determine if a similar relationship exists between *B. terrestris* male emergence and flower abundance, further investigation is necessary.

White lupin was not a favoured food source. However a succession of lupin species could provide an almost continuous 'secondary' pollen source to complement more preferred 'primary' bee forage. Growing the following lupins in sequence would provide such an alternative: white lupin > blue lupin > yellow lupin = Russell lupin, *L. polyphyllus*.

Maintenance of the corolla tube of fodder radish for 2-3 days (chapter 4) theoretically provides a barrier to nectar exploitation by bees other than *B. terrestris* queens and long-tongued species, with a proboscis of the appropriate length. However, as observed in the field and in cages, *B. terrestris* workers with tongues too short to reach the nectar successfully bit holes in the base of the calyx with mandibles and proceeded to extract nectar with their proboscis through these perforations. While this 'robbing' behaviour has been recorded for *B. terrestris* on red clover (Gurr 1955) and tick bean (Newton and Hill 1983), this behaviour has not previously been recorded on fodder radish. Honey bees were observed removing nectar through holes perforated by *B. terrestris* (secondary 'robbing'), but honey bees did not bite holes in the calyx of fodder radish flowers (primary 'robbing'). Both honey and bumble bee workers could also 'rob' nectar from a few fodder radish flowers that separated at the base of the calyx after 1-2 days or from flowers where the calyx had fully separated after 2-3 days. Honey bees were therefore, partly excluded from nectar removal from fodder radish. 'Robbing' by *B. terrestris* workers is adaptively beneficial because: a) it provides a method of obtaining nectar from flowers initially unexploitable, and b) it improves handling efficiency of nectar gatherers on these flowers by avoiding anthers and minimising the time required for grooming pollen from the body.

3.4 Summary

1) Kale, fodder radish, broccoli and borage were identified as potential *B . terrestris* fodder crops based on flowering time, duration, density and morphology.
2) Honey bee numbers were 2.4- 8.6 times higher than *B. terrestris* on the four preferred crops with the highest honey bee density on borage.
3) Data suggested *B. terrestris* collected pollen from borage early in the day before honey bee numbers increased. *B. terrestris* also foraged on windier days (>2.0ms^{-1}) than honey bees.
4) Tongue length of honey bees and *B. terrestris* workers was similar, with queens having significantly longer tongues. Tongue length was related to body weight.
5) *B. terrestris* workers robbed nectar from fodder radish by biting holes at the base of the calyx because workers were unable to reach the nectar legitimately.

CHAPTER 4

CHARACTERISTICS OF FOUR FLOWERING CROPS

4.0 Introduction

Floral attractants entice the bee to the flower (Kevan and Baker 1983) where 'rewards' are harvested and pollination of the flower is effected. Faegri and van der Pijl (1979) introduced the rather confusing terms of primary and secondary attractants. The terms floral attractants (e.g. flower colour, scent and structure) and floral rewards (e.g. pollen and nectar) seem more appropriate.

Bumble bee flower choice is influenced by a complex of factors including availability of nectar and pollen, flower shape and colour and inflorescence size (Brian 1954). A correlation exists between tongue (proboscis) length or head shape of bumble bees and the corolla tube length of flowers visited (Brian 1957; Hobbs *et al.* 1961; Teras 1976). However, factors such as nectar secretion and synchronisation of bloom period with the bee's life cycle may be more important influences on the composition of bumble bees on each flowering plant than tongue length (Macfarlane 1974). Floral preference is influenced by flower abundance, flower structure, nectar sugar composition (Teras 1985), and concentration of sugar and volume of nectar secreted. Although factors such as flowering time in the season, competition from other pollinators (Teras 1985) and proximity of colonies to flowers (Webb 1961) may influence the distribution of bumble bees on crops. Factors affecting nectar secretion (e.g. temperature, humidity, soil moisture, wind and vigour of plants) may determine the degree of attractiveness of each flowering species to potential pollinating bees (Howes 1948; Percival 1961). Temperature and humidity may also influence sugar concentration and pollen availability (Percival 1965).

Pollen harvesting by bumble bee workers depends on pollen availability from flowers (Webb 1961). This is limited by either flower opening or anther dehiscence. Whichever process occurs last is the limiting factor (Synge 1947). If a flower normally releases pollen in the morning during fine weather, anther dehiscence may occur at a different time of day during poor weather (Prys-Jones and Corbet 1987).

Nectar secretion and anther dehiscence are normally controlled by an intrinsic diurnal rhythm (Percival 1961). Hence foraging behaviour of bees may not necessarily be due to meteorological conditions but indirectly due to food availability (Goodwin 1987).

Field preference of forage crops by *B. terrestris* in 1986 indicated the following crops had potential as bee fodder: fodder radish, kale, broccoli and borage. Field trials during

1986 indicated that kale cv. Maris Kestrel was a suitable crop worthy of further testing, but the seed supplied and sowed in 1987 turned out to be swede and so the trial had to be with swede. Hence a more detailed evaluation considering criteria 5-11 (chapter 3) was implemented in the 1987 season with swede replacing kale.

The aim of this chapter was to evaluate characteristics (criteria 5, 6, 9 and 10 in chapt. 3) of four bee forage crops grown as food for *B. terrestris*, which may be attractive to foragers for use in colony development.

4.1 Flower structure

The aim was to measure corolla depth and stage of calyx and corolla separation, which could aid or hinder nectar removal by *B. terrestris*.

4.1.1 Methods

Corolla tube depth (nectary to top of fused petals) was measured by inserting a micropipette into the flower and marking the distance on the pipette. Twenty flowers from each of the four forage crops were examined and mean values calculated. Data were analysed with one-way ANOVA, using Tukey's test for treatment mean comparisons.

To determine at what stage the calyx and corolla separated during anthesis ten flowers were randomly tagged on 22 February 1988 from each of the four crops grown in small 4 x 2m plots. The calyx and corolla were examined at midday for three days after the flowers opened to determine when separation occurred.

4.1.2 Results

Corolla depths of the four species examined were significantly different (F_S=961.18; df=3; $p<0.001$), with borage having the shortest corolla (2mm), (fig.4.1). Broccoli and swede corollas were the same length (5.5-6.0mm) and shorter than fodder radish (9.9mm)

The calyx and corolla of borage, broccoli and swede split open completely on the first day; while for fodder radish, the calyx in some flowers took 2-3 days to split. In some cases the calyx of fodder radish split at the base first then later (1-2 days) split completely (table 4.1).

4.2 Flower density and flower production

The aim of this section was to determine flower density and production of the four crops throughout the season.

Figure 4.1. Flower corolla depth of 4 crops

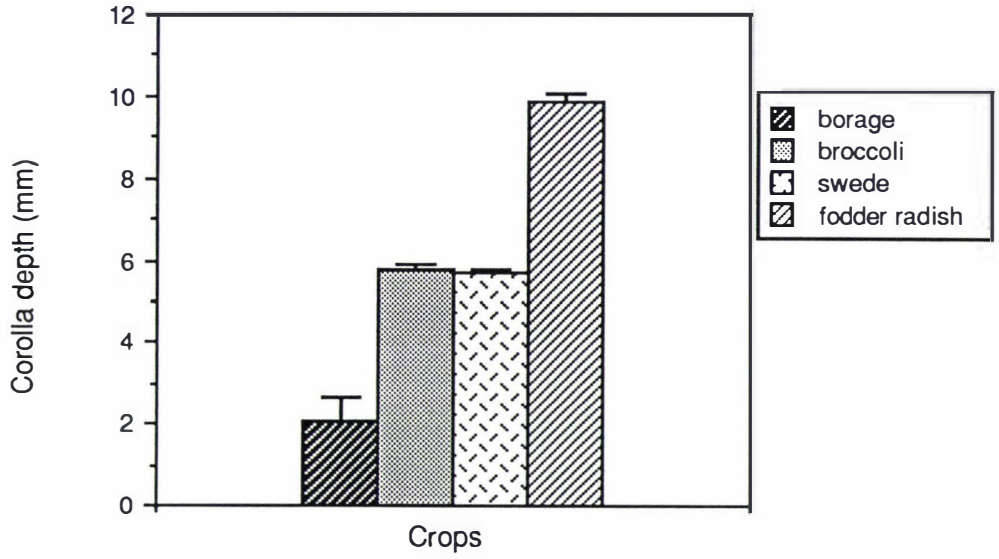


Figure 4.2. Layout of the 4x4 Latin square plot design for the 1987 field trial: Four plots of each of the 4 crops were grown adjacent to Sheepfarm Road near Massey University. A caravan for rearing bumble bees and 4 foraging cages were also sited near the crops.

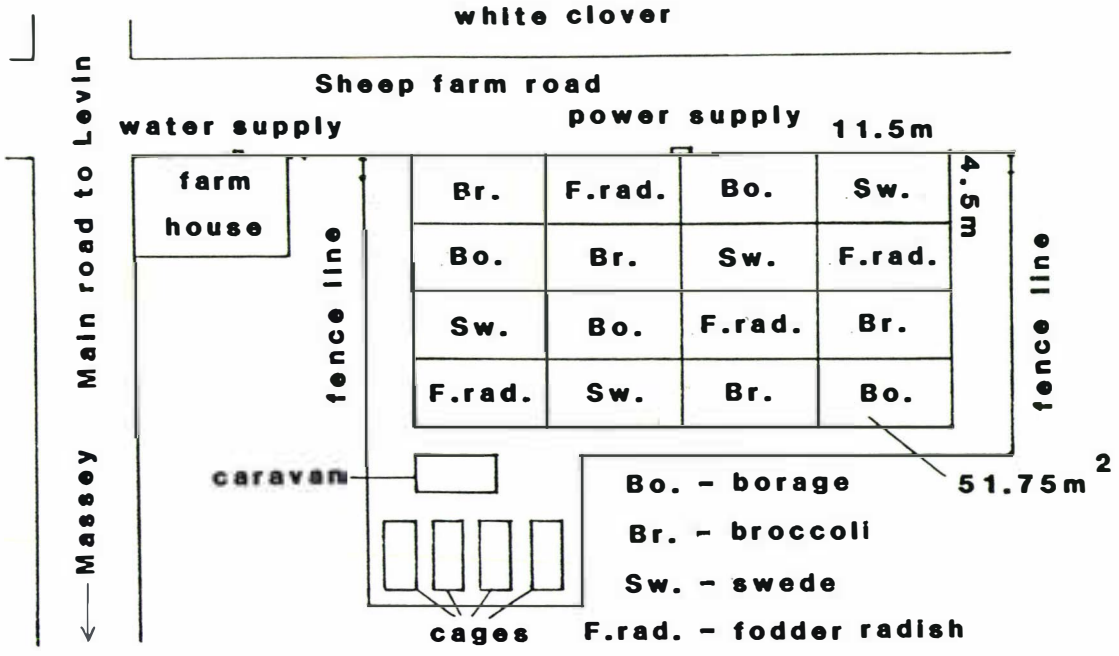


Table 4.1. Time of splitting of calyx on 4 crops (22-24 February 1988)

Percentage of 10 flowers with split calyces				
Day	F. radish[#]	Swede	Broccoli	Borage
1	44	100	100	100
2	78	-	-	-
3	100	-	-	-

[#]=calyces split either at base or completely split

Table 4.2. Sowing rates, area, amount and cost of seed required for 1987 field trial. Crops were sown on 30 March 1987.

Crops sown	Borage	F.radish	Swede	Broccoli
Sowing rate (kg/ha)	20	10	5	5
Total area sown (m^2)	207	207	207	207
Area of plots (m^2)	51.75	51.75	51.75	51.75
Total seed required (g)	414	207	104	104
Seed/plot (g)	104	52	26	26
Cost of seed/100g (1987)	$18.33	$0.33	$0.76	$14.69

Table 4.3. Percentage flowers open from 4 crops at different times on morning of 19 November 1987.

Normal time		5.00am	6.00	7.00	8.00	9.00	10.00
Daylight saving time		6.00am	7.00	8.00	9.00	10.00	11.00
Percentage of total flowers open	[#]Fodder radish	39	67	100	100	100	100
	[#]Swede	94	100	100	100	100	100
	[*]Broccoli	15	40	80	90	95	100
	[*]Borage	95	100	100	100	100	100
Temperature (C)		7.5	12.5	12.0	14.5	14.0	15.5
Light ($\mu Em^{-2}s^{-1}$) [&]		58	570	830	1320	1650	1900
Wind speed (ms^{-1})		2.6	0.6	3.3	3.9	2.5	2.7
Relative humidity		86	80	77	70	66	65

[#]=total of nine flowers
[*]=total of ten flowers
[&]=sunrise approx. 5am(normal time)

closed=stamens enclosed by petals(0%)
half open=some stamens visible (5%)
fully open=all stamens visible (10%)

4.2.1 Methods

Crop preparation

Equal areas of four crops broccoli, swede, fodder radish cv. Neris and borage were established on 1.3ha of land, 1km southwest of Massey University (table 4.2). Site preparation consisted of grazing, followed by herbicide (glyphosate and dicamba on 11 March 1987), ploughing and sowing (cone seeder, rows 15cm apart, to a depth of 15mm) on 30 March 1987. The land was surrounded, in a 1km radius, by ryegrass, *Lolium perenne*, white clover, tree lucerne, barberry, *Berberis vulgaris*, and bedding plants from the nearby farmhouse . This ensured bumble bees foraged mostly on the crops provided at least until white clover first flowered in late October. The closest honey bee hives were about 1.0km from trial site. The site was exposed to strong westerly and easterly winds with little shelter.

The crops were sown in a 4 x 4 Latin square (fig. 4.2 and 4.3) to avoid plots of the same species occurring adjacent to one another, which may have influenced the bees' floral preference.

Flower density

Flower density was monitored fortnightly from 10 September to 23 November. Five random co-ordinates for each 4.5 x 11.5m (51.75m^2) plot were chosen from a computer generated list. A 1m^2 quadrat was lowered over the crop at each co-ordinate point. The number of plants/m^2, stems/plant and flowers/stem were recorded. An assessment of the square meters of flowers/plot took into account bare patches of ground with non-uniform crop cover. Hence density and production were recorded in flowers/plot rather than flowers/m^2. Flower density was calculated as follows:

Flowers/stem x stems/plant x plants/m^2 x m^2 of flowers/plot

Flower production was determined fortnightly from ten tagged stems/plot. Two random co-ordinates were selected per plot. At each point two stakes were positioned and the nearest plant to each stake was tagged on five stems at the most recently opened flower. The plants were examined again after seven days and the number of newly opened flowers with anthers visible beyond each tag were recorded. Flower production was calculated as follows;

Newly opened flowers/stem/week x stems/plant x plants/m^2 x m^2 of flowers/plot /day

Figure 4.3. Field plots, caravan and foraging cages for 1987 field trial: Foreground: flowering borage and swede behind, caravan for rearing bees, field cages. Background: Massey University.

Mean flower density and flower production/crop was determined for each two week interval.

4.2.2 Results

Borage began flowering on 20 August, broccoli and fodder radish on 1 September and swede on 12 October. Broccoli had the highest flower density (591/m^2) during the first two weeks with borage second (406/m^2) and fodder radish third (290/m^2) (fig. 4.4 a,c,d). Broccoli declined in flower density with less than 39 flowers/m^2 after week six. Borage had between 309-425 flowers/m^2 until week six then also declined to below 39 flowers/m^2 Flower density of fodder radish peaked at 1894 flowers/m^2 during weeks 5-6, then declined rapidly. Swede had a short burst of flowering during weeks 7-10 peaking at 560 flowers/m^2 during weeks 7-8 (fig. 4.4b).

Production of new flowers/day followed a similar trend to flower density (fig. 4.5a-d). Broccoli had the highest initial flower production during weeks 1-2 (60/m^2/day), peaking at 184 new flowers/m^2/day during weeks 3-4. Fodder radish increased to 734/m^2/day during weeks 5-6, followed by swede peaking at 340/m^2/day during weeks 7-8. Borage had 39-50 flowers/m^2/day during weeks 1-6. Flower production declined significantly in all crops four weeks after reaching a peak, to below 58 flowers/m^2/day.

4.3 Nectar and pollen availability

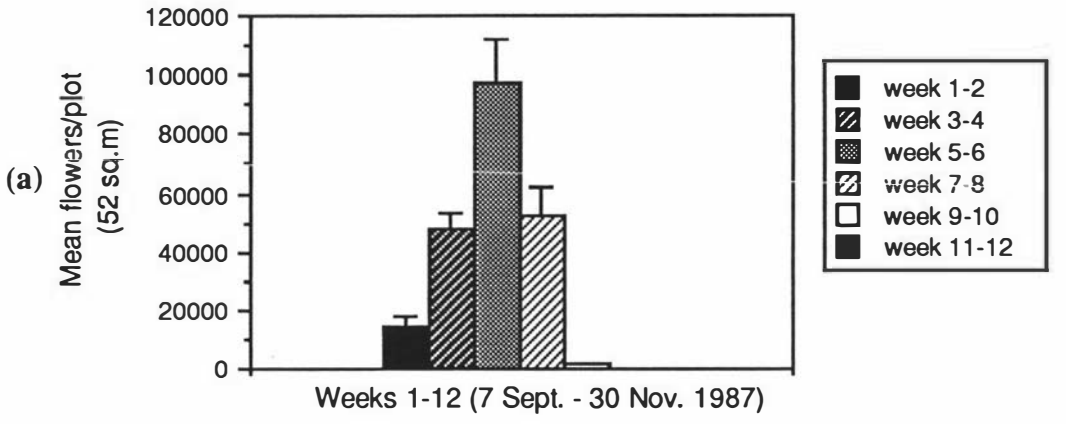
The aim of this section was to determine the flower pollen content of each crop, the timing of first flower opening and the longevity of individual flowers. The diurnal change in food availability (energy from nectar secretion and pollen from anther dehiscence) during each recording day for each of four crop species, from bagged and exposed flowers was also determined.

4.3.1 Methods

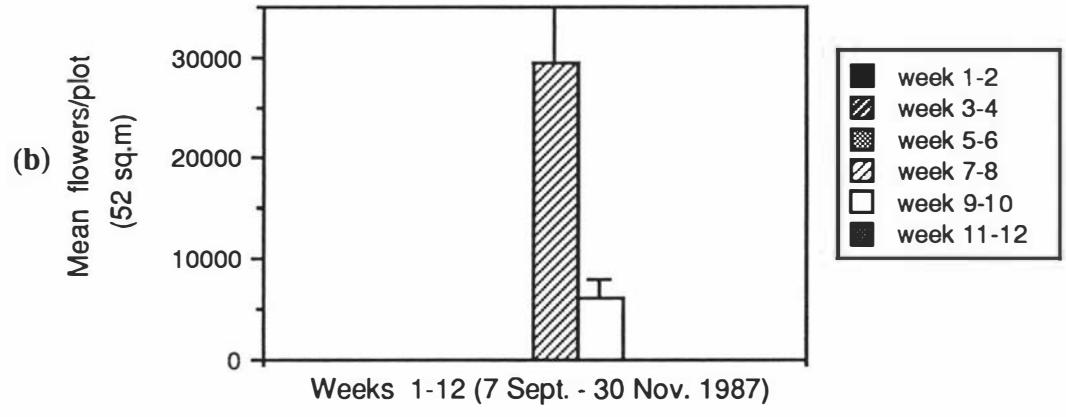
Flower pollen content

Determination of pollen grains/flower from each crop was necessary to evaluate the total potential pollen available to bees for collection. Undehisced anthers were removed from young unopened flowers. The anthers were held at 60 C for 24 hours to initiate anther dehiscence. The pollen was suspended in 4ml of water; ten samples were pipetted off and a few drops of suspension placed on a haemocytometer and viewed at 400x magnification. The grains were left to settle and the number of grains in ten squares was determined. The average for the ten samples was calculated. This was repeated for ten

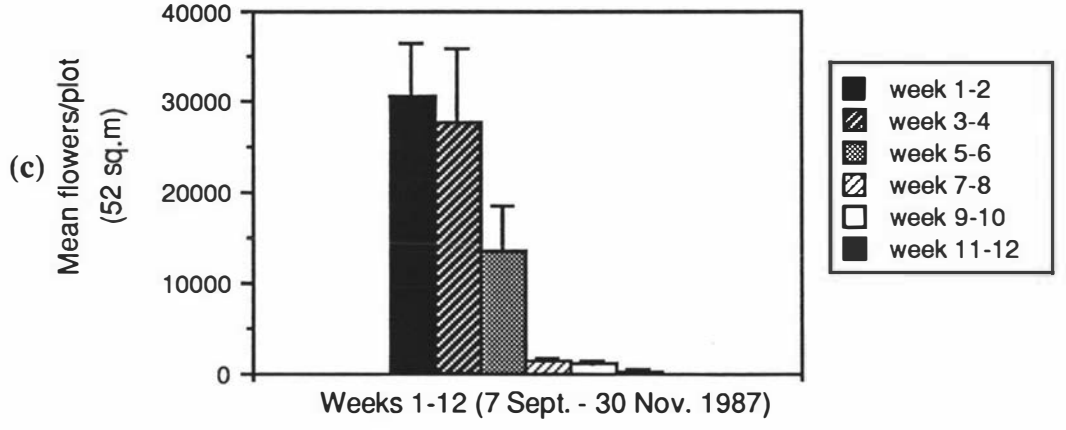
Figure 4.4. Flower density for fodder radish over 12 weeks



Flower density for swede over 12 weeks



Flower density for broccoli over 12 weeks



Flower density for borage over 12 weeks

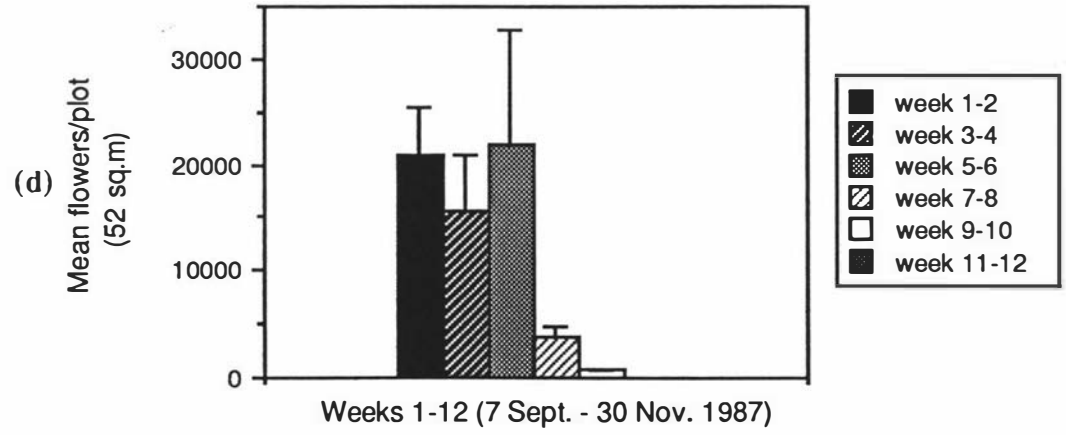
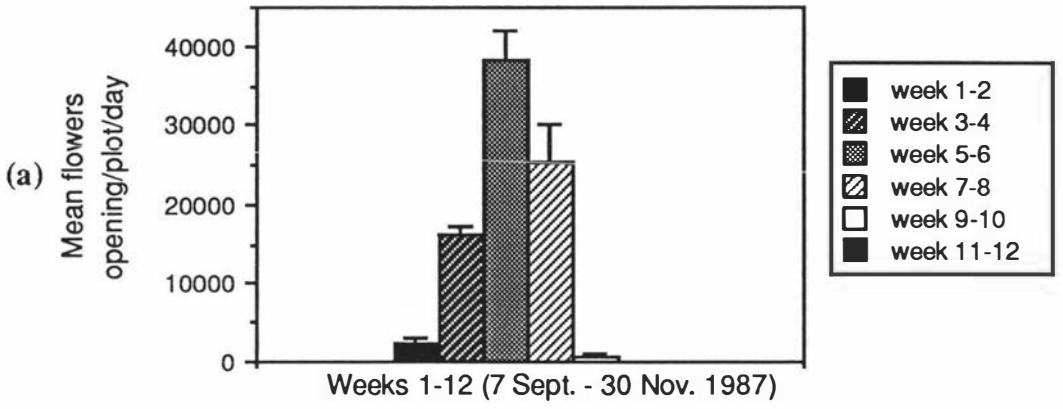
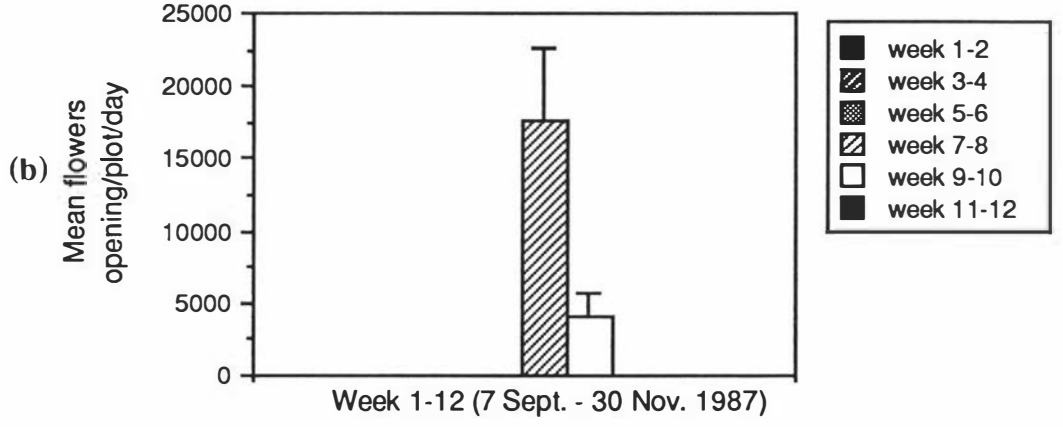


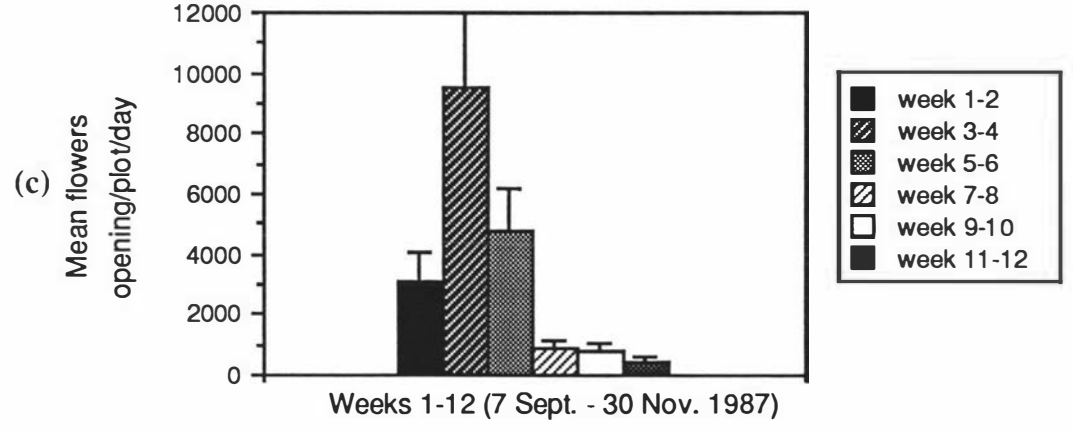
Figure 4.5. Flower production for f. radish over 12 weeks



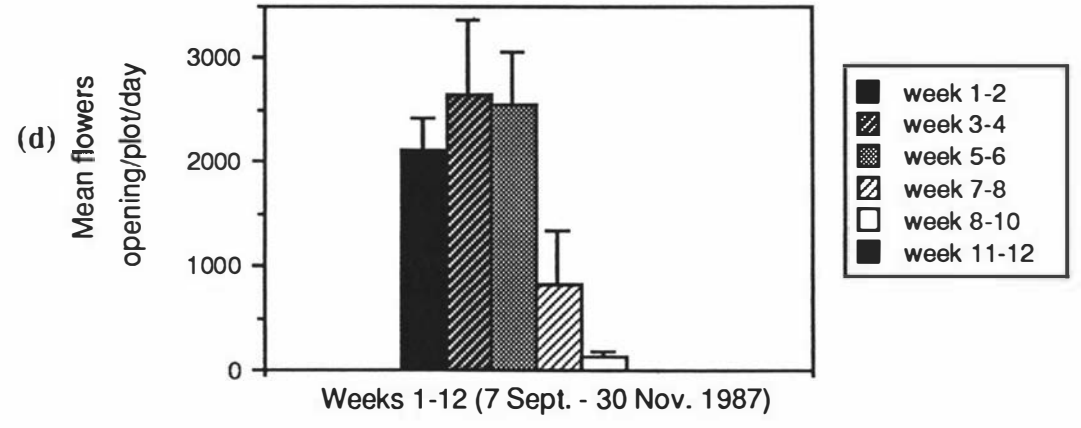
Flower production for swede over 12 weeks



Flower production for broccoli over 12 weeks



Flower production for borage over 12 weeks



flowers of each species. The mean number of grains/ml and grains/flower were calculated. Data were transformed (square root) and analysed with a one-way ANOVA with treatment means compared using Tukey's test.

The mean grains/flower was compared with the pollen grain count from ten pollen loads of various sizes (2-22mg) from bees captured foraging on borage and crucifers. The pollen load was removed, weighed, suspended in 10-20ml of water and ten samples removed and counted as above. Wet weight to dry weight conversions for pollen loads were calculated by placing five crucifer and five borage pollen loads at 60 C for 24 hours and recording weight loss (Mettler balance, 0.01mg). From the average grains/mg of pollen from pollen loads and grains/flower/species from flower anthers, the average milligrams of pollen/flower/species was calculated. Data were transformed and analysed with Student's t test and one-way ANOVA.

Diurnal change in food availability

To determine more specifically the diurnal timing of first flower opening for each crop, ten flowers/species from randomly chosen plots and plants were individually tagged. These flowers were unopened when tagged in the evening but were expected to open the following day. Each flower was examined hourly from 6am to 12noon on 19 November and recorded as closed, partially open (some anthers visible) or fully open (all anthers visible). Temperature, light intensity, wind speed and relative humidity were recorded each hour (see 4.4.1).

To determine the longevity of individual flowers, two trials were run beginning 21 September and 5 November. One bee exclusion bag was randomly positioned in one of four plots for each species (swede was not flowering during first trial). Ten flowers were individually numbered on plants inside each bag, with another ten flowers exposed to foraging being tagged within a 1m radius of each bag. Only flower buds on the verge of opening were tagged. Each of the ten exposed and bagged flowers for each species were monitored daily at midday for pollen availability, nectar volume and sugar concentration (see below).

Nectar and pollen availability were recorded for each of the four crops from 8am to 6pm on each Tuesday and Saturday from 8 September to 21 November. Bee exclusion bags were constructed from 32% green shade cloth (Donaghy's Ltd.) of dimensions 1.5 x 1.0m. On each sampling day, two points were randomly selected in each of two randomly selected plots for each crop. At each point a bag was placed over 1-2 flowering plants, supported by two, 1.5m bamboo stakes and secured to the ground with two metal pegs. The bags were positioned between 5-6pm the night before recording. Between 8-10am, 12-2pm and 4-6pm all bags were temporarily removed and ten flowers from plants from each bag were picked and sampled for pollen and nectar (20/species). Bags were then replaced until the next recording.

Light intensity was compared between bagged and exposed flowers for the four crops at three time intervals (8-10am, 12-2, 4-6pm) on 17 November 1987. The light meter sensor (see 4.4.1) was placed at a height of 1m inside and outside bags and gave mean readings at ten second intervals. Light intensities incident on bagged and exposed flowers were compared with a student's t test.

For each set of five flowers, total nectar volume was recorded using a 5 µl micropipette (Drummond). The pooled nectar sample was discharged onto a hand-held Atago refractometer (15-55%) for measurement of percentage total sugars. Nectar energy (joules) was calculated from nectar volume and sugar concentration using the formula from Prys-Jones and Corbet (1987).

$$E = V \times ((3.7291 \times 10^{-3} \times C) + (1.78 \times 10^{-5} \times C^2) + 0.9988603) \times (C/100) \times 15.5$$

where E =energy of nectar (joules)

V =volume of nectar (µl)

C =percentage sugar in nectar (weight of sucrose per 100g solution)

Because the change in flower pollen dry weight content for dehiscing anthers could not be determined from the four species on a two hourly basis, due to the time required for measurement, a more practical method was implemented. This method did not take account of differences in pollen grain number per flower species.

Pollen availability revealed not only whether anther dehiscence had occurred but also whether pollen remained within the anther locule. Pollen availability was recorded by rubbing the dehiscent area of the anther locule with a micropipette and observing whether pollen was released. Minute amounts of pollen on the micropipette were recorded as zero. Data were recorded as the proportion of five flowers with pollen present. Some flowers were examined under a dissecting microscope (Nikon SMZ-1) at 40x magnification to determine whether flowers with no pollen available had not dehisced or alternatively whether the anther locule was empty of pollen.

Ten flowers exposed to bee foraging were selected within a 1m radius of the bagged flowers. Once analysed the flowers were discarded preventing the same flowers from being reanalysed. Twenty flowers from each species were analysed in the same way as bagged flowers, but at five time intervals (8-10am, 10-12, 12-2, 2-4, 4-6pm).

The data were ranked, normalised and three-way ANOVAs analysed (pollen and nectar energy by day, crop and time). Polynomial functions for day and time were incorporated. Subsequently, data were reanalysed for each of 22 days for bagged and exposed pollen availability and nectar energy for flowers from four crops, using a two-way ANOVA. Data were analysed for five time intervals for exposed and three time intervals for bagged flowers using a square root transformation. Swede was excluded

from the analysis for the first 11 recording days. Treatments were compared using L.S.D. calculated from S.E.D.

Standing crop of pollen and nectar

The mean standing crop of pollen (mg/flower) and nectar energy (joules/flower) was calculated for the four crops.

The standing crop of pollen was estimated from pollen dry weight/flower (see below fig. 4.6c) while nectar energy was estimated from the maximum energy/flower from bagged flowers taken from weeks 1-10. Pollen and nectar energy/flower were multiplied by flower production to obtain the production of new pollen and nectar.

4.3.2 Results

Flower pollen content

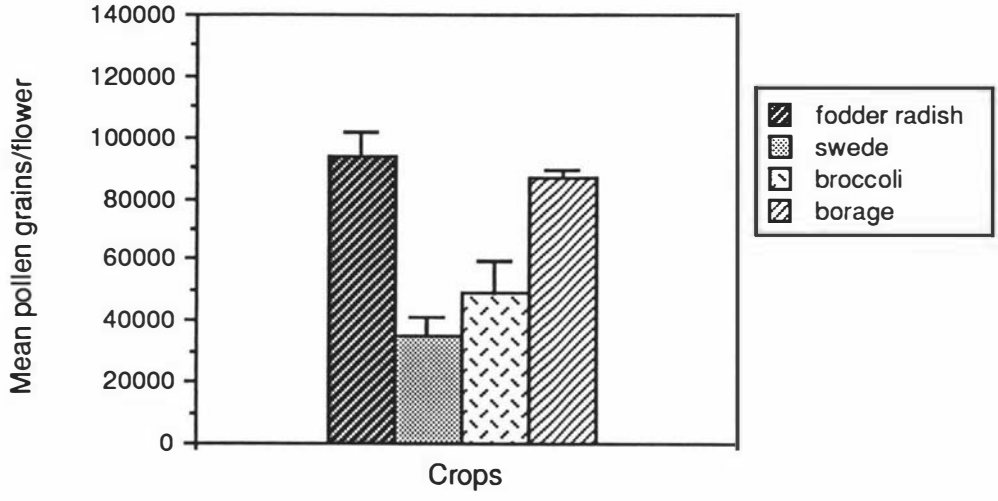
Fodder radish flowers had the highest number of pollen grains/flower (93,280) with borage second (86,360), broccoli third and swede fourth (fig. 4.6a). Pollen grain content/flower was significantly different between crops (F_S = 13.79; df=3,39; $p < 0.001$) in the order from highest to lowest: fodder radish = borage > broccoli = swede. The number of pollen grains/mg from pollen loads removed from foraging bees was 197,412 for cruciferous crops but only 78,972 for borage (fig. 4.6b; t=-12.75 ;df=18; $p<0.001$). Fodder radish, broccoli and swede were recorded together as cruciferous crops because it was not possible to distinguish the pollen between these three species (see chapter 6).

Pollen dry weight/flower was significantly different between crops (F_S=69.53; df=3,39; $p<0.001$). This difference in borage pollen dry weight/flower is shown in figure 4.6c where borage had 2.3 times more pollen/flower than fodder radish, and 6 times that of swede.

Lower density of pollen grains in bee loads collected from borage compared to crucifers may be related to grain size. A comparison of the dimensions between borage pollen grains (0.026mm wide x 0.038mm long; n=20) and fodder radish (0.020mm wide x 0.038mm long) indicated borage grains were slightly larger than fodder radish pollen grains. Fresh borage pollen grains have a dumbbell shape, common in Boraginaceae (Howes 1948), while cruciferous crops have grains with a narrow elliptic shape. If we assume pollen grains are shaped like rectangular boxes (which they are not, but for ease of calculation) with width equal to height and estimate the volume, we find borage pollen grains have a volume of $2.56 \times 10^{-5} mm^3$, while fodder radish grains have a volume of $1.48 \times 10^{-5} mm^3$. Thus, the volume of borage grains is 1.7 times that of

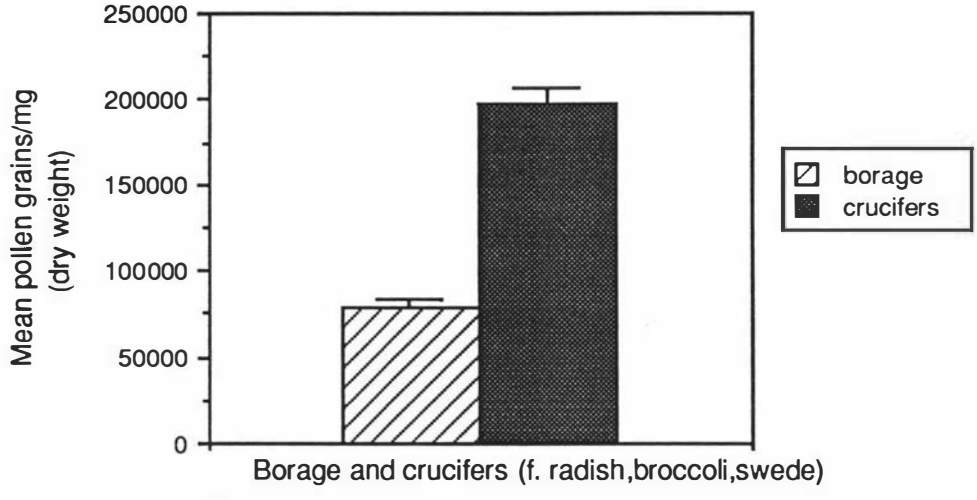
Figure 4.6. Pollen grains per flower from 4 crops

(a)



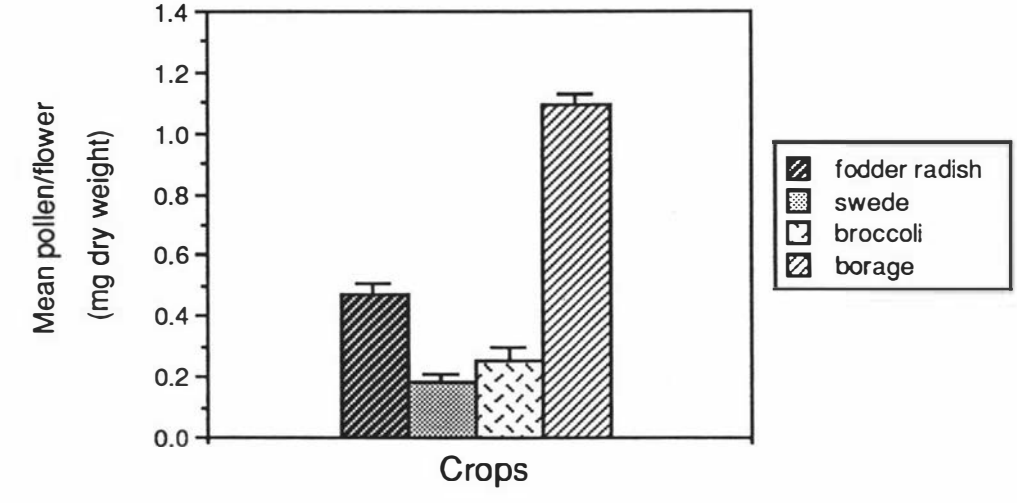
Pollen grains per mg bee load from 4 crops

(b)



Pollen dry weight per flower from 4 crops

(c)



fodder radish. The dumbbell shape of borage would only accentuate this difference. This could help explain the lower density of borage pollen grains/mg of bee load.

Diurnal change in food availability

Borage and swede flowers opened early in the day with all flowers open by 6am (standard time, table 4.3). Fodder radish flowers were fully opened by 7am, while broccoli flowers opened slowly between 5-9am all being fully opened by 10am. Temperature and light intensity increased rapidly between 5-6am which may have influenced flower opening for all except broccoli. This crop may require higher light intensity or lower relative humidity.

Borage and broccoli flowers lasted longer in September than November, and longer when not exposed to foraging (table 4.4). Pollen availability and nectar secretion followed the same trend. Borage flowers lasted 2-3 days in September and one day in November, secreting nectar and releasing pollen for as long as flowers were open. Broccoli flowers lasted four days in September (three days exposed to foraging); while in November, flowers lasted 2-3 days.

Fodder radish flowers opened for 2-3 days in September and two days in November. Pollen was available on the first two days but was mostly removed by the second day in exposed flowers. Nectar was available on the second day in September and on the first day in November.

Swede flowers, unopen in September, lasted 1-2 days in November. Pollen and nectar were available on the first day. Food was rapidly depleted in exposed flowers.

Generally, nectar was rapidly removed from exposed flowers of all species, but this was not so with pollen.

Borage, and to a lesser extent broccoli, secreted nectar over a wide range of weather conditions during both trials. Fodder radish and swede, however, secreted more nectar in milder weather with less range in sugar concentration. More energy was recorded from broccoli overall, due to longer lasting flowers (table 4.5). From diurnal nectar secretion results (see below), it was apparent that borage generally had the highest nectar volume and energy levels, but this was difficult to detect in this experiment because of the short life of individual flowers and rapid depletion by bees.

Nectar energy from exposed flowers

Energy of nectar recorded from five flowers from the four crops exposed to bee foraging indicated significant differences between crops (appendix table A4.1). Borage had the highest nectar energy on 12 and 29 Sept., 10 and 13 Oct. and 14 Nov. and fodder radish on 3, 6, 24 and 31 Oct. and 3 Nov. with both crops being equal on the

Table 4.4. Phenology of bagged and exposed flowers from 2 trials of 10 flowers for each of 4 crops beginning 22 September and 5 November 1987.

		Bagged flowers						Exposed flowers				
	Days	1	2	3	4	5	6	1	2	3	4	5
	Crops											
						Trial 1						
	F.radish	100	100	20	0	0	-	100	100	30	0	-
	Swede		not	flowering					not	flowering		
	Broccoli	100	100	100	100	30	0	100	100	80	40	0
Percentage	Borage	100	100	30	0	0	-	100	100	60	0	-
of flowers						Trial 2						
still open	F.radish	100	100	0	0	-	-	100	100	0	-	-
	Swede	100	60	0	0	-	-	100	44[#]	0	-	-
	Broccoli	100	100	70	0	-	-	100	100	0	-	-
	Borage	70	0	0	0	-	-	80	0	0	-	-
						Trial 1						
	F.radish	100	100	-	-	-	-	100	50	-	-	-
	Swede		not	flowering					not	flowering		
Percentage	Broccoli	90	90	80	50	-	-	100	60	13	-	-
of open	Borage	60	88	0	-	-	-	80	13	0	-	-
flowers						Trial 2						
with	F.radish	100	70	-	-	-	-	100	0	-	-	-
pollen	Swede	100	17	-	-	-	-	56	11	-	-	-
available	Broccoli	100	100	100	-	-	-	100	10	-	-	-
	Borage	89	-	-	-	-	-	100	-	-	-	-
						Trial 1						
	F.radish	0	60	0	-	-	-	0	30	0	-	-
	Swede		not	flowering					not	flowering		
	Broccoli	0	60	30	-	-	-	0	0	0	0	-
Percentage	Borage	10	60	0	-	-	-	-	-	-	-	-
of open						Trial 2						
flowers	F.radish	80	0	-	-	-	-	0	-	-	-	-
secreting	Swede	90	17	-	-	-	-	11	0	-	-	-
nectar	Broccoli	90	30	-	-	-	-	10	0	-	-	-
	Borage	20	0	-	-	-	-	0	-	-	-	-

[#]=only 9 flowers opened

Table 4.5. Nectar secretion/flower from bagged and exposed treatments for 2 trials (see table 4.4).

	Nectar volume (µl)		Sugar conc. (% sugar)		Nectar energy (joules)	
	Min	Max	Min	Max	Min	Max
F.radish	0.5	1.0	27	55+	2.3	5.4
Swede	0.5	1.0	55+	55+	5.4	10.7
Broccoli	0.5	2.0	17	55+	2.8	21.5
Borage	0.5	2.5	16	55	2.6	8.6

Table 4.6. Incident light intensity ($\mu Em^{-2}s^{-1}$) from bagged and exposed flowers from 4 crops at 3 time intervals (8-10am,12-2,4-6pm) on 17 November 1987.

Time	8 - 10 am		12 - 2 pm		4 - 6 pm	
Crop	Exposed	Bagged	Exposed	Bagged	Exposed	Bagged
Fodder radish	1930	900	2150	1240	270	230
Swede	2130	1140	2200	1300	380	220
Broccoli	1600	900	1800	1300	390	236
Borage	1925	1000	1900	1000	260	140
Mean	1894	985	2013	1210	325	207
t test (bagged vs. exposed) Signific.	t=7.37	**	t=6.68	**	t=2.87	*

$t_{0.05(1)[3]}=2.353$
$t_{0.01(1)[3]}=4.541$
$t_{0.001(1)[3]}=10.213$

Table 4.7. Standing crop and production of pollen and nectar energy for bagged flowers from September to November 1987.

Pollen and nectar energy standing crop and production	Crops			
	Fodder radish	Swede	Broccoli	Borage
Pollen/flower (mg)	0.47	0.18	0.25	1.09
Nectar energy/flower(joules)	0.87	1.51	1.27	3.47
Flowers/m^2 mean for 10 weeks	828	137	285	243
New flowers/m^2/day mean for 10 weeks	320	84	73	32
Pollen/m^2/day mean for 10 weeks (mg)	150	15	18	35
Nectar energy/m^2/day mean for 10 weeks (joules)	278	127	93	111

remaining recording days (figs. 4.7a, 4.8a, 4.9a). Broccoli had very low levels of nectar. Swede flowered from 17 Oct. onwards and had little nectar in exposed flowers.

Fodder radish had little nectar before 10am, whereas borage produced energy rich nectar throughout the day with an increase from 8-10am and 4-6pm, possibly when bee numbers were lower. Swede nectar was available early in the day only in exposed flowers.

Seasonal trends suggested the overall order of highest energy content of exposed flowers from the four crops was: borage > fodder radish > broccoli > swede (appendix table A4.2). Energy content of flowers from the crops differed from day to day due to weather changes. Time of day was of comparatively minor importance in influencing nectar yield.

Light intensity was consistently higher on exposed flowers compared to flowers in bags (table 4.6); this difference being less in the evening.

Nectar energy from bagged flowers

Nectar energy accumulation in five bagged flowers of four crops indicated significant differences between crops (appendix table A4.1). Daily energy analysis indicated borage secreted more nectar, especially early in the season, with fodder radish having higher energy accumulation than borage after 17 Oct. Broccoli had comparatively low levels of energy, while swede, on some days e.g. 24 Oct. had the second highest nectar energy available (figs. 4.7b, 4.8b, 4.9b).

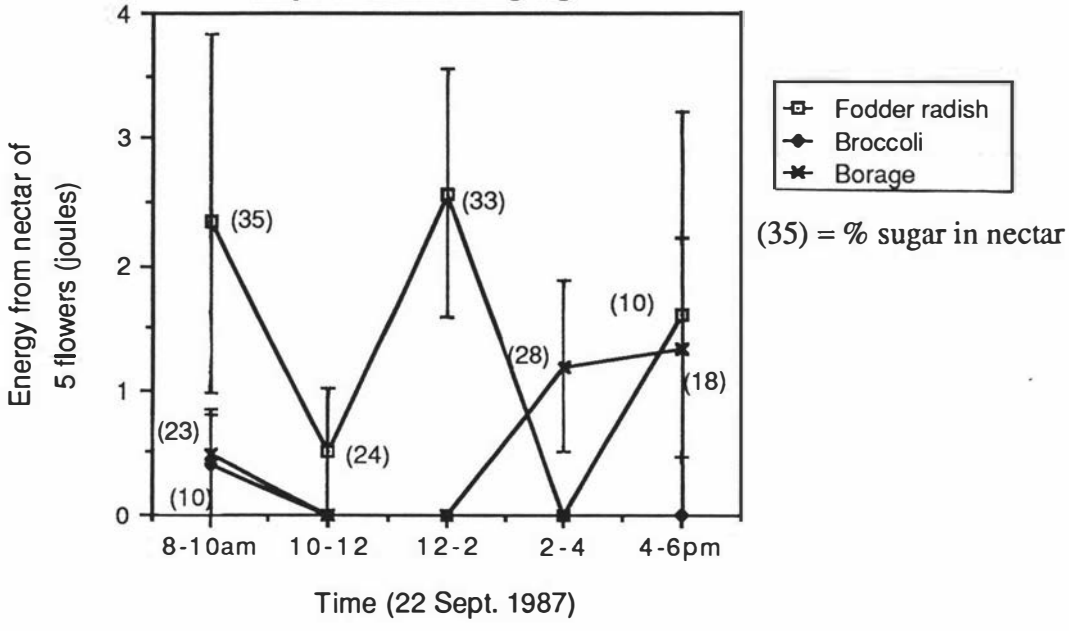
The order of mean nectar energy from bagged flowers during the season was: borage >> fodder radish = broccoli > swede (appendix table A4.3). This order, however, underestimated nectar levels from swede because this crop only flowered for 50% of the recording days. Energy of nectar varied between days due to weather changes far more than during each day.

Pollen availability from exposed flowers

Pollen availability recorded from the proportion of pollen in five exposed flowers from four crops indicated significant differences between crops throughout the recording period (appendix table A4.1). The order of pollen availability throughout the season was: fodder radish > broccoli > borage, before swede flowered (e.g. fig. 4.7c) and fodder radish > broccoli > swede > borage when all crops flowered (fig. 4.8c, 4.9c) (appendix table A4.4).

Figure 4.7. **Energy from nectar of 3 crops exposed to foraging**

(a)



(35) = % sugar in nectar

(b)

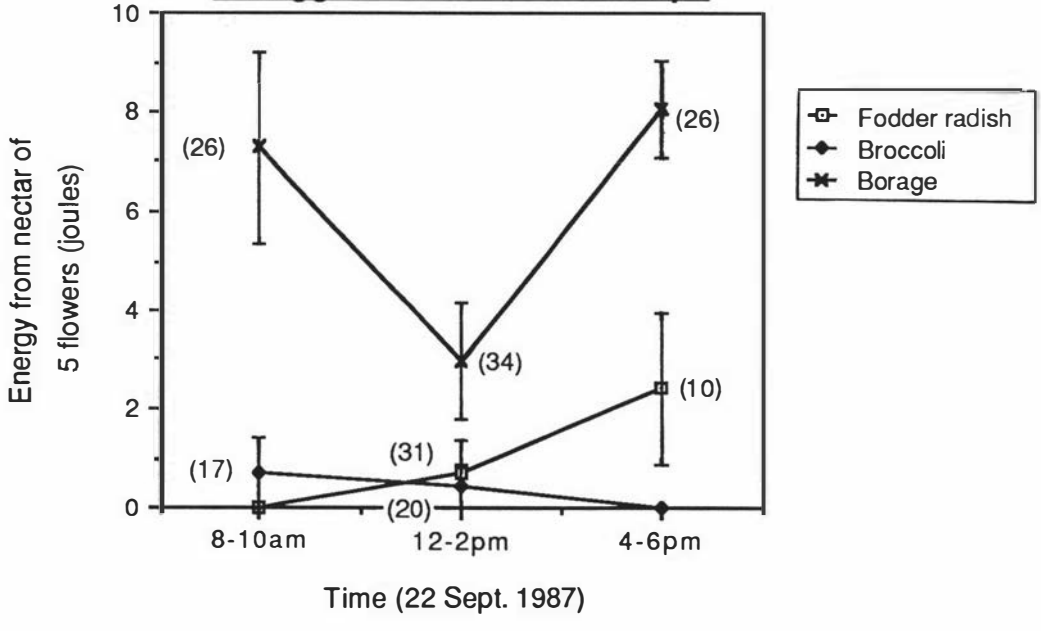
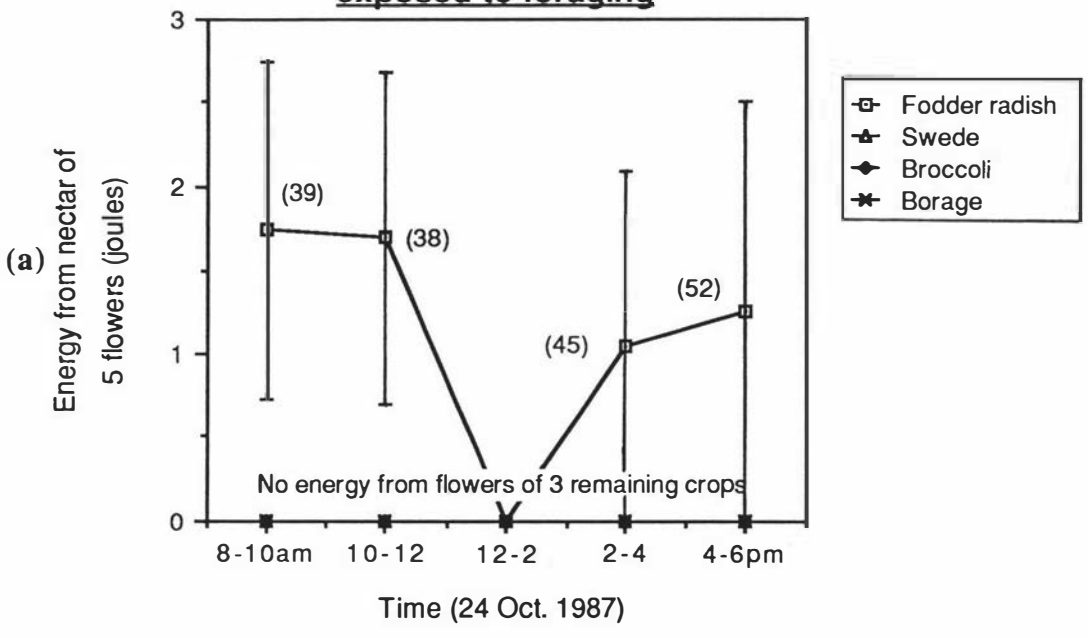


Figure 4.8. Energy from nectar of 4 crops exposed to foraging



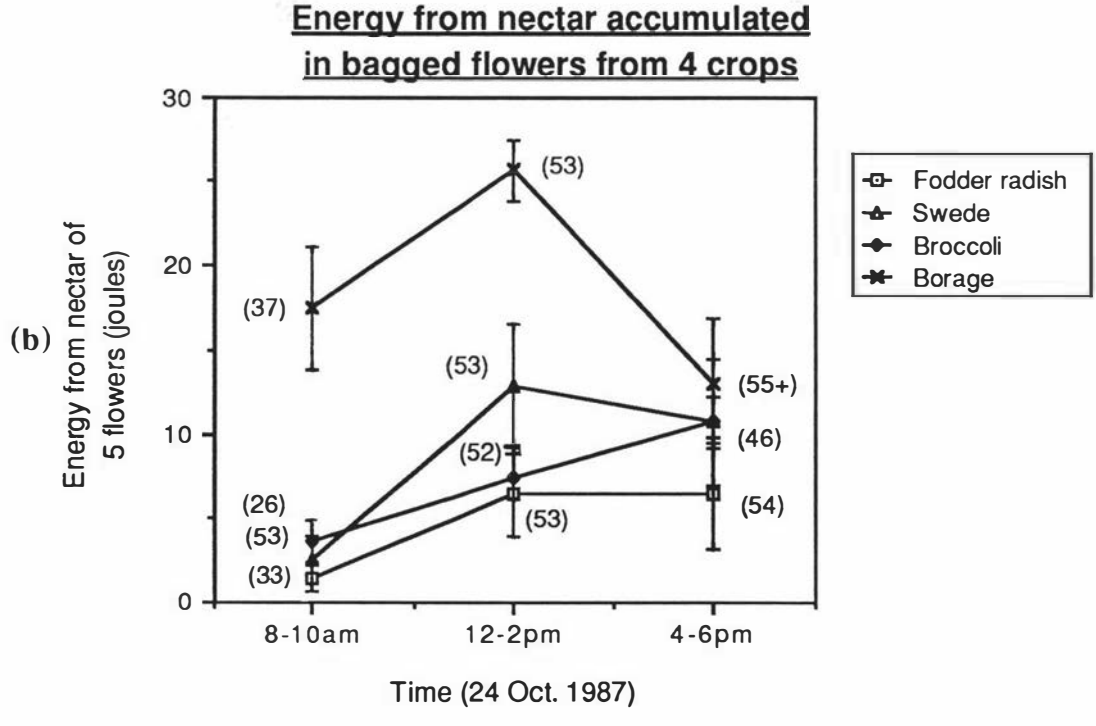
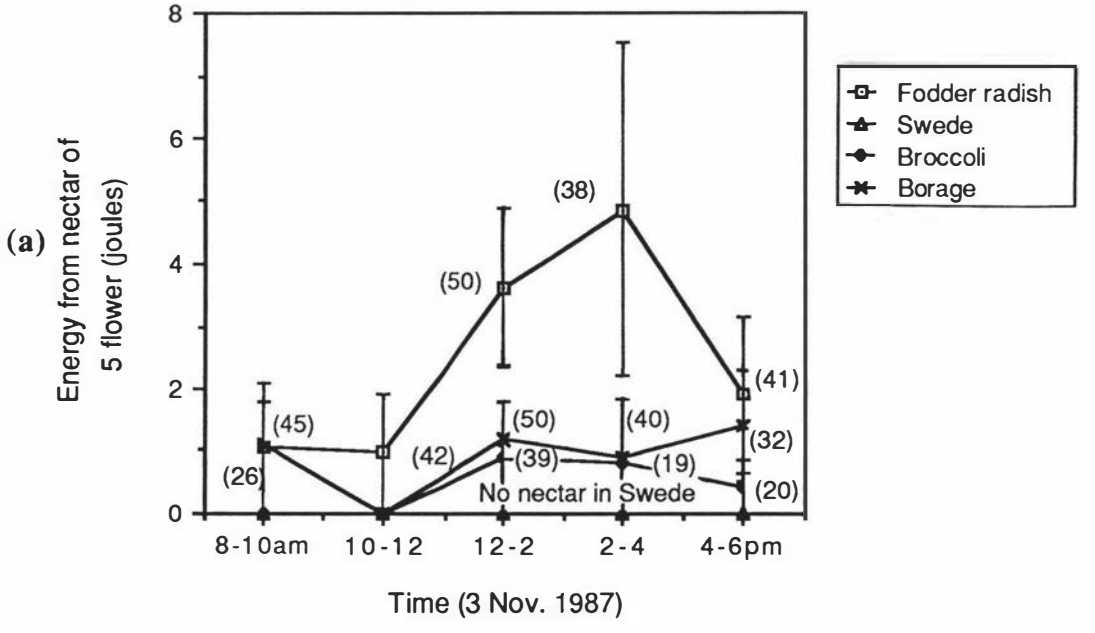


Figure 4.9. Energy from nectar of 4 crops exposed to foraging



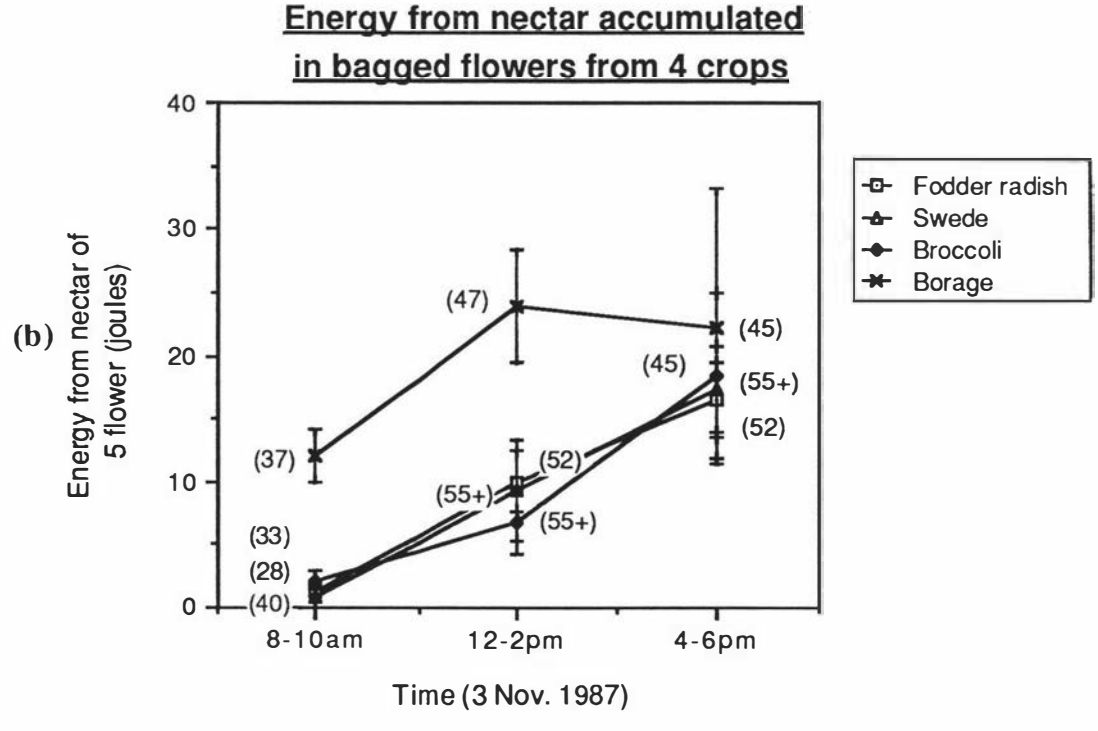
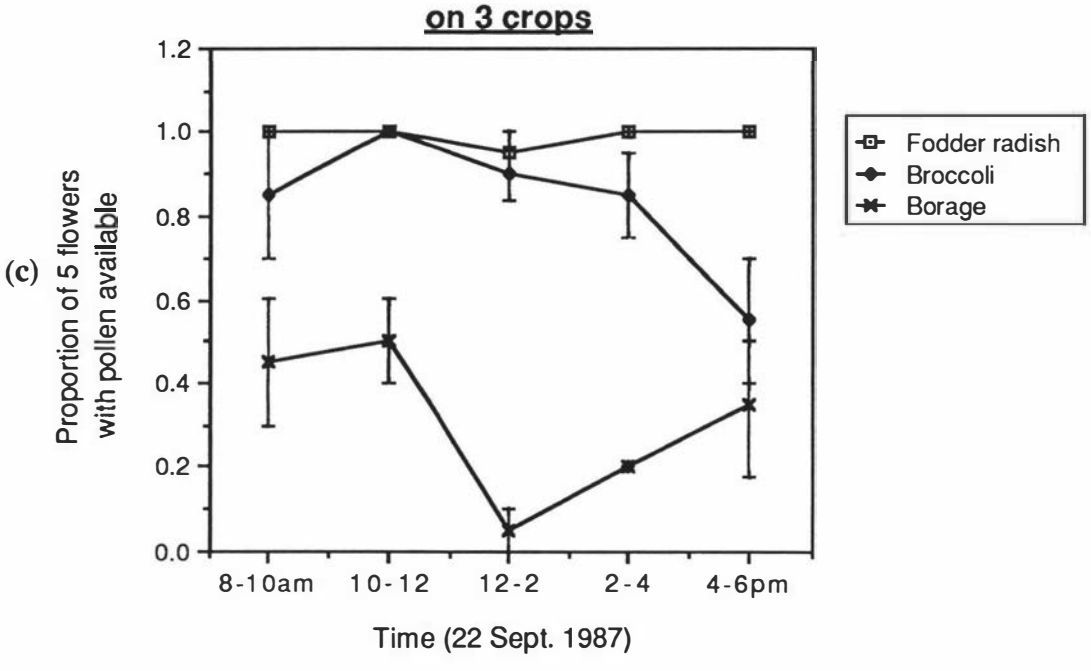


Figure 4.7. Pollen available from exposed flowers on 3 crops



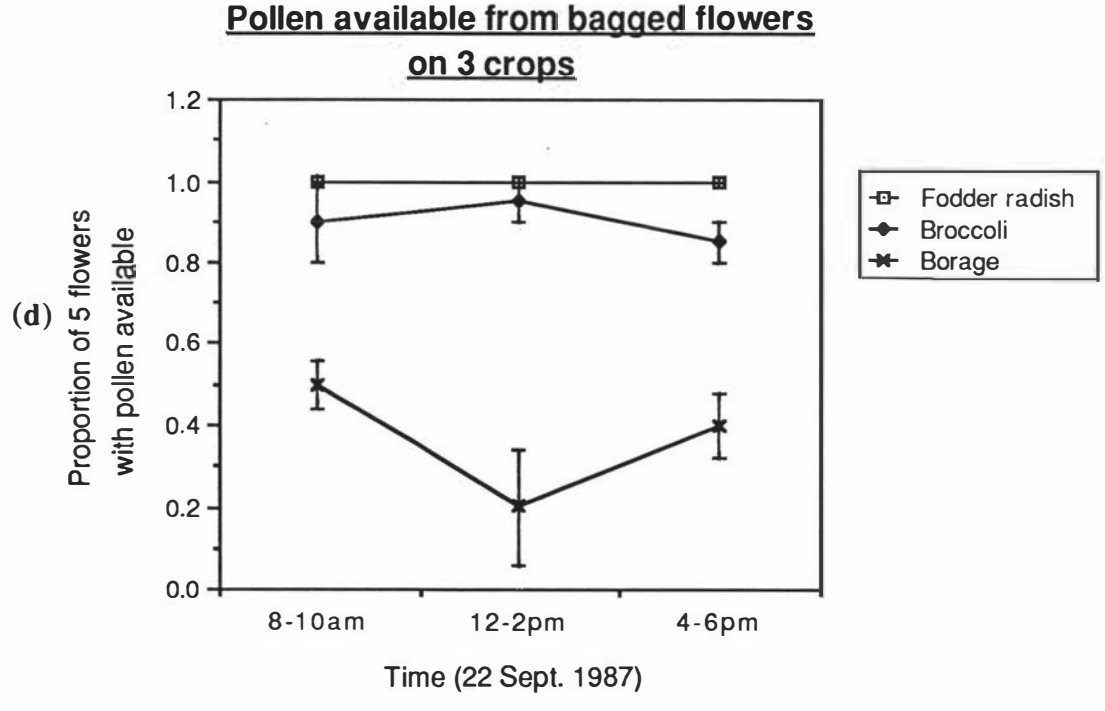
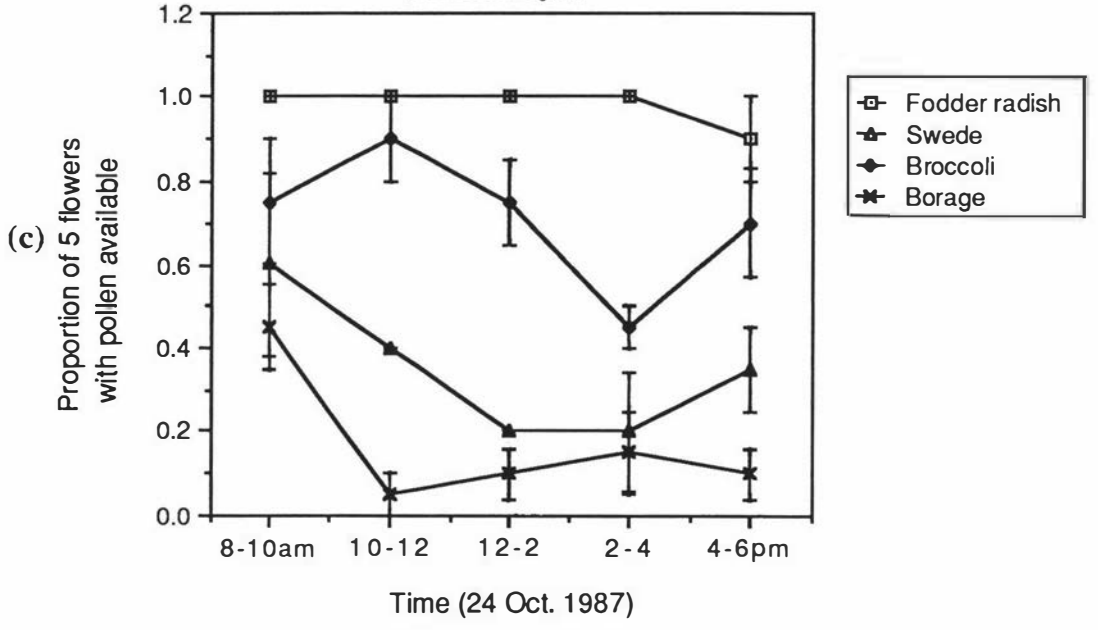


Figure 4.8. **Pollen available from exposed flowers on 4 crops**



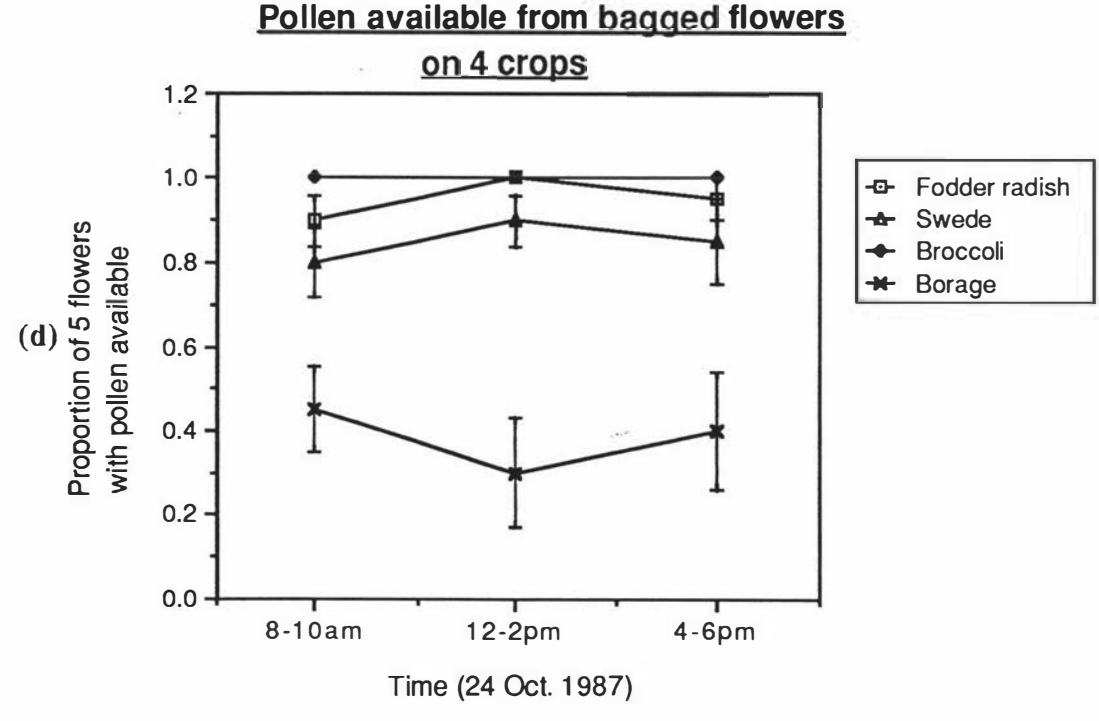
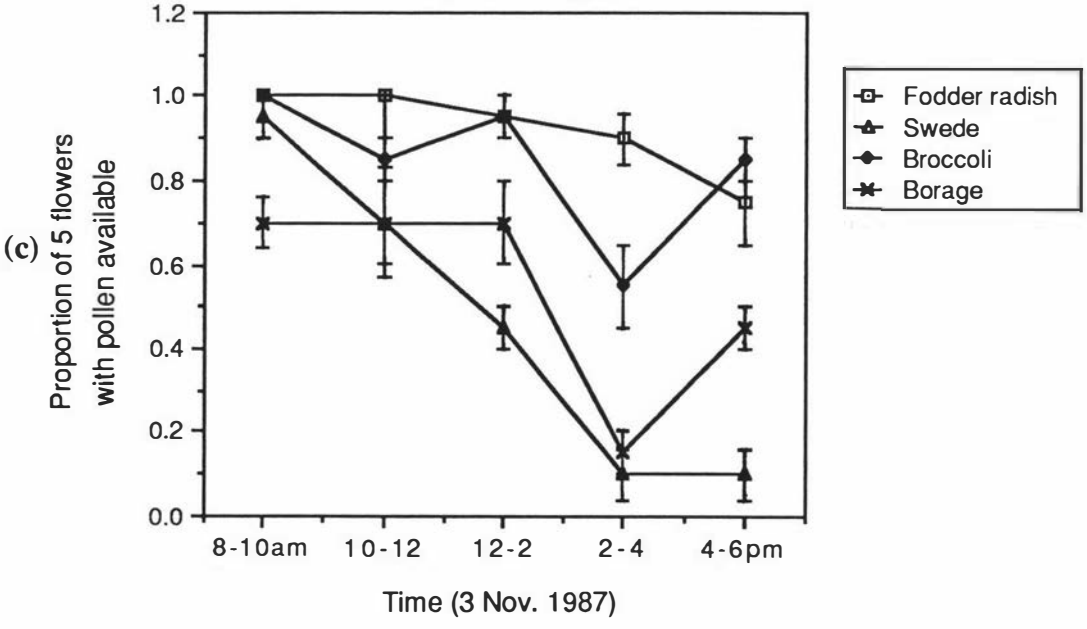
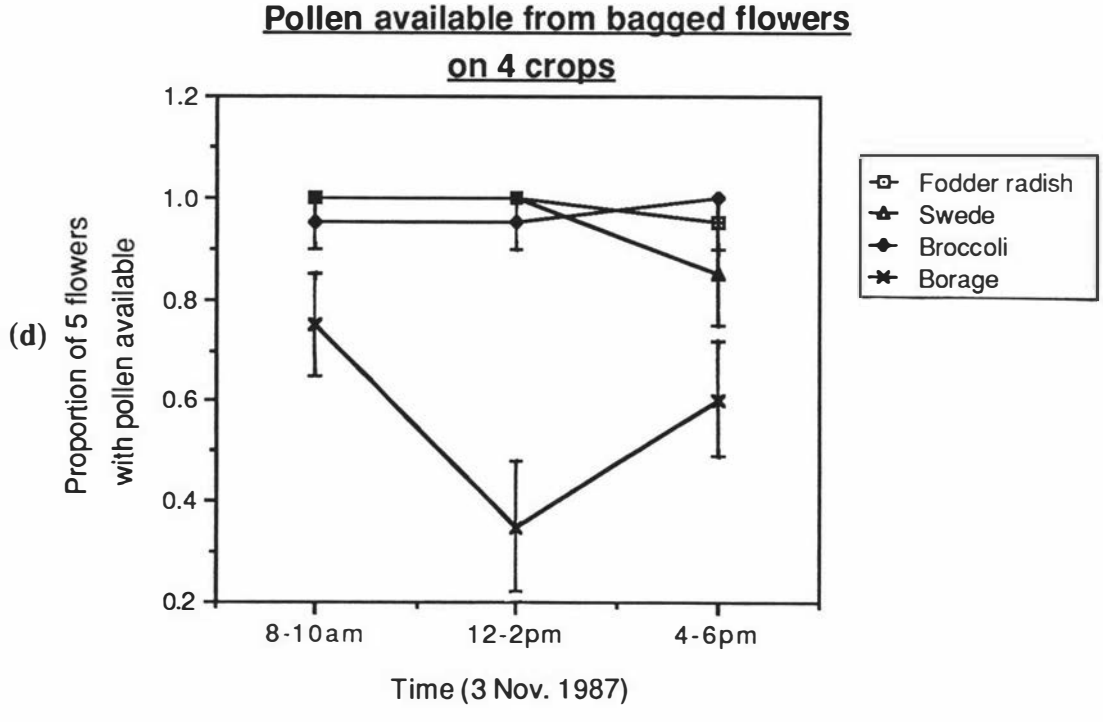


Figure 4.9. Pollen available from exposed flowers on 4 crops





Crops utilised most for pollen should show a decline in pollen availability throughout the day. This occurred in borage where the order of pollen availability was: 8-10am > 10-12noon > 12-6pm. Swede pollen declined after midday, broccoli after 2pm and fodder radish after 4pm.

Microscopic examination of anthers from the four crops showed that borage anthers, with no pollen available, were completely empty of pollen. By comparison anthers from the three cruciferous crops, also with no pollen available, had not yet dehisced.

Pollen availability from bagged flowers

Pollen availability from bagged flowers (protected from bees) exhibited significant differences between crops throughout the recording period (appendix table A4.1). The order of pollen availability throughout the season was the same as for exposed flowers. Crop differences accounted for 38% of ANOVA variation (appendix table A4.5), while differences between days due to weather, accounted for 16.4% of variation. Pollen availability from the four crops increased linearly throughout the season with some fluctuations.

Time of day was of comparatively minor importance for influencing pollen availability. Less pollen was available at 4-6pm than 12-2pm. Pollen was available on all crops from 8-10am onwards. However, on fodder radish, the greatest available pollen occurred from 12-2pm. Borage had more pollen available in the morning in bagged flowers (figs. 4.7d, 4.8d, 4.9d). Note that bagged pollen availability was recorded at three time intervals each day (8-10am, 12-2pm, 4-6pm).

Standing crop of pollen and nectar

The order for the production of pollen/m^2/day during flowering was: fodder radish > borage > broccoli > swede (table 4.7). The order for nectar production/m^2/day was: fodder radish > swede > borage > broccoli. Fodder radish had high flower density and flower production while borage had high levels of pollen and nectar energy per flower.

4.4 Effect of weather conditions on pollen and nectar availability

The aim of this section was to relate the availability of pollen and nectar energy on the four crops to weather variables recorded throughout each of 22 recording days.

4.4.1 Methods

Weather parameters were recorded every two hours from 8am-6pm on recording days. Wind speed was recorded with a hand-held anemometer AM500, held 1.5m above ground level for one minute and values converted to ms^{-1}. Light was recorded with a

Licor light meter using a quantum sensor positioned on a post near the crop 1m above ground level. This recorded the photosynthetically active radiation (P.A.R.) from 400 to 700nm (in microEinsteins/m^2/s; $\mu Em^{-2}s^{-1}$). The light meter was set to give mean readings over ten seconds. Two-hourly temperature, relative humidity, rainfall and weekly evaporation and soil temperature records were taken from a meteorological recording station 300m from the trial plots as follows: temperature and relative humidity were recorded continuously on a drum thermohydrograph inside a Stephensons screen 1.5m above ground level; rainfall was recorded on a drum chart giving continuous recordings of rainfall in millilitres; weekly soil temperature was obtained from a 30cm deep thermometer; weekly evaporation was recorded from a raised pan evaporimeter.

Daily sunshine hours were taken from the Department of Scientific and Industrial Research climatological recording station 2km from the trial site.

A correlation matrix between temperature, relative humidity, wind speed, light intensity and rainfall was calculated.

A correlation matrix and multiple regression analyses of pollen availability and nectar energy for the 22 recording days at five time intervals from exposed and bagged flowers (three time intervals for bagged flowers) were compared with the five weather variables.

To examine the effect of individual weather variables on nectar secretion of two preferred nectar producing crops of *B. terrestris* (see chapter 5), bagged borage and fodder radish nectar energy levels were calculated, and each compared with temperature, relative humidity, wind speed, rainfall and light intensity recorded at three time intervals throughout the 22 recording days using Pearson's correlation.

4.4.2 Results

As expected, temperature was highly correlated with light intensity and negatively correlated with relative humidity. Rainfall was positively correlated with R.H. and negatively correlated with light intensity. Wind speed was correlated with light intensity (table 4.8).

Nectar energy from exposed flowers independent of crop species, was negatively affected by light intensity and temperature (appendix table A4.6). As light intensity and temperature increased, nectar secretion increased, but more bees foraged removing more nectar; hence exposed flowers overall had less nectar energy available during more favourable conditions for foraging. Less nectar was removed early in the season with low light intensity and temperature.

Nectar production (rate of secretion) from bagged borage and fodder radish flowers was not significantly correlated with weather variables (appendix table A4.7).

Table 4.8. Correlation matrix of weather variables

	Temp. (C)	R.H.	Wind (ms^{-1})	Light #	Rain (mm)
DF = 108					
Temp.	1.000				
R.H.	-0.252**	1.000			
Wind	-0.082n.s.	-0.129n.s.	1.000		
Light	0.373***	-0.658***	0.209*	1.000	
Rain	-0.117n.s.	0.413***	-0.146n.s.	-0.272**	1.000

$r_{0.05(2)[108]}=0.188$
$r_{0.01(2)[108]}=0.245$
$r_{0.001(2)[108]}=0.310$

= ($\mu Em^{-2}s^{-1}$)

Table 4.9. Ranking of 4 crops according to anthesis and food availability in relation to their suitability for *B. terrestris* workers for the 1987 season.

Features of crops	Crops			
	Fodder radish	Swede	Broccoli	Borage
Flower structure	4*	2=	2=	1
Seasonal flowering time	1=	4	1	1
Flower duration	1=	4	1=	1=
Flower density	1	3	2	4
Flower production	1	2	3	4
Pollen/flower (mg)	2	4	3	1
Proportion of bagged flowers with pollen available	1	3	2	4
Nectar energy/flower (joules)	4	2	3	1
Pollen/m^2/day (mg)	1	4	3	2
Nectar energy/m^2/day (joules)	1	2	4	3
Overall rating	1st	4th	3rd	2nd

* assumes no hole biting

Pollen available from exposed flowers was not significantly influenced by the weather (appendix table A4.6). Honey bees were affected by weather and, in turn, influenced pollen availability (see chapter 5).

Pollen availability of bagged flowers was positively influenced by temperature and negatively influenced by rainfall. The combined effects explained 42.9% of total variance.

4.5 Discussion

The crops were evaluated as potential bee forage for *B. terrestris* colony development (table 4.9) using criteria 5,6,9 and 10 (chapt. 3). Fodder radish was the most suitable crop with high flower density and production, flowering over an extended period and had ample pollen and nectar available. Early in the season, fodder radish was less attractive due to a lack of nectar.

Borage would be the second most suitable crop, with broccoli third. Swede was unsuitable as a bee forage crop because of the very short flowering duration.

Borage flowered for most of the 11 week trial. Borage flower density and production were low, but the pollen/flower was high. Some pollen appeared to be lost in bagged flowers, however, possibly due to strong wind. The amount of borage pollen and nectar energy/flower was high, but because of low flower density and flower production, the turnover of new pollen and nectar was lower than fodder radish. Nectar was secreted throughout the season. In the case where equal weights of pollen were collected from borage and crucifers, although borage had fewer pollen grains/bee load, the larger volume would compensate. Therefore crucifers and borage would have similar food potential for larvae. Brian (1951) calculated pollen grain volume assuming grains were spherical, recording the average length x breadth for non-spherical grains. She found more *Lotus corniculatus* pollen grains (34) than red clover grains (25) in a *B. agrorum* nest, but as red clover grains were 15 times larger in volume, she concluded this species was of greater importance as a food source. If *B. terrestris* could harvest the same number of pollen grains/unit time from borage as crucifers, then borage would be a more important food source because of the greater grain size.

Broccoli flowered throughout the trial; flower density and production were high (although ranked second and third resp.). However, the amount of pollen and nectar/flower was low with nectar becoming scarce in wet weather.

The proboscis length (chapter 3) of worker bumble and honey bees (5.5mm) enabled nectar collection from borage with a corolla depth of 2mm, and these bees probably also had little difficulty with broccoli (5.8mm) or swede (5.7mm), but may have been excluded from fodder radish (9.9mm). *Bombus* species prefer flowers with a corolla

tube the same or slightly shorter than the length of their proboscis (Free and Butler 1959; Percival 1965; Hobbs *et al.* 1961; Hobbs 1962b). *B. terrestris* queens, with a tongue length of 11.25mm, could utilise all flowers, while males with a 6.9mm tongue were excluded from fodder radish. While the corolla tube of fodder radish may be too long for *B. terrestris* workers, the behaviour of biting holes in the base of the flower (chapt. 3) would circumvent this problem.

The rapid splitting of the calyx and corolla in broccoli and swede would have assisted in worker exploitation of these crops, with flower handling efficiency increasing through removal of nectar by 'robbing'. However, as suggested by Percival (1965) for some long-tubed crucifers with polysepalous calyces e.g. fodder radish, the strong imbrication of the four sepals forms and preserves the flower tube and protects the nectar, maintaining the flower shape long enough to enable legitimate exploitation by long-tongued insects.

When measuring the quantity of nectar that accumulates in bagged flowers, the bagging process may affect apparent rates of secretion (Raw 1953), although light levels recorded in bags on 17 November 1987 were unlikely to be limiting in this trial. Corbet *et al.* (1981) suggest that this bagged nectar reflects the rate of secretion in bagged flowers only which may be lower than the rate of secretion of nectar in exposed flowers where nectar is constantly being harvested and replenished. Unfortunately, time restraints prevented an accurate assessment of the effect of nectar removal on nectar secretion in bagged flowers. As a result it was not possible to determine whether bagged nectar secretion was an underestimate of nectar secretion in exposed flowers. Corbet (1978) suggests that because of resorption it is not possible to assess sugar production from that yielded from flowers protected from insects. However in situations where nearly all the nectar from exposed flowers is removed by foragers, such as in this trial, it may be the only method available for determining nectar production.

The decline in nectar energy levels in bagged flowers later in the day could be due to a number of factors. Possibly the destructive sampling procedure resulted in newly recruited flowers being sampled which, having only opened a few hours earlier, had less nectar. However, data indicated all borage flowers were open by 6am in November 1987. Alternatively, nectar resorption may have occurred. Corbet, Unwin and Prys-Jones (1979) explained that the balance between rates of secretion and resorption may determine the rate of accumulation or depletion of nectar in flowers. An increase in nectar results from secretion of new nectar or recruitment of newly opened flowers containing more nectar than others. Decrease in nectar may be due to removal by insects, resorption of nectar or recruitment of new flowers containing less nectar than remaining flowers. Difficulty in removal of nectar using micropipettes due to high sugar content was not a problem as sugar concentration usually decreased in the late afternoon.

The decrease in nectar energy levels later in the day can therefore be explained by a drop in sugar concentration not a drop in nectar volume.

Use of a refractometer to estimate percentage total sugar concentration of nectar assumes a correlation between refractive index and percentage composition by weight of sucrose, glucose and fructose. Fortunately, these sugars have very similar refractive indices (Corbet *et al.* 1979). It is convenient to assume nectar is simply a sugar solution. This is not quite correct as small amounts of other substances, such as amino acids and proteins, may be present and affect the readings slightly (Prys-Jones and Corbet 1987).

Two factors influencing visits to flowers for nectar are the sugar concentration in nectar (quality) and the calorific content (Corbet 1978) which takes account of sugar content and nectar volume (quantity). Feeding of honey and bumble bees may depend on sugar concentrations (Free 1955, Pouvreau 1974) with bees favouring concentrations between 20-50% (Eickwort and Ginsberg 1980), although uptake may be highest at 50% sucrose (Prys-Jones 1982). Diurnal variation in calorific reward may be a major determinant of bee foraging strategy (Corbet *et al.* 1979).

Rain may dilute nectar in open flowers. However, the pendulous nature of borage flowers would counter this effect. Nectar is a product of photosynthesis and therefore often increases with light intensity (Free 1970a). In some plant species high light intensity may impede nectar secretion; however, this did not appear to be the case for this trial. The effect of temperature and light intensity on nectar availability was probably related to the influence of these weather variables on foragers removing nectar from flowers.

Higher temperature with infrequent rain increased pollen availability on the four crops. This was recorded by Percival (1965) for a number of plant species. Rain and R.H. above 90% may inhibit dehiscence. However, the poricidal-like anthers of borage were probably less susceptible to high moisture than the longitudinally dehiscent anthers of the crucifers. As the opening of flowers and dehiscence of anthers occurred early in the morning, pollen availability was highest during this period.

4.6 Summary

1) Fodder radish was the most suitable crop for *B. terrestris* colony development based on flower density, flower production, length of flowering and pollen and nectar standing crop. However, little nectar was available early in the season.

2) Borage was second most suitable with a high standing crop of pollen and nectar and the highest pollen dry weight/flower of the four crops. Nectar was secreted throughout the season from pendulous flowers. Both nectar and pollen were well protected and unaffected by weather conditions. However, flower density and flower production were low.

3) Although the four crops had different corolla lengths, *B. terrestris* workers could still remove nectar from all crops.

CHAPTER 5

FORAGING PERFORMANCE: FIELD STUDY

5.0 Introduction

Bumble bees are eusocial and the colony survives throughout the flowering season. The life of one bee extends throughout the period of several flowering species,so foragers must be polytropic (Free 1970a).

Floral attractants (Kevan and Baker 1983) lure bees from a distance and stimulate sampling of rewards. Bees gathering nectar must carry this out efficiently i.e. maximise their nett energy intake (Pyke *et al.* 1977; Pyke 1978a, 1978b, 1979, 1980; Eickwort and Ginsberg 1980). Bumble bees have high energy requirements partly because they regulate their temperature (Heinrich 1979a).

Flower preference is influenced by a complex of factors (chapter 4) and has been subjectively studied in the past. However Hobbs *et al.* (1961) and Hobbs (1962a, 1962b) made a quantitative study of bee attractiveness of four legumes. Honey, leafcutter and bumble bees were assessed diurnally on crops grown in a 4 x 4 Latin square. Floral preference was determined by the length of the proboscis and the depth of the corolla tube.

Bumble bee foragers assess nectar availability using visual and olfactory cues at a distance from flowers and pollen availability for *Anemonopsis macrophylla* through age-related morphological cues of the flower (Pellmyr 1988).

Pollen availability may influence foraging behaviour affecting the size of the foraging area, distance foragers work from the hive, trip duration and size of pollen loads.

The main objectives of this trial (chapter 5) were to determine the relative preferences of *B. terrestris* on four selected crops and the influence of food (pollen and nectar) availability, weather and competition on this preference (criteria 7,8,9 chapter 3). The method of food gathering by workers was also examined.

Because a management system required food for colonies throughout an extended period (Sept.- Nov.), it was inappropriate to base crop preference on numbers of foragers recorded on any one day at any single time. Also crop preference was likely to be influenced by other factors (chapters 1 and 4). Crop preference was therefore studied throughout the season. A concurrent trial monitored the growth and food gathering of ten colonies maintained on site in heated observation hives housed in a caravan (chapter 6). Workers from these colonies

foraged on the test crops and were distinguished from feral bumble bees by white markings painted on the thorax.

5.1 Daily and seasonal crop preference of *B. terrestris* and honey bees

The aim of this section was to determine the daily and seasonal trends of crop preference for *B. terrestris* and honey bees. A comparison of *B. terrestris* and honey bees determined the extent of interspecific competition for bee forage. Male, queen and worker *B. terrestris* were compared to assess differences in foraging preference. Feral and laboratory reared foragers were compared to determine the degree of intraspecific competition and whether differences in foraging preference occurred.

5.1.1 Methods

Bee density

Bee density was monitored at two-hourly intervals (from 8am to 6pm) on the four crops twice weekly (Tuesday and Saturday) for 11 weeks (8 September - 21 November). Note: Daylight Saving started 25 October 1987 so for standard time, subtract one hour from subsequent times recorded after this date. The same route was walked by two people, on either side of the 16 plots every two hours. Relative distributions of five bee classes/plot on four crops were recorded as follows:

1) *B. terrestris* nectar gathering workers.
2) *B. terrestris* pollen gathering workers.
3) *A. mellifera,* honey bees
4) *B. terrestris* queens.
5) *B. terrestris* males.

Bee classes 1 and 2 were further subdivided into marked and unmarked.

Relative distributions of five bee classes on the four crops at five daily time intervals over 22 recording days were analysed using a three-way ANOVA, treating rows and columns of the Latin square as blocks. Data for the five bee classes were examined separately to determine conformity to ANOVA assumptions. Normality and variance equality assumptions were not met and transformations were unsuccessful in improving data normality. Finally, data were ranked and normalised using a nonparametric ANOVA; this being necessary to take account of the large number of zeroes. A full factor three-way ANOVA of ranked bee numbers by bee class, crop, time and day was calculated. This included linear, quadratic, cubic and quartic polynomials to indicate the shape of data distributions. While the validity of this ANOVA of 8800 observations was questionable,

due to differences in variances between bee classes and between days and because days and bee classes were not strictly treatments, the analysis did illustrate overall trends not obtained when the data were separated into individual recording days. Subsequently, the data were reanalysed for bumble bees only.

To assess the significance of bee distributions on each day, the data were split by bee class for each day and reanalysed with a square root transformation and a two-way ANOVA of transformed bee numbers by crop by time interval. Swede failed to flower for the first 11 days so was excluded from the analysis for this period. The treatment means were compared using least significant differences (L.S.D.) calculated from standard errors of differences of means (S.E.D.).

A comparison of marked and feral nectar and pollen gatherers was analysed for days 9-22. The data were split by bee class for each day and reanalysed as above.

5.1.2 Results

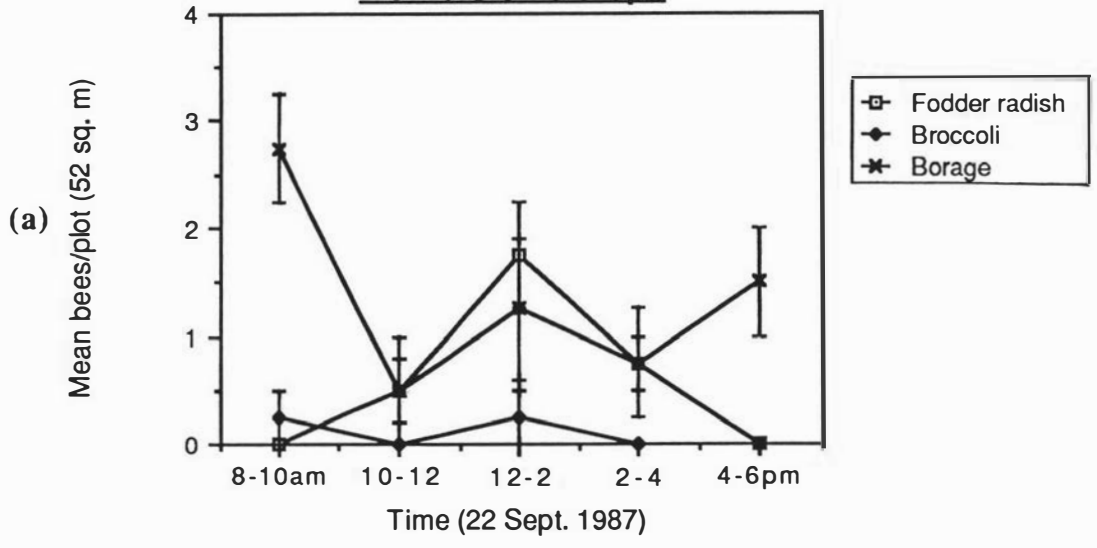
B. terrestris workers

During the first half of the season (8 Sept.-13 Oct.), workers foraged throughout the day, preferring borage, with broccoli second and fodder radish third choice. Swede did not flower during this period. The crop preference changed very little later in the season with the overall order of crop preference for nectar gatherers as follows: borage > fodder radish > swede = broccoli; and for pollen gatherers: borage > fodder radish = broccoli > swede (appendix tables A5.1,A5.3,A5.4).

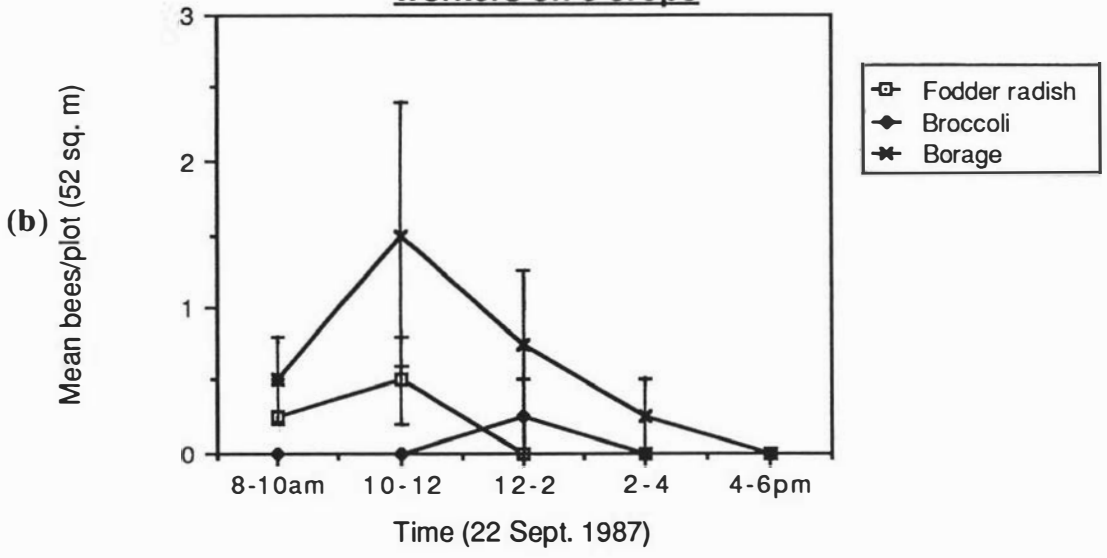
On cold days (e.g. 12 Sept. and 10 Oct.), with temperature maxima of 12 C, borage was the only crop foraged upon. However, on milder days (e.g. 22 Sept. and 6 Oct.; daily maxima 16 and 20 C resp.) with higher light intensity, pollen gatherers still preferred borage, while nectar gatherers were found in higher numbers on fodder radish (figs. 5.1a,b,d,e,f). From 17-24 Oct. both nectar and pollen gatherers foraged on borage from 8-10am and again after 2pm and on fodder radish from 10am to 6pm (figs. 5.2a,b,d,e). From 27 Oct.- 3 Nov. nectar gatherers were equally divided between fodder radish and borage. Borage was preferred from 8am-12noon, while fodder radish was preferred from 10am-6pm (figs. 5.3a,b,d,e). Pollen gatherers showed no crop preference after 27 Oct., harvesting pollen from all four crops.

From 6 Oct. - 21 Nov. marked nectar and pollen gatherers from laboratory rearing also foraged on the crops with numbers and distribution being compared with unmarked feral foragers. Feral nectar gatherers had crop preferences on 11 days; the preference being; borage > fodder radish > swede = broccoli. Marked nectar gatherers had significant

Figure 5.1. Number of B.terrestris nectar gathering workers on 3 crops



Number of B.terrestris pollen gathering workers on 3 crops



Number of honey bees on 3 crops

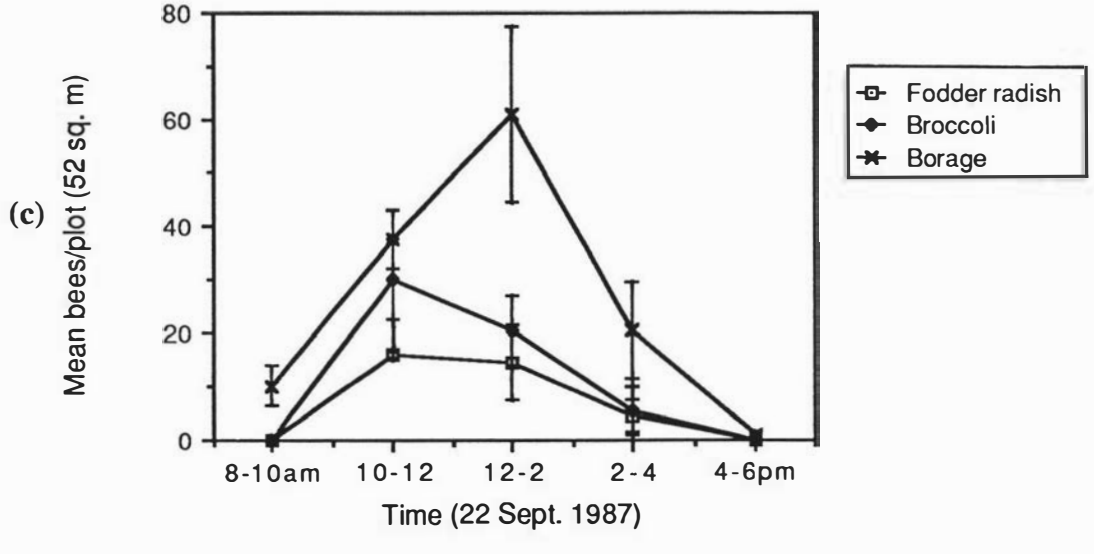
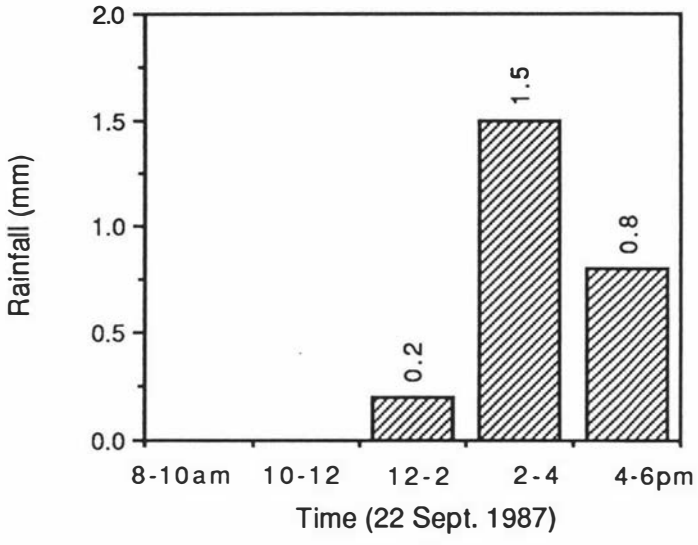
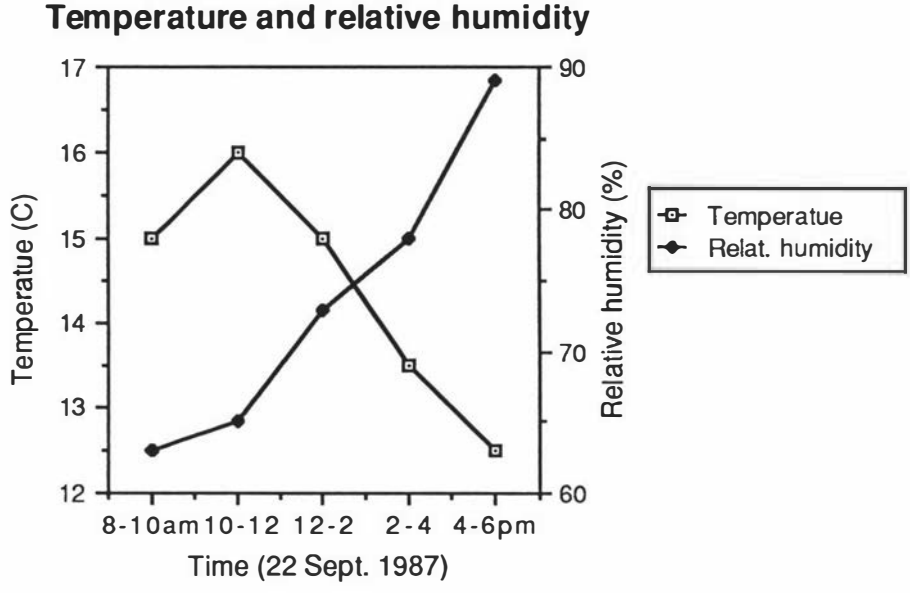


Figure 5.1. **Rainfall**

(d)



(e)



(f)

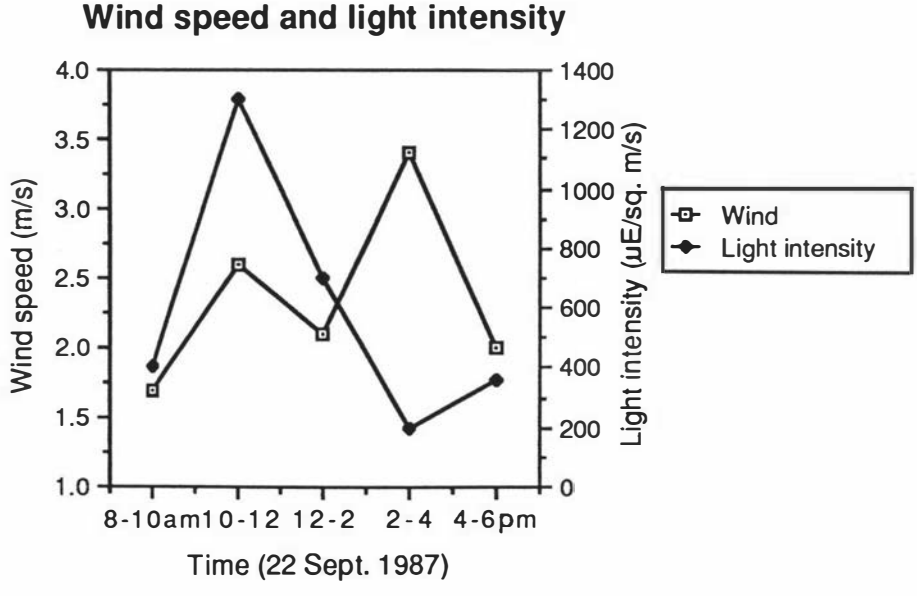
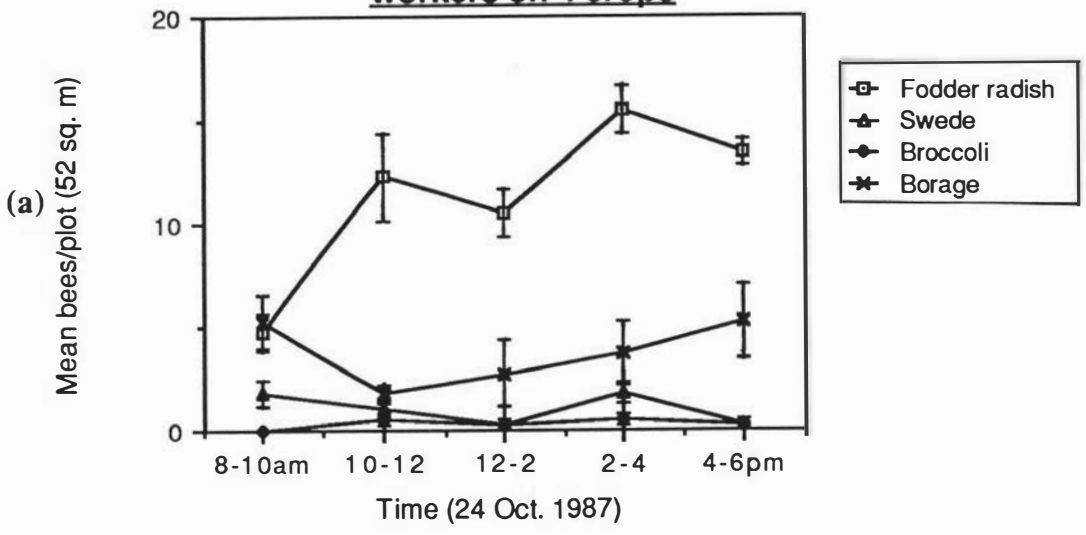
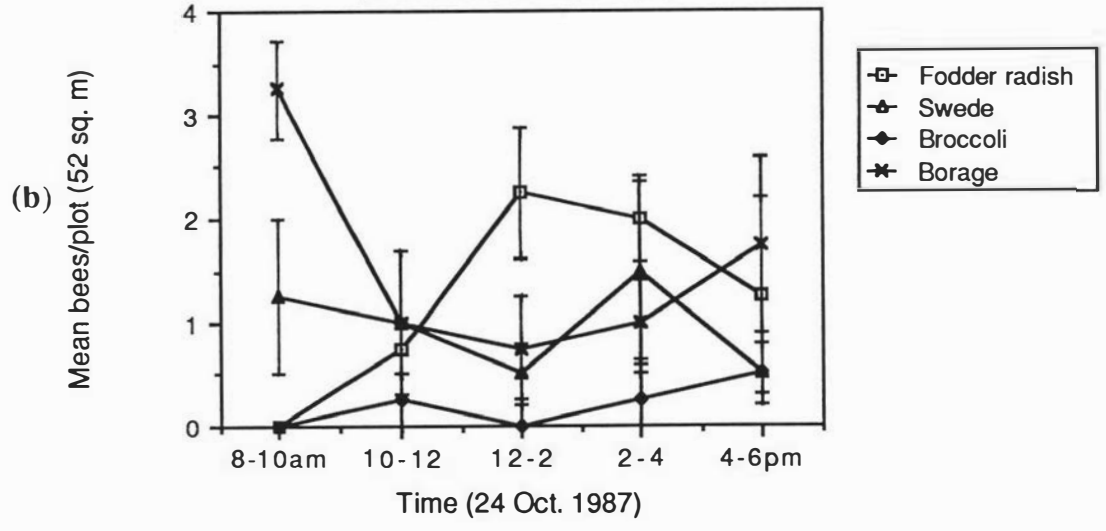


Figure 5.2. Number of B.terrestris nectar gathering workers on 4 crops



Number of B.terrestris pollen gathering workers on 4 crops



Number of honey bees on 4 crops

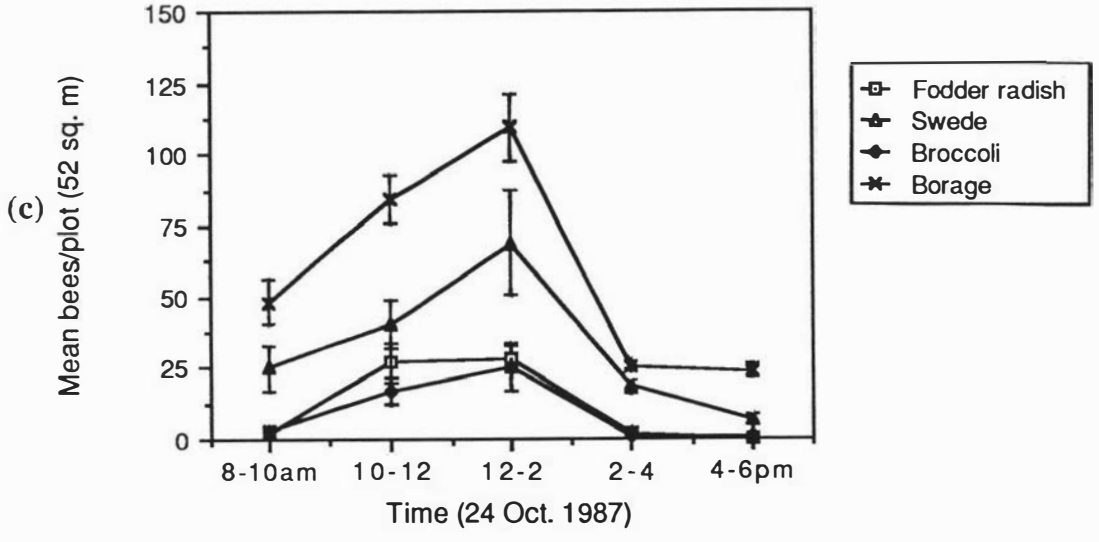
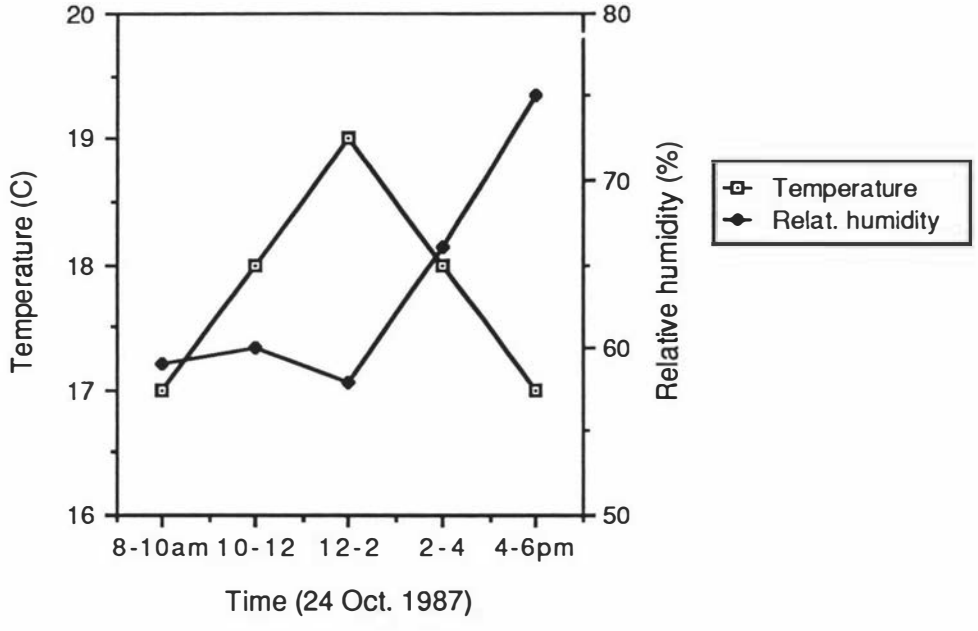


Figure 5.2. Temperature and relative humidity

(d)



(e)

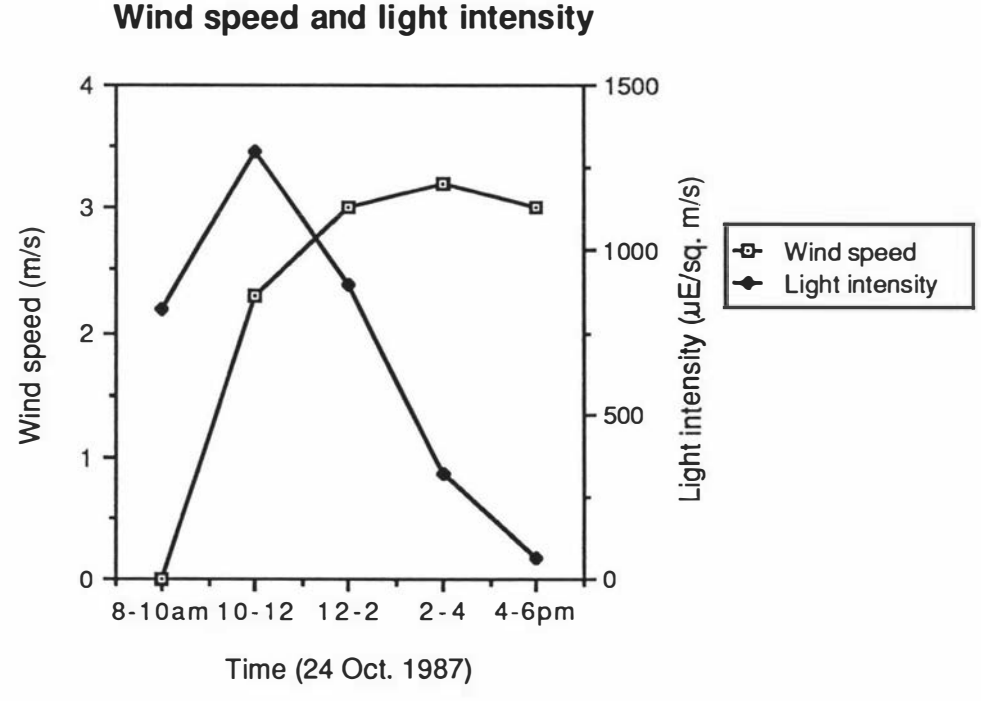
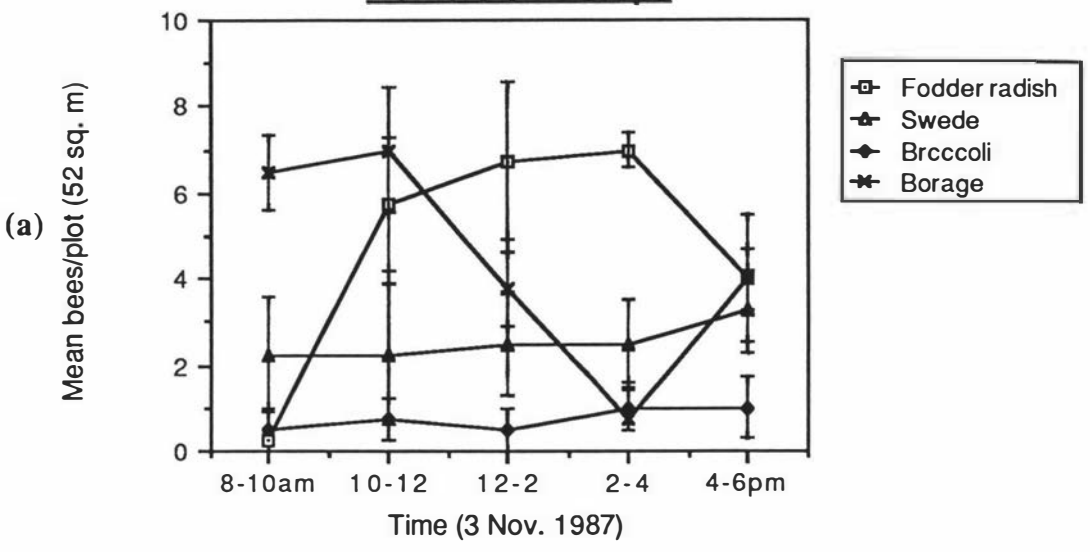
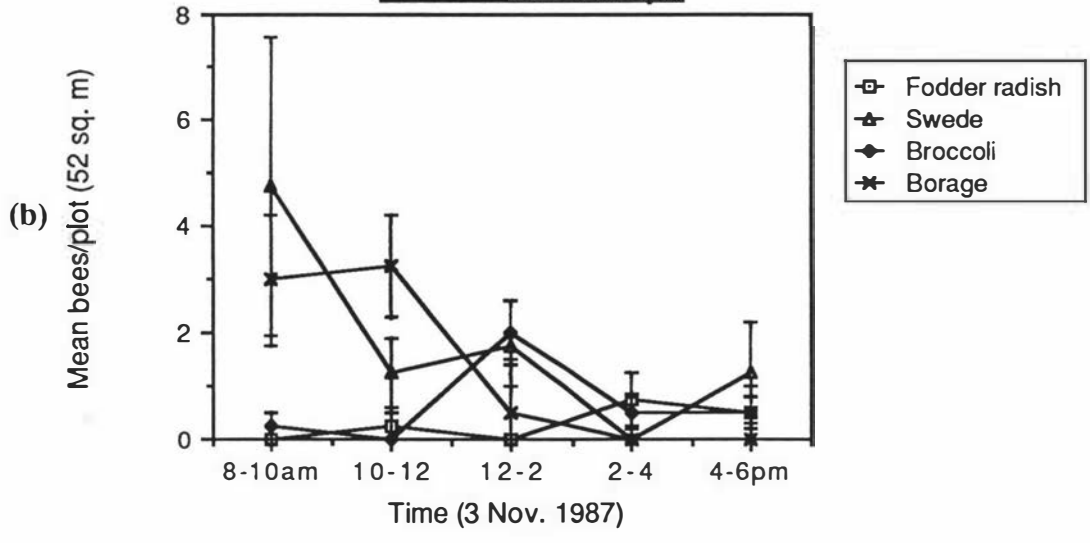


Figure 5.3. Number of B.terrestris nectar gathering workers on 4 crops



Number of B.terrestris pollen gathering workers on 4 crops



Number of honey bees on 4 crops

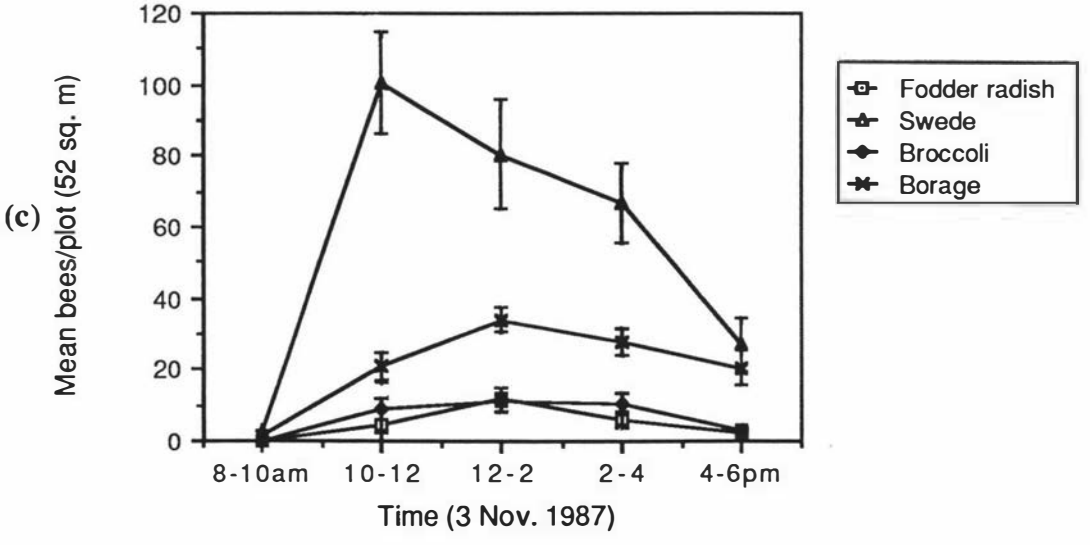
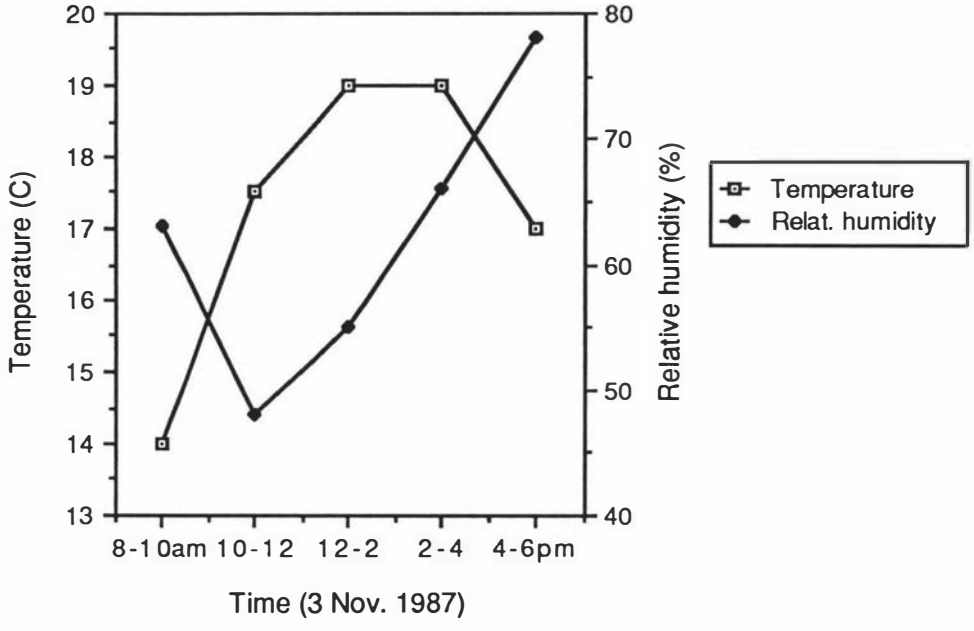
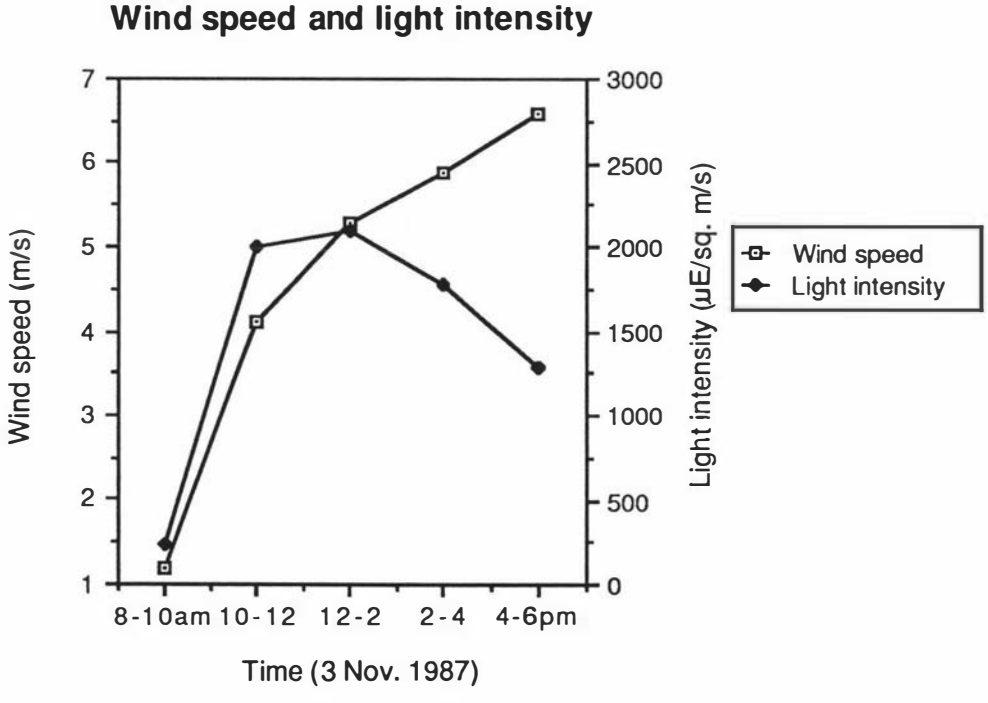


Figure 5.3. Temperature and relative humidity

(d)



(e)



preferences on ten of the 14 days of comparison; this preference being: borage = fodder radish > swede = broccoli (appendix tables A5.2,A5.5). Whereas marked nectar gatherers foraged on borage from 8am-12noon and on fodder radish from 10am-4pm, feral nectar gatherers foraged for longer periods on borage (8am-4pm) and fodder radish (10am-6pm).

Feral pollen gatherers exhibited significant crop preferences on six days, the preference was: borage > fodder radish = broccoli = swede. Marked pollen gatherers exhibited preferences on only two of the 14 days (appendix table A5.2) with little overall preference among the crops. While marked pollen gatherers foraged on borage from 8am-12noon showing no time preference on other crops, feral pollen gatherers also preferred borage before midday and fodder radish from 10am onwards.

B. terrestris queens

During the first half of the season, queens foraged throughout the day preferring borage with broccoli second and fodder radish third. From 3-6 Oct., with warmer temperatures, queens were found in higher numbers on fodder radish. Between 17-27 Oct. queens preferred fodder radish with borage second. Overall, the seasonal preference was: borage = fodder radish > broccoli = swede. Queens foraged on fodder radish between 10am-4pm with no time preference for other crops. Queens showed no preference after 27 Oct. (appendix table A5.1). Queens were not observed collecting pollen from any of the crops, only nectar.

Queens were all of feral origin with numbers decreasing after 17 Oct., and no queens were recorded after 8 Nov.

B. terrestris males

Numbers were too low to show any preferences before 26 Sept. Between 26 Sept. - 13 Oct. males preferred borage with broccoli second and fodder radish third (appendix table A5.1). Males foraged in the afternoon on borage and broccoli. Although borage was preferred during this period, higher numbers were found on fodder radish on milder days. From 17-27 Oct., males foraged on borage from 8-10am then after 2pm and on fodder radish from 10am-6pm. From 31 Oct. - 16 Nov. males foraged equally on broccoli and swede, preferring swede before and after the peak in honey bees and on broccoli from midday onwards. The overall seasonal crop preference was: broccoli = borage > fodder radish = swede.

After the initial low numbers of males the numbers peaked on 17 Oct. All males were of feral origin.

A. mellifera

During the first half of the season, honey bee numbers were low; the preferred crop being borage with broccoli second and fodder radish third (appendix table A5.1). Honey bees foraged mainly from 10-4pm with few honey bees early or late in the day (fig. 5.1c). On 3-6 Oct. (daily maxima 16 and 20 C resp.), light intensity was higher and honey bee density increased to 100 bees/plot during midday on borage.

Between 17-27 Oct. honey bee numbers were high on borage (> 100/plot) especially between 10am-4pm (fig. 5.2c). Swede flowered from 17 Oct. onwards and peaked in bloom from 31 Oct. - 10 Nov. Honey bees switched to foraging on swede initially (e.g. 3 Nov, fig. 5.3c), then foraged equally on swede and borage from 8-10 Nov. The overall seasonal crop preference was: borage > broccoli > fodder radish = swede.

White clover flowered in nearby paddocks from late October providing an additional flower source for both honey and bumble bees.

Seasonal abundance of *B. terrestris* and *A. mellifera*

The order of seasonal bee abundance for the five bee classes was: honey bees > *B. terrestris* nectar gatherers > pollen gatherers > males > queens (appendix table A5.3, figs. A5.1a-e). Comparing feral with indoor reared bee abundance indicated more feral *B. terrestris* workers than indoor reared bees were present. The overall bee abundance was: feral nectar gatherers > marked nectar gatherers > feral pollen gatherers > marked pollen gatherers.

5.2 Bee distribution in relation to weather conditions and pollen and nectar availability.

The aim of this section was to determine whether diurnal changes in *B. terrestris* and honey bee foraging were related to diurnal changes in weather and/or food availability of the four crops.

5.2.1 Methods

Bee distribution on crops was analysed in relation to pollen and nectar availability in exposed flowers. The food variables were treated as covariates to take account of any relationship between daily timing of pollen availability and nectar secretion. This was independent of the crop species and may have been a negative relationship.

The five bee classes were normalised, and separate three-way ANOVAs, (factors of recording day (which accounted for weather variation), crop and time (of day)) adjusted for covariates for each bee class, were calculated.

During five time intervals (three for bagged food data) throughout 22 recording days, multiple regression analysis compared the mean number of five bee classes (transformed ln(x + 1)) on four crops with:

1) Five weather variables (temperature, R.H., light intensity, rainfall, wind speed).
2) Pollen and nectar energy available from exposed flowers (mean from four crops).
3) Pollen availability and nectar energy production from bagged flowers.

Weather variables were compared with, firstly, exposed pollen and nectar and, secondly, bagged pollen and nectar production and were regressed against each bee class. Regression analysis assessed the data and selected the independent variable which explained the greatest percentage variance of bee numbers on the first 'run'. On subsequent 'runs', the second most important variable was selected, then the third and so on. In cases where an independent variable explained no further percentage variance for a particular bee class, that variable was not added to the final analysis.

To determine what factors influenced the changeover from nectar and pollen foraging on borage to nectar collection on fodder radish, the pollen and nectar gatherers on these crops were compared over the 22 day period with variables which may have influenced this change in foraging. Weather variables, pollen availability, nectar production and numbers of *B. terrestris* on both crops and honey bees on borage, were analysed using a multiple regression.

5.2.2 Results

Covariate analysis suggested the distribution of nectar gatherers, queens and males was not significantly affected by the covariates ($p=0.627$, $p=0.496$, $p=0.733$ respectively, appendix tables A5.6,A5.7,A5.8). This does not necessarily mean that these three bee classes are uncorrelated with food availability. However, a smaller amount of the variation was explained by the mean pollen and nectar energy availability from exposed flowers of all crops combined compared to that explained by the weather and crop effects. But, it may be possible that only one crop was important in explaining bee distribution in relation to the food available. In contrast, pollen gatherers and honey bees were significantly influenced by covariates ($p=0.024$, $p<0.001$ resp., appendix tables A5.9, A5.10). However, pollen and nectar in this analysis only accounted for a small amount of the variance respectively and the analysis did not indicate whether pollen or nectar energy or both were influencing bee

numbers. The covariance efficiency (COV EF) was lowest for the crop effect (0.290) in all five ANOVAs, indicating the different crops accounted for the greatest variation in pollen and nectar energy availability. As seen from chapter 4, this was mainly due to pollen availability; whereas nectar energy was more influenced by weather conditions of light intensity and temperature. The ANOVAs also indicated the comparative importance of time of day on foraging of honey bees and males (appendix tables A5.8,A5.10). These results were inconclusive, so regression analysis was introduced.

Multiple regression analysis indicated the order of sensitivity to weather influencing foraging for the five bee classes was: *A. mellifera* (50.9%) > *B. terrestris* nectar gatherers (31.3%) > *B. terrestris* males (23.8%) > *B. terrestris* pollen gatherers (7.0%) > *B. terrestris* queens (5.6%) (appendix table A5.11). Foraging increased with an increase in temperature and decrease in relative humidity (R.H.). Honey bees were very sensitive to weather and only foraged in numbers on fine, calm and warm days. Pollen gatherers and males were negatively influenced by light intensity possibly suggesting that more of these bees foraged earlier or later (males) in the day when light levels were lower.

The most informative multiple regression analysis (i.e. that explained the greatest percentage variation) indicated the order of sensitivity of the five bee classes to weather and food availability was: *A. mellifera* (light intensity, temperature and wind; 51.9%) > nectar gatherers (temperature, nectar production and R.H.; 47.6%) > males (temperature, rain and exposed pollen; 35.7%) > queens (light intensity, exposed nectar and wind; 26.9%) > pollen gatherers (15.3%) (appendix tables A5.12, A5.13). From the regressions and correlation matrix (table 5.1), it can be concluded that honey bees, *B. terrestris* nectar gatherers and males increase their foraging with temperature. Also honey bees and *B. terrestris* nectar gatherers forage more when there is high nectar production (rate of secretion) but 'graze' the standing crop of nectar so heavily that the nett availability of nectar in exposed flowers is lower than when fewer bees are foraging.

Nectar and pollen gathering by *B. terrestris* workers on borage were highly correlated (r=0.534); this food gathering increased with an increase in borage nectar production and with more pollen available in borage flowers. Less pollen was collected in strong wind and low temperature. The switch to nectar gathering on fodder radish was associated with an increase in honey bees on borage, a decrease in nectar and pollen in borage flowers, an increase in nectar production in fodder radish flowers and an increase in temperature (table 5.2, appendix tables A5.14, A5.15). The relation between nectar gatherers and honey bees on borage although negative was not significant, while some results suggested a positive correlation between nectar gatherers on borage and fodder radish.

Table 5.1. Correlation matrix of 5 bee classes with weather variables, food from exposed flowers, bagged pollen and nectar production (rate of secretion).

DF = 107	Nectar gatherers#	Pollen gatherers#	Honey bees#	Queens#	Males#
#Temperature	0.493***	0.093n.s.	0.513***	-0.063n.s.	0.452***
#R.H.	-0.371***	-0.073n.s.	-0.553***	-0.219*	-0.239*
#Wind speed	-0.031n.s.	-0.082n.s.	-0.142n.s.	-0.102n.s.	0.019n.s.
#Light intensity	0.256**	-0.111n.s.	0.558***	0.161n.s.	0.121n.s.
#Rainfall	-0.201*	-0.073n.s.	-0.217*	-0.118n.s.	-0.135n.s.
Exposed pollen	0.073n.s.	-0.118n.s.	0.011n.s.	-0.012n.s.	-0.137n.s.
Exposed nectar (energy)	-0.202*	0.085n.s.	-0.411***	0.162n.s.	-0.094n.s.
DF= 64					
Bagged pollen	0.297*	0.217n.s.	0.210n.s.	-0.071n.s.	0.273*
Nectar production	0.477***	0.205n.s.	0.299*	-0.054n.s.	0.237n.s.

= transformed $\log_e (x + 1)$

$r_{0.05(2)[64]}=0.242$ $r_{0.05(2)[107]}=0.188$
$r_{0.01(2)[64]}=0.315$ $r_{0.01(2)[107]}=0.246$
$r_{0.001(2)[64]}=0.396$ $r_{0.001(2)107]}=0.311$

Table 5.2. Correlation matrix of variables associated with nectar and pollen gathering on borage and the 'switch' to nectar gathering on fodder radish.

DF = 107	Nectar gatherers on borage#	Pollen gatherers on borage#	Nectar gatherers on f. radish#
Nectar gatherers on borage	1.000	0.534***	0.147n.s.
Pollen gatherers on borage	0.534***	1.000	0.086n.s.
Nectar gatherers on f.radish	0.147n.s.	0.086n.s.	1.000
Pollen gatherers on f.radish	0.018n.s.	0.136n.s.	0.658***
Honey bees on borage	- 0.093n.s.	- 0.059n.s.	0.673***
Exposed nectar on borage	0.088n.s.	0.080n.s.	- 0.385***
Exposed pollen on borage	0.255**	0.033n.s.	- 0.201*
Exposed nectar on f.radish	0.120n.s.	0.221*	0.017n.s.
DF = 64			
Nectar production on borage	0.390**	0.255*	- 0.045n.s.
Nectar production on f.radish	0.181n.s.	- 0.033n.s.	0.354**

= transformed $\log_e (x + 1)$

5.3 *B. terrestris* nectar and pollen gathering

The aim was to observe free and confined foraging workers to determine how food was removed, how much food was removed and what proportion of food was left in the flower.

5.3.1 Methods

5.3.1.1 Workers confined on borage and broccoli

Comparison between foraging on borage and broccoli provided data on worker foraging strategies on flowers with different rewards, different presentation mechanisms and contrasting arrangement of the inflorescence.

Two wooden cages, 4 x 2 x 1.75m high were constructed and covered in 32% 'Donaghy's' shade cloth. One cage was positioned on an $8m^2$ plot of borage and another on the same area of broccoli.

From 15 Oct. - 16 Nov. 1987, individual workers leaving from free foraging colonies (chapter 6) were introduced into a wooden box, 12 x 8 x 6 cm high, after weighing each bee (Mettler balance AE160) to the nearest milligram. The box was transferred into a cage and the trapdoor opened allowing the bees to forage on the crops provided. Temperature, wind and light intensity were recorded at a height of 1m within the cage before and after observations using a shaded max/min thermometer, hand-held anemometer AM500 and Licor light meter, respectively (see chapter 4).

Recorded parameters were: foraging time, change in bee weight, percentage of time grooming, number of flowers visited, mean flower handling time, weight of pollen collected, sugar concentration of nectar and volume of nectar. The volume of nectar collected by each bee was calculated from change in bee weight, using a conversion factor to account for the difference in weight of equal volumes of sugar solution and water (for given temperature and sugar concentration, Iscotables 1974). Pollen loads were removed from corbiculae prior to measuring bee weight.

Sugar concentration of regurgitated nectar was determined with a refractometer and volume of nectar from flowers was recorded with a micropipette. Foragers were caught when they lost interest in the crop or when grooming stopped. Samples of visited flowers (n=12) were, in some cases, analysed to determine the volume of nectar remaining in the flowers.

5.3.1.2 Free foraging on borage

Few *B. terrestris* workers could be encouraged to collect pollen in cages,so observations had to be made on unconfined pollen gatherers.

Twenty-five borage flowers were examined prior to and after bee visits; the latter being recorded by picking flowers visited as the bee moved on to adjacent flowers. Visited flowers were examined to determine stage of development and percentage of pollen remaining in anthers. Each anther was examined,and an estimate of the percentage of pollen remaining was made from the length of the longitudinal split of each anther locule. Although a correlation between length of dehiscence and pollen content was not determined,the undehisced length of the locule contained pollen;whereas the dehisced length was empty.

A separate trial of tagged flowers examined exposed flower development and anther dehiscence. Ten borage flowers were tagged on 19 October 1988, the night before opening. Progressive development of stigma/style and percentage pollen dehiscence of anthers was monitored at midday for the next two days.

5.3.2 Results

5.3.2.1 Workers confined on borage and broccoli

The data for borage and broccoli are summarised in table 5.3 (see appendix tables 5.16a,b). Nectar gatherers on borage brushed pollen from the body surface with forelegs, transferred it to mid and hindlegs from where it was finally removed altogether. Grooming of all body regions often occurred while the bee was suspended from a flower or leaf attached only by the tarsal claw of one foreleg. Foragers spent considerable time basking in the sun. Nectar gatherers in cages did not vibrate ('buzz') anthers for pollen. In contrast the one pollen gatherer observed, buzzed 21% of flowers visited, and pollen dispersed on the ventral surface of the abdomen was transferred to the hind legs where it was packed onto the corbiculae. Some foragers sampled flowers that had fallen to the ground, which still appeared to have small amounts of nectar.

Foragers on broccoli worked up the spike of flowers before moving to the base of the next spike on the same plant. Most flowers on one plant were visited before the bee transferred to the next plant. The most efficient foragers 'robbed' nectar through the separating calyces and corolla or alternatively bit holes through the calyx with their mandibles. Most workers walked between flowers. 'Robbing' reduced the amount of pollen deposited on the head of the bee,so less time was wasted grooming pollen and more

Table 5.3. Comparison of *B. terrestris* worker foraging efficiency, food availability and weather conditions while foraging on $8m^2$ of borage and broccoli in cages (Oct.-Nov.1987),n=7.

	Borage Mean±S.E.	Broccoli Mean±S.E.	df	t test T value	Prob.	Signif.
BEES						
Foraging time(min)	15.2± 2.6	17.9± 1.7	12	-0.89	0.393	n.s.
Grooming time(min)	9.4± 1.2	10.1± 1.0	12	-0.43	0.677	n.s.
No.flowers visited	34.6± 6.5	59.6± 6.8	12	-2.66	0.021	*
Mean handling time/flower (s)	29.1± 3.5	19.0± 2.3	12	2.42	0.032	*
Volume nectar collected (µl)	36.7± 9.6	33.6± 7.9	12	0.25	0.805	n.s.
Conc. of nectar (% sugar)	54.4± 0.6	54.9± 0.1	6.8	-0.73	0.491	n.s.
Weight of pollen collected(mg;n=1)	25	6	-	-	-	-
FLOWERS						
Mean nectar/ flower (µl) n=20	1.5± 0.3	0.5± 0.0	6.2	3.52	0.012	*
Mean nectar conc./ flower (% sugar)	50.1± 1.5	52.0± 1.8	12	-0.78	0.449	n.s.
Mean proportion flowers releasing pollen	0.9± 0.1	1.0± 0.0	6.1	-1.83	0.117	n.s.
Predicted no. flowers visited #	31.7±11.5	69.4±14.6	12	-2.03	0.066	n.s.
WEATHER						
Mean light intensity ($\mu Em^{-2}s^{-1}$)	1431±176	1467±111	12	-0.18	0.863	n.s.
Mean temperat. (C)	17.3± 1.1	19.3± 0.3	7.0	-1.65	0.143	n.s.
Mean wind speed (ms^{-1})	1.6± 0.1	0.9± 0.2	12	3.21	0.008	**
No. flowers visited on borage	Observed 34.6± 6.5	Predicted 31.7±11.5	12	-0.22	0.833	n.s.
No. flowers visited on broccoli	59.6± 6.8	69.4±14.6	12	0.61	0.552	n.s.

\# = (nectar collected)/(nectar per flower)

time spent foraging for nectar. Handling time of robbing bees was about 12.5 seconds/flower compared with 15-30 seconds/flower for bees making 'legitimate' visits. In some cases, flowers without petals were visited. Grooming with hind legs sometimes occurred while probing for nectar. Only one of seven foragers tested per crop collected pollen during approaches to the flowers.

Foraging on borage compared to broccoli was made under similar light and temperature levels. But wind speed was higher on borage making the comparison questionable (table 5.3). The volume of nectar was higher on borage than broccoli. This may explain the significantly longer handling time/flower for borage. However, the densely packed flowers on broccoli allowed foragers to visit more flower per unit time than on borage. Thus although broccoli had less nectar/flower than borage, more flowers were processed, enabling foragers to collect as much nectar (µl/minute) on broccoli as on borage.

Two workers confined on borage during 1988 (Sept.-Oct.) with different rewards/flower, showed different foraging strategies. On 29 September, one worker was released into a cage with three foraging honey bees. The mean nectar/ flower was 2µl at 55% sugar concentration. The calculated number of flowers visited (increase in nectar volume per bee/mean nectar volume/flower) was 21. The observed number of flowers visited was 39; hence the bee should have removed a mean of 1.1µl of nectar/flower, leaving an estimated 0.9µl/flower. In fact, a sample of 12 flowers visited had 0.5µl remaining/flower. The bee remained in a small area, revisiting several flowers. On 17 October, another worker was released in the cage with ten honey bees and three bumble bees foraging. The nectar volume/flower was 0.05µl at 55%. The worker showed no weight gain during foraging. No nectar was recorded remaining in flowers visited and the forager visited flowers which were widely dispersed.

5.3.2.2 Free foraging on borage

The proboscis was extended during foraging and nectar collection was observed as the bees vibrated flowers for pollen. A number of flowers were either landed upon or approached to within 1cm then suddenly avoided, probably as these flowers contained little pollen, nectar or both. Variation in handling time and percentage of flowers vibrated was recorded (table 5.4). Most of the flowers visited were blue and staminate i.e.the stamens were mature with a short stigma enclosed within the anthers (in pistillate flowers, the stigma/style extended above the ring of stamens). The estimate of pollen remaining in flowers after bee harvesting (40-62%) was more than the mean amount recorded from a representative sample (n=25) of surrounding flowers (32%).

Table 5.4. *B. terrestris* worker pollen harvesting on borage (13 October 1988) at 20 C.

Forager	1	2	3	4
No. flowers visited	16	28	11	19
% flowers 'sampled,' vibrated (buzzed) for pollen	100	36	100	100
Mean handling time/flower (s)	6.8	5.5	7.8	4.5
% blue flowers	-	86	67	83
% staminate flowers	-	86	100	100
Mean % pollen (n=25) in exposed flowers	32	32	32	32
Mean % pollen remaining in visited flowers (±S.E.)	-	48.5±6.0 (n=6)	51.7±7.4 (n=6)	40.0±6.7 (n=12)

Of the ten flowers tagged and recorded for two days, all flowers were staminate on day one with a mean of 20% of pollen remaining by noon on the first day. On the second day, all anthers were empty. However, eight out of ten flowers were still staminate, while a number of untagged flowers appeared to have developed to the pistillate stage. Heavy rain and strong winds may have affected the outcome of this trial.

Honey bees collecting borage pollen were uncommon, especially towards midday during October-November 1988. Pollen loads of honey bees on borage were small (approximately 2-6mg) while bumble bee loads were often very large (16-30mg). Pollen appeared to be collected secondarily to nectar by honey bees on borage, while honey bees observed on nearby plots of kale were collecting comparatively larger loads (6-12mg).

5.4 Discussion

Borage was the major crop utilised by *B. terrestris* workers early in the season. High nectar energy yields and poricidal-like anthers made this crop particularly attractive for nectar and pollen. Fodder radish, a minor source of food early in the season, became a major nectar source for *B. terrestris* later in the season when honey bees depleted the nectar standing crop on borage.

Heinrich (1976, 1979a, 1979b) explains that in a field of mixed flowers, individual bumble bees specialise by 'majoring' on a single flowering species (e.g. borage) while occasionally sampling flowers with 'minor' rewards (e.g. remaining crucifers). This strategy enables individual foragers to monitor food rewards on less favourable flowers and, in cases where nectar levels shift among these flower species (e.g. fodder radish), foragers can switch their foraging onto flowers which are becoming more favourable as their major food source (borage) declines (Oster and Heinrich 1976). Flower constancy allows specialisation without dependence on a single flower species (Eickwort and Ginsberg 1980).

Major shifts in food (resource) availability were influenced by weather conditions and inter- and intraspecific competition. Early in the season intraspecific competition from feral *B. terrestris* was unlikely to have made a significant impact on the foraging behaviour of artificially reared colonies because numbers of feral workers were too low. Later in the season this competition increased as numbers of workers increased. Central place foraging theory (Prys-Jones and Corbet 1987) would predict marked workers would be at a competitive advantage due to proximity to the crop with minimal time devoted to transporting food to the colony. This may also explain greater crop constancy of feral pollen gatherers. Due to greater distances to return to hives, these bees may have foraged on the most long term rewarding crop for longer periods of the day rather than making quick profits by

foraging on a wider variety of crops, thus feral bees show greater crop fidelity than workers from nearby hives.

Honey bee numbers were low early in the season due to a high sensitivity to weather conditions. However, later in the season, improving weather resulted in higher numbers of bees on the crops due to increasing temperature and light intensity and reduced wind, rain and relative humidity.

When two species share the same resource (e.g. pollen and nectar) and the available supply of this resource is smaller than the sum of the requirements of the coexisting species, competition may occur (Sale 1974; Vintrova 1981). This appeared to be the situation between *B. terrestris* workers and honey bees. Overlapping requirements for a shared resource do not necessarily mean competition unless the resource is limiting (Heinrich 1976). Two factors were responsible for niche overlap between *B. terrestris* and honey bees. The tongue lengths were the same (5.5mm, chapter 3). This is the major factor determining niche overlap of flower visiting bees (Inouye 1978), and secondly both species preferred borage as their major food source. The area of borage and the amount of pollen and nectar per unit area were limited and food, especially nectar, was rapidly depleted when honey bee numbers increased to over 100 per plot ($2/m^{2)}$

In order to demonstrate that competition exists, it would be necessary to show that both species prefer the same resource and that one species modifies its behaviour to accomodate the competitor, and that in the absence of competition the original species resumes 'normal' behaviour. *B. terrestris* and honey bees both foraged for nectar and pollen from borage later in the season as weather improved. On mild days, fodder radish also secreted considerable nectar. However, the length of the corolla provided a barrier for nectar removal by *B. terrestris* workers and honey bees.

Food is partitioned on the basis of tongue length and corolla tube length. Two species with the same proboscis length may be able to coexist if one species can 'rob' flowers while the other does not (Inouye 1977). This was the case with *B. terrestris* workers. They robbed nectar from fodder radish by biting holes at the base of the corolla ('primary robber') to obtain nectar from a crop otherwise unexploitable to either species. This also enabled honey bees to behave as 'secondary robbers' removing nectar from holes bitten by *B. terrestris* workers. Honey bees did not bite holes in the calyx of fodder radish flowers. Both honey and bumble bee workers and males could also 'rob' nectar from a few fodder radish flowers that separated at the base of the calyx after 1-2 days or from flowers where the calyx had fully separated after 2-3 days. Honey bees and males were, therefore, not completely excluded from nectar removal from fodder radish.

This 'exploitative' competition (Inouye 1978; Heinrich 1976) from honey bees on borage resulted in a shift of *B. terrestris* from borage to fodder radish apparently during warm weather. Some evidence for relocation of *B. terrestris* at certain times of day also existed. Early in the season, *B. terrestris* workers foraged for pollen and nectar on borage throughout the day. Later in the season on mild days, when honey bee numbers increased, *B. terrestris* foraged on borage early (pollen and nectar) and later (nectar) in the day, switching to fodder radish (nectar) in mid-morning and staying in relatively high numbers on this crop throughout the rest of the day. This behaviour avoided the high numbers of honey bees on borage from mid-morning to mid-afternoon.

Borage anthers dehisce early in the day; thus cold-tolerant *B. terrestris* pollen gatherers had an opportunity to harvest borage pollen by vibration of anther locules prior to the arrival of other 'non-buzzing' bees e.g. honey bees (Heinrich 1972; Thorp and Estes 1975). The remaining crops were harvested for pollen after borage had been exploited.

It could be argued that *B. terrestris* simply preferred fodder radish over borage at certain times of the day and the season and that competition did not influence their preference. However, diurnal results of three recording days (22 Sept., 24 Oct., 3 Nov.) and seasonal trends indicated a transfer of bumble bees from borage to fodder radish as honey bee numbers and temperature increased. When honey bee numbers were divided between borage and swede, numbers of *B. terrestris* workers were divided between borage and fodder radish. With few honey bees, most *B. terrestris* workers foraged on borage. With more honey bees foraging on crops, greater amounts of pollen and nectar were removed. Also data from bagged and exposed flowers indicated that on days when bumble bees switched to fodder radish, the nectar and pollen levels in exposed borage flowers were very low, but somewhat higher in exposed fodder radish. The bagged flowers indicated that while fodder radish had high nectar production borage had by far the highest nectar energy levels. It seems unlikely that bumble bees alone would have depleted the nectar as this did not occur early in the season when few honey bees foraged. Levels of exposed borage pollen declined during the day when honey bees were abundant. Hence, if bumble bees were not 'early risers', much of the pollen would have been harvested by honey bees later in the day or lost by wind causing vibration of the dry pollen from the anther locule. The cruciferous crops showed little reduction in bagged pollen, possibly due to the presence of pollenkitt (Percival 1965) binding the pollen grains together.

Finally, it would seem likely that 'robbing' nectar from fodder radish by hole biting would increase handling time compared to nectar removal on borage, and if *B. terrestris* was not outnumbered on borage, it would be expected to remain on that crop.

The high numbers of honey bees recruited from nearby hives to forage on borage rapidly reduced the standing crop of nectar and pollen. Such exploitative competition between honey bees and bumble bees has also been reported by Wratt (1968), Liu *et al.* (1975) and D'Albore and D'Ambrosia (1981). The former two authors suggest that depletion of nectar by honey bees on a preferred crop to bumble bees either during the middle of the day or with increasing temperature, resulted in either a switch to pollen gathering (Wratt 1968) or a switch to other more attractive flowers (Liu *et al.* 1975). However, competition between honey and bumble bees may have an 'interference' component as some authors suggest (Holmes 1961; Benest 1976; Laroca and Winston 1978). Holmes found a tendency for bumble bees to leave areas crowded with honey bees when both were foraging on exposed honey bee comb. Benest (1976) found honey bees better tolerated joint foraging with bumble bees on dwarf dahlias than bumble bees did.

The ability of honey bees to communicate the whereabouts of the most rewarding crops results in very high numbers of bees recruited to a single crop during a certain period of the day. Honey bees remain in a small area approximately $100m^2$, returning to this area if food remains available (Free 1960). However, bumble bees, lacking communication, have to individually conduct their own sampling to 'test' flower rewards and are thereby less constant to one crop (Plowright and Laverty 1984).

A word of warning has been suggested by Prys-Jones and Corbet (1987) on the interpretation of bee count data. They suggest when nectar is abundant, a worker may spend a small proportion of a foraging trip actually on flowers compared with time spent travelling to and from the colony and depositing the load. Conversely, when nectar is scarce (often in the middle of the day), a large proportion of a worker's time will be spent on flowers. This may result in resources decreasing as numbers of bees increase and secondly, when estimating the extent of competition e.g. between *Bombus* and *Apis*, an overestimation of the times when large bee numbers are present but little food is available to any foragers may result. Both *Bombus* and *Apis* may forage during the middle of the day when nectar availability is often low. However, *Bombus* also forages earlier and later in the day when honey bees are not abundant and when nectar is abundant.

While some overestimation of competition at midday may have occurred for feral workers, the proximity of marked bumble bee colonies to the crop would have reduced this; also, the low nectar levels at midday resulted from high honey bee numbers. Removal of food early in the day by *B. terrestris* avoided competition on borage from honey bees. Bumble bee numbers were often relatively high in the morning even though in some cases nectar levels were low. A similar problem has been reported for interpreting bee counts in relation to pollen availability by Synge (1947), where pollen gathering numbers may drop

with high pollen availability. Synge suggests that if the number of pollen gatherers is related to pollen availability, then bee numbers should decline as pollen availability declines, otherwise other factors may be involved. This occurred for borage and swede but less for broccoli and fodder radish, indicating the level of utilisation of each crop.

Feral queens preferred borage early in the season for nectar, but they were not observed collecting pollen. As the standing crop of borage nectar was depleted, queens with a longer tongue (11mm) than workers foraged legitimately on fodder radish with a corolla tube depth of 10mm.

Males did not collect pollen but foraged for nectar from borage initially, then the remaining crucifers, especially broccoli, later in the season. The main foraging period was from midday onwards. Male bumble bees are solitary, visiting flowers to meet their own needs. Bertsch (1984) showed that males may gain water from flight metabolism and from nectar faster than they can lose it. They must therefore excrete large droplets of fluid and evaporate nectar by regurgitation onto the tongue as well as altering their foraging activity to acquire highly concentrated nectar sugar. This often means foraging later in the day when sugar concentrations are higher on crops. This may explain the afternoon foraging of males exhibited in this trial. Workers do not need to evaporate nectar or excrete large amounts of water except on very damp days (Brian 1952) because nectar can be concentrated by evaporation within the colony.

The preference of males for foraging during warm weather with low R.H. and rainfall recorded for this trial may have resulted from their small nectar demand, foraging only for themselves during these conditions. Due to competition for nectar on borage and being unable to reach nectar in fodder radish or bite holes in the corolla with undeveloped mandibles (but behaving as a 'secondary robber' after holes were bitten by workers), males may have resorted to broccoli as a nectar source. During bad weather males, may become inactive requiring little sustenance.

No direct correlation existed between flower density, flower production (chapter 4) and the distribution of bumble and honey bees on the four crops. If bees were foraging on crops according to flower density and flower production, most bees would be expected on broccoli and borage initially, then switching to fodder radish and borage and finally all converging on swede. But this did not appear to be the case. While an increase in *B. terrestris* nectar gatherers on fodder radish did occur, a decline on borage throughout the season was not evident as would be expected from flower density except during periods of high honey bee numbers on borage. Broccoli was not as attractive as expected from flower density or as a result of longer lasting flowers. However, a switch by honey bees to foraging on swede,

when this crop peaked in density, was evident mainly because of the low flower density on other crops, especially borage at that time.

While peak flower density and flower production in fodder radish and swede may explain a small proportion of the distribution of bumble bees and honey bees respectively during these periods, other factors such as pollen and nectar availability and interspecific competition played a more significant role.

B. terrestris workers exhibited considerable variation in handling time of flowers on broccoli and borage, which probably reflected previous experience of individual bees on these crops. Bees exhibited certain behaviours, which allowed them to optimise foraging time for the best reward. Such behaviours, e.g. walking between flowers and 'robbing' flowers, may minimise energy expenditure and maximise nett energy profit respectively, as suggested by Heinrich (1979a). Nectar gatherers collected the same amount of nett energy on low reward flowers (broccoli) as high reward flowers (borage) per unit time by changes in foraging behaviour as suggested in optimal foraging theory (Pyke 1978a; 1978b; 1979; 1980). On a single crop, with high reward flowers (full borage), not all nectar was removed. Each bee remained in a small area, whereas on low reward flowers (nearly empty borage), all nectar was removed and the forager moved over a wider area as a result of nectar depletion. Thus it appeared that the 'effort' required to remove all the nectar from a few high reward flowers was costly (in time) compared to 'creaming' the greater proportion of nectar from many more flowers as suggested by Heinrich (1979a). However, further trials would be needed to substantiate this for *B. terrestris* on borage.

Pollen collection by *B. terrestris* workers on crucifers involved incidental dusting of pollen on body hairs while bees probed for nectar. This method was suggested by Free (1970a) for pollen gathering bees on many flowers. By contrast, harvesting of borage pollen is a highly evolved, efficient process for which *B. terrestris* workers are well adapted, by their ability to vibrate indirect flight muscles to dislodge pollen from the poricidal-like anthers of borage (Buchmann 1983). The dry, concealed pollen of borage facilitated rapid removal by vibration of anthers, so bumble bees collected large loads of pollen compared to smaller loads harvested by honey bees gathering nectar.

Borage flowers develop through a staminate stage, usually on the first day of opening, with stamens releasing pollen while the stigma/style remains enclosed in the ring of anthers and is probably unreceptive to pollen germination thus avoiding self-pollination. *B. terrestris* pollen gatherers appeared to be attracted to staminate flowers, but after pollen harvesting, 40-62% of pollen remained. This was more than the mean residual amount of pollen remaining in a sample of surrounding flowers suggesting the pollen gatherers were actively selecting flowers that were full of pollen. By the second day, some borage flowers

developed to the pistillate stage with the stigma/style extending beyond the ring of anthers. However, this did not appear to occur in poor weather. Some pollen still remained within the anther locule. Nectar secretion was more prolific on the second day in bagged borage flowers on 22 September 1987 (chapter 4). Thus, borage flowers would still attract nectar and/or pollen gatherers on day two and, if pistillate, effect cross-pollination. Alternately, in poor weather, flowers remaining staminate may become receptive to their own pollen, effecting self-pollination. Further study of receptivity of the stigma on days one and two would be required to test this idea.

5.5 Summary

1) *B. terrestris* and honey bees preferred borage. Fodder radish was the second choice for *B. terrestris* workers and queens. Broccoli was second choice for males and honey bees.
2) Honey bees were more abundant and more sensitive to weather conditions than *B. terrestris* workers. Queens foraged independent of weather conditions.
3) Pollen and nectar gathering on borage increased with higher nectar production and pollen availability. As temperatures increased, numbers of honey bees on borage increased with a consequent depletion in the nectar and pollen standing crop. *B. terrestris* workers switched from borage to gathering nectar on fodder radish.
4) *B. terrestris* nectar gatherers were capable of harvesting the same amount of nett energy on low reward flowers (broccoli) as high reward flowers (borage) per unit time by changes in foraging behaviour.

CHAPTER 6

FORAGING PERFORMANCE AND COLONY DEVELOPMENT: OBSERVATION HIVE STUDY

6.0 Introduction

B. terrestris is an opportunist forager of a wide range of food sources extending to honeydew and sap from wounded trees (Gurr 1957a; Alford 1978). The ratio of pollen to nectar gatherers depends on the stage of colony development, the length of the colony life cycle and the species (Free and Butler 1959; Webb 1961; Prys-Jones and Corbet 1987). Pollen collection by bees depends upon colony demand, the attractiveness of and ability to locate pollen sources, seasonal and diurnal synchronization of activity with anthesis and anther dehiscence, morphological adaptations to plants and the degree of intra- and inter-specific competition affecting food availability (Eickwort and Ginsberg 1980; Goodwin 1987). Anther dehiscence may, in turn, depend on weather conditions (Prys-Jones and Corbet 1987).

Colony development depends on the regular supply of pollen and nectar to feed growing larvae and for general colony maintenance. During times of bad weather, food intake may be reduced, and so larval growth of *Bombus* is often a series of bursts followed by food deprivation (Plowright and Pendrel 1977).

Foragers may be stimulated to collect pollen by direct contact with the brood, so pollen collectors probably receive a greater stimulus than nectar collectors. For indoor colonies, a close correlation between rate of pollen consumption and total larval biomass was found for and *B. terricola* Kby. (Pendrel and Plowright 1981). A linear relation was also found for free foraging *B. terrestris* colonies (Tod 1986). Pomeroy (1977) found a similar relation for *B. ruderatus* colonies.

Scent from the predominant pollen in the colony may induce novice foragers to seek this crop (Brian 1951; Free 1970b). Bumble bee workers assess whether pollen is available using age-related morphological cues of the flower prior to alighting on *Anemonopsis macrophylla* (Pellmyr 1988), rather than the nutritional value, colour, reflectivity or moisture content of the pollen (Levin and Bohart 1955).

Little work has been conducted on pollen and nectar preference of bumble bees returning to hives after foraging on crops grown as bee forage. Most researchers have concentrated on

assessment of foraging preference of pollen gatherers on wild flowers by analysis of pollen in the larval meconia (Brian 1951; Liu *et al.* 1975; Yalden 1982).

Pollen preference of a colony can be assessed by recording corbicular pollen loads returning to the hive, by analysing pollen residue from the larval meconia (Brian 1951), or by monitoring foraging behaviour in the field. Analysing pollen residues may be difficult if the colony is damaged, e.g. by wax moth. Pollen grains can be distorted by larval digestion and may be less easily identified. Towards the end of the season, pollen collected may not be fed to brood but consumed by emerging sexuals. Therefore, this pollen would not be found in the meconia. Also pollen preference on specific days and throughout the day could not be determined from analysis of larval meconia.

Recording pollen loads on worker corbiculae requires diurnal 'trapping' of foragers. Honey bee pollen traps are unsuitable because of bumble bees worker size variation. Other methods such as photographing incoming foragers (Pomeroy 1977) or use of an automatic bee counting and recording device ('Apicard') (Burrill and Dietz 1981) may be useful. However, with the use of a 'trapping' system, pollen size, colour and the total number of returning foragers can be recorded without physically handling the bees. Also, labelled bees can be monitored and where necessary, removed and analysed for nectar and pollen quantity and quality.

With the exception of Heinrich (1979a), little attempt has been made to estimate total colony consumption and consequent colony development of 'free foraging' colonies.

Sladen (1912) constructed a bumble bee house in which an observer could be protected from the weather while observing free foraging colonies in unheated observation hives. A similar system was adopted in the present work. Incoming food and forager movements were monitored from heated observation hives in a caravan during the 1987 season.

The aim of this trial was to determine which crops were being foraged upon for nectar and pollen by analysing returning foragers at the hive entrance, also what factors (biotic and abiotic) influenced the amount of food returning to the colony and how this food intake affected colony development.

6.1 Pollen species preference of foragers

The aim was to determine which of the available pollen sources was most preferred by *B. terrestris* workers.

6.1.1 Methods

Rearing system

During 1987 a similar rearing system to the indoor 1986 trial was employed but with hives ducted outdoors to enable free foraging. The latter equipment was set up inside an aluminium caravan (2 x 4m) supplied with 240V electricity and maintained similar to indoor colonies at 24±4 C by a thermostatically controlled 'Shacklock' 2KW fan heater. Within the caravan, ten observation hives were controlled at 30.5±2 C, preventing the construction of a wax canopy and allowing for brood manipulation and measurement. Tunnels leading from the hives exited through the caravan floor to the outside. The tunnels exited through two wooden panels. Each panel (0.15 x 1.5m) provided for five exit holes 30cm apart with each separated by a wooden partition. The ten holes were each decorated with different three dimensional objects partly obscuring the tunnel entrance (fig. 6.1). Tunnel exit numbers 1-5 faced WNW with tunnels 6-10 facing NNE. The former received the sun from 11.30am to 6.30 pm, the latter from 6.30am to 2.30pm. An area of ground 1m in front of each entrance was kept clear of weeds. Entrances were checked regularly to prevent blocking. Tunnels were made of rolled shade cloth, covered in black cloth to exclude light; this reduced worker disorientation within the tunnel system. Each tunnel was of similar length (3-4m) (figs. 6.2 and 6.3).

B. terrestris queens were removed from artificial hibernation in laboratory refrigerators, (4-6 C) between 5-17 August 1987. These queens were all sisters mated by males from 1-2 other colonies (cross-mating). Emerging queens were fed sugar solution for seven days inside a 25 x 25cm plastic mesh cage before introduction into modified rearing boxes. Ten non-male producing colonies with 5-10 workers each were transferred to the caravan (between 16-24 September 1987) in a conical shaped 'Netlon' liner. Each liner was fitted inside a heated hive (chapter 2), so the liner could be removed later if the original colony died. Additional indoor reared workers from other colonies were added to bring worker numbers to ten/hive. Each hive had an aluminium queen excluder to confine the queen. As new workers emerged they were marked, after refrigeration for 30 minutes, with quick drying, white, volatile typing fluid. Each worker was marked on the interalar band of the dorsal thorax, avoiding wing bases and the head (fig. 6.4).

Monitoring foragers

As workers adapted to the tunnel system, trapping vestibules were inserted 20-30cm from the hive. Each trap had four compartments; exiting foragers moved through an exit compartment while returning foragers moved through a separate returning compartment so

Figure 6.1. Three dimensional objects decorating entrances of 2 panels of 5 holes each exiting from tunnels of *B. terrestris* colonies.

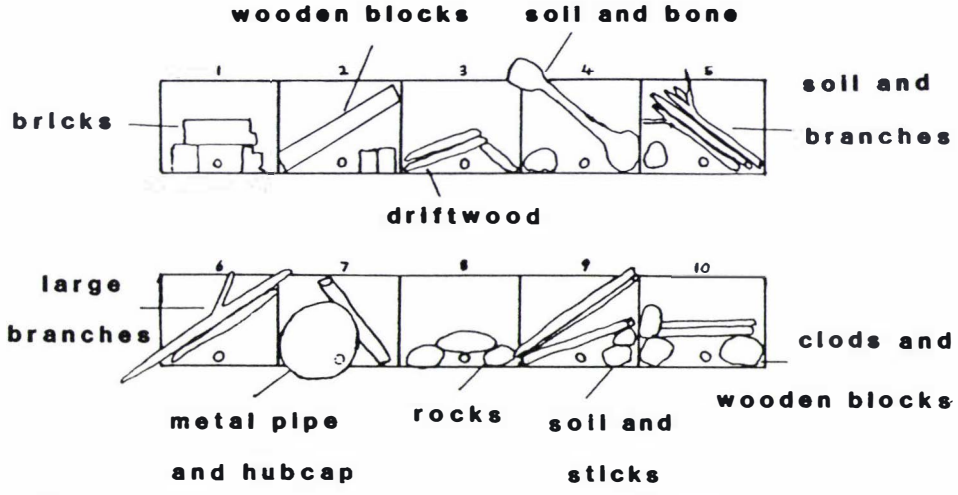


Figure 6.2. Arrangement of 10 observations hives inside caravan with 3-4m tunnels exiting externally into 2 panels through hole in side of caravan.

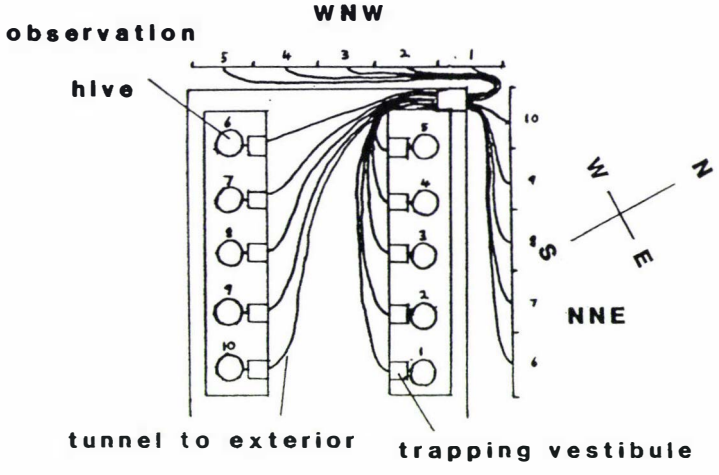


Figure 6.3. Arrangement of 10 observation hives, traps, tunnels and electronics, inside caravan (1987).

Figure 6.4. Range of bee sizes: Left to right: size of pollen loads returning to observation hive (Sept.-Nov. 1987); range in size of marked workers; pollen gatherers; numbered workers; males; queens; honey bees. Top: refractometer (15cm long) used for recording nectar sugar concentration.

Figure 6.5. Trapping system used to trap incoming foragers before returning to observation hive (top): This is an anticlockwise trap. The trapdoor is in place (right middle) and the trap is set. Foragers exit through left chamber, returning through right chamber.

that leaving and returning workers travelled along different routes through the trapping system (fig. 6.5). The traps were designed so that in five traps workers moved clockwise through the chambers and in the remaining five, workers moved anticlockwise. Trapdoors could be inserted and removed by the recorder so that returning foragers, temporarily confined, could be counted, weighed (if necessary) and the corbicular pollen loads examined for size and colour while other workers were free to leave the hive.

This trapping method allowed foragers to exit with short delays on entry (0-20 minutes). While some 'house' bees (non-foraging workers) were observed moving through the trapping system without foraging ('loopers'), the proportion of these non-foragers during any two hour period was only about 15% of the total incoming workers. However, this did not include workers that disappeared down the tunnels for short periods without foraging, so the number of 'loopers' may have been higher.

Pollen intake

Twice weekly for 12 weeks and then once/week for two remaining weeks, ten hives were 'trapped' throughout the day. The returning trapdoor was 'set' late at night on the day before recording and cleared at 8am on the recording day and every 15-20 minutes thereafter until 6pm, when the trap was set and cleared again after dark. The total number of nectar and pollen gatherers was recorded for each two hour interval. Nectar gatherers were defined as workers without pollen, but not all workers without pollen foraged (i.e. some were 'loopers'). Pollen loads on returning workers were assessed visually for size and colour. The size of pollen loads, which in most cases were the same on each leg, were compared to four standard pollen sizes pre-weighed at 6, 12, 18 and 24 mg. Tod (1986) found that pollen loads on returning forager corbiculae fell into four size classes. These size classes were used as standards for this trapping experiment. Occasionally workers were removed from the trap, refrigerated and the pollen loads removed with a fine paint brush. The pollen loads were then weighed (Mettler balance AE 160) and the estimated and actual values compared. A sample of 12 pollen load pairs removed from returning foragers were weighed, oven dried at 60 C for 24 hours, removed to a desiccator with indicator Silica gel for two hours then reweighed. Fresh weight to dry weight conversions were calculated, and a mean value determined. Pollen intake was divided into seven, two-hour intervals for each day (6am-8pm), and borage intake was compared with crucifer intake (total for three crops) throughout each recording day.

Samples of pollen loads were prepared for examination under a compound Olympus Ch microscope at 400 or 1000x (oil immersion) magnification. Pollen colours were assigned to

plant species so that preference of pollen species could be determined. For some pollen the host plant could not be located and the exact identification to species was not possible.

Pollen loads from corbiculae of honey and bumble bees captured foraging on broccoli, swede and fodder radish could not be accurately differentiated. The yellow shade of pollen loads from broccoli and swede were virtually identical. Fodder radish pollen appeared slightly greenish-yellow when fresh, but as the pollen dried, the colours became indistinguishable from broccoli and swede. Under 1000x magnification, broccoli had more collapsed grains, but the structures of the exine of the three species were identical. As a result, the total dry weight of these pollens was determined and divided by three to approximate the amount per species. This was compared with the amount of borage pollen collected from 6 Oct. - 21 Nov. This assumed that equal quantities of pollen were collected from the three cruciferous crops which was probably incorrect but nevertheless enabled a comparison with amounts of borage pollen collected early in the season and of white clover pollen collected late in the season. Thus from 6-31 Oct., the total amount of borage pollen returned to hives was compared with one third of the amount of cruciferous pollen, while from 3 Nov. - 8 Dec. the total amount of white clover pollen was similarly compared with one third of the cruciferous pollen, however the area of white clover was far greater than the whole trial site area. One-way ANOVA tested differences between treatment means while 95% confidence intervals indicated which treatments differed significantly.

Pollen loads were removed from the corbiculae of workers foraging on borage and on kale interspersed with broccoli and fodder radish (crucifer pollen), during October 1988. The pollen was frozen until required.

A feeding tray was constructed from two perspex squares 4 x 4 x 0.4cm. In one square, holes, 4mm in diameter, were drilled 1cm apart in a 3 x 4 configuration. The second square was secured to the base of the first with tape producing 12 'pollen pots' 4mm deep. Each pot was filled alternately with either borage or crucifer pollen. The tray was then introduced into the 'outer' chamber of a rearing box containing a colony of 32 workers, and the number of empty pollen pots recorded at approximately three minute intervals. For the second trial, a colony that had been free foraging on borage flowers was used. This colony had 17 workers and took considerably longer to consume the pollen. Observations were therefore taken at approximately one hour intervals. Pots were considered empty when a few 'crumbs' of pollen were left in the bottom.

6.1.2 Results

White to off-white pollen returned to hives was identified as borage. Brown to dark brown pollen was identified as white clover and was collected in corbiculae of bumble bees in kidney shaped loads of approximately 6-12 mg. Similar sized loads were collected by honey bees from white clover (Hodges 1974). Brick-red pollen was identified as lupin, probably yellow lupin. Orange pollen had an exine structure identical to dandelion. Green pollen with an exine structure similar to false acacia, *Robinia pseudo-acacia*, at 1000x magnification, could not be confirmed, as this species was not located in the area. Alternatively, it could have been apple, *Malus* spp.

Pollen from the four sown crops was returned to hives from 6 Oct. when trapping began and declined after 10 Nov. Crucifer pollen returned after 17 Nov. was probably broccoli or wild mustard as other crucifers were not flowering during this period. White clover and dandelion pollen were first collected on 20 Oct., while green pollen was collected on 24 Nov. and 1 Dec. only. The latter two pollen types were collected in very small amounts.

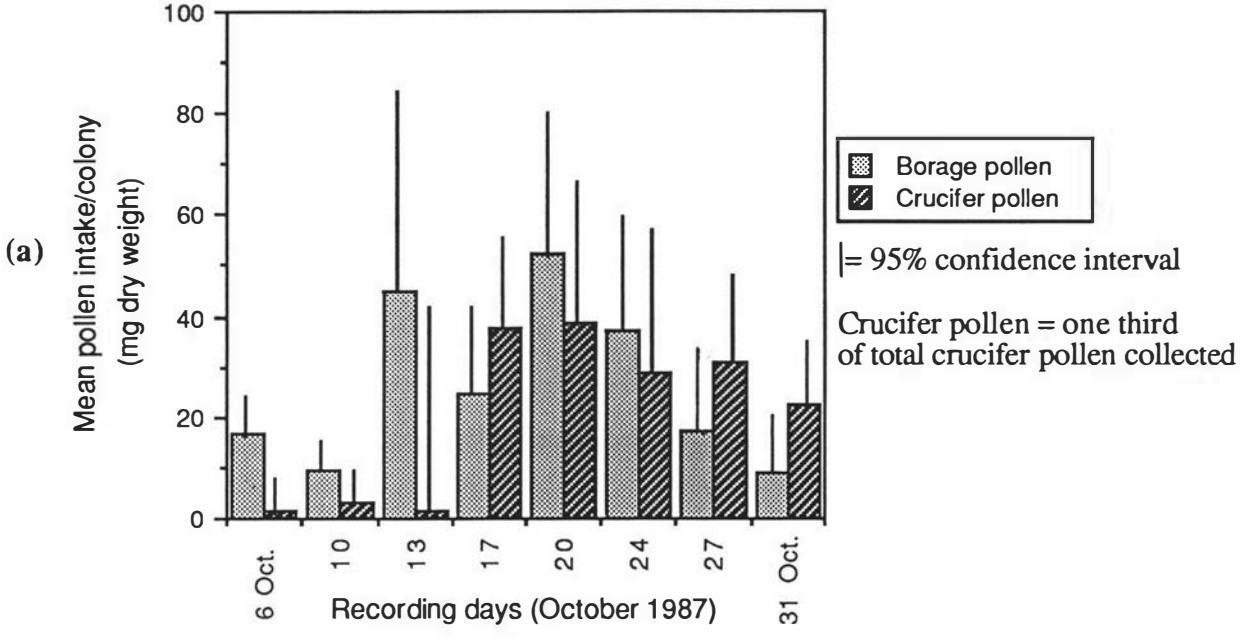
Throughout the recording period there appeared to be little preference for one pollen type, only on 6 Oct. for borage and on 3 and 8 Nov. for crucifers, was any significant preference recorded (fig. 6.6a, appendix table A6.1). Later in the season, the amount of white clover pollen increased but only on 24 Nov. was the difference significant (fig. 6.6b).

In both pollen consumption trials, crucifer pollen was consumed sooner than borage pollen (appendix table A6.2). All pollen was consumed eventually. The longer time required for consumption in the second trial was probably due to fewer workers per colony. Difficulties in obtaining sufficient pure lines of pollen reduced the number of possible trials, hence the significance of the above result could not be tested further.

The diurnal trends of pollen collection on 13, 24 Oct. and 3 Nov. (recording day 11, 14 and 17) are presented in figures 6.7a-f. On 13 October (day 11), the maximum temperature was 14.5 C, overcast (light intensity max. 650$\mu Em^{-2}s^{-1}$), with light rain during midday (1mm rainfall 10-2pm) and heavy rain in the afternoon (7.8mm 2-6pm). The wind speed increased throughout the day from 1.2ms^{-1} at 7am to 3.4ms^{-1} at 5pm, with an average of only five honey bees/borage plot and less honey bees on other crops. Nectar and pollen gatherers returning to observation hives declined after 4 pm (fig. 6.7a) with a peak between 10-12noon. Pollen collection also peaked between 10-12noon, during which 66-100% of pollen collected was borage (fig. 6.7d). This was the general trend on cool, overcast days with little honey bee activity.

On 24 Oct. (day 14), temperatures increased to 19 C, wind increased in the afternoon from 0ms^{-1} at 9am to 3.2ms^{-1} at 3pm with a decline in light intensity from 1300 (11am) to

Figure 6.6. Daily pollen intake into 10 free foraging colonies



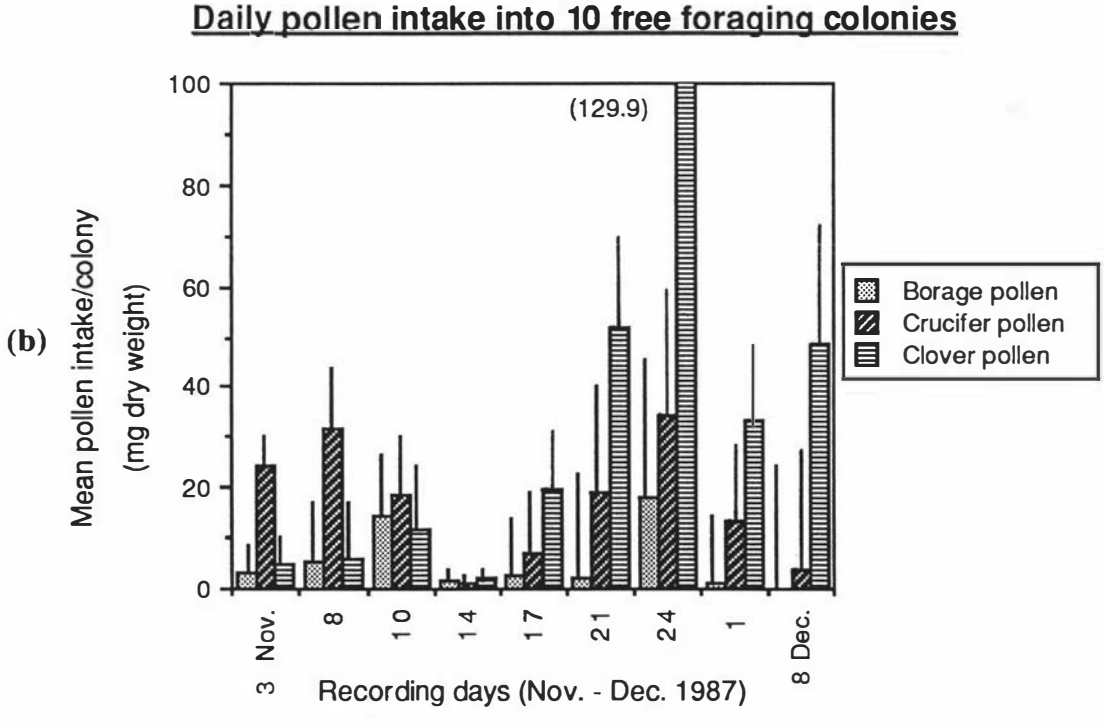
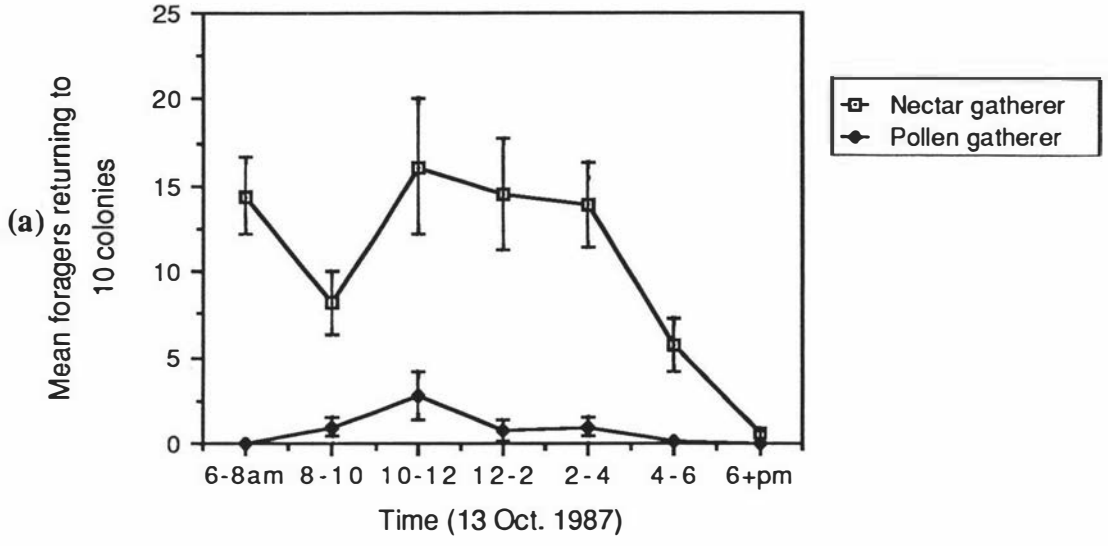
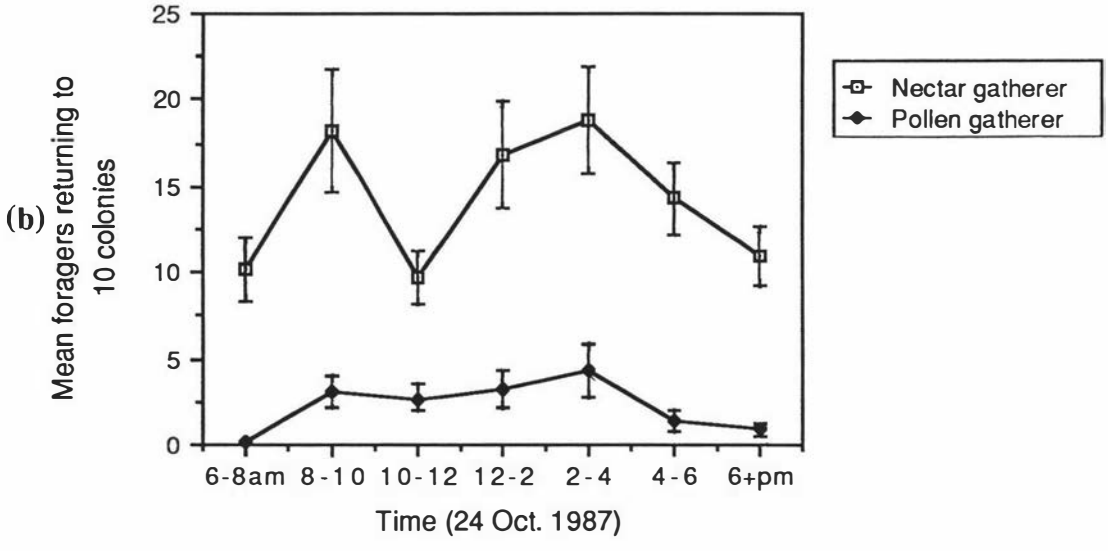


Figure 6.7. B.terrestris pollen and nectar gatherers on day 11



B.terrestris pollen and nectar gatherers on day 14



B.terrestris pollen and nectar gatherers on day 17

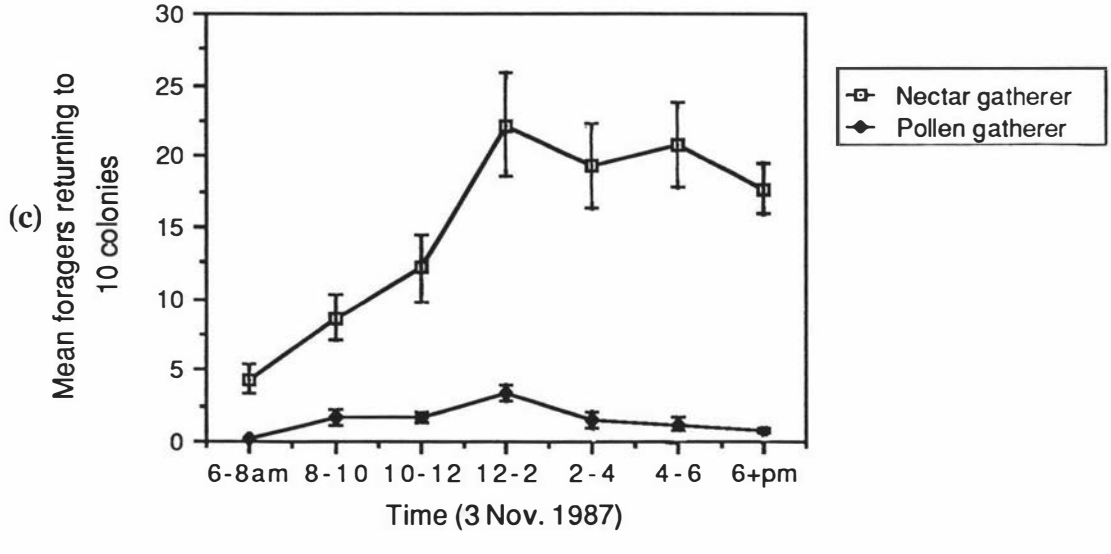
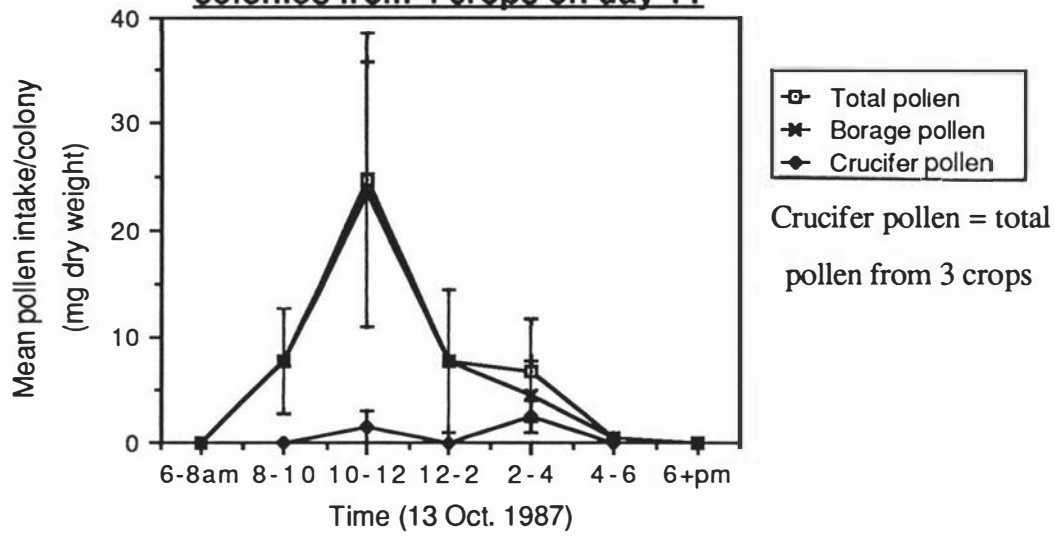
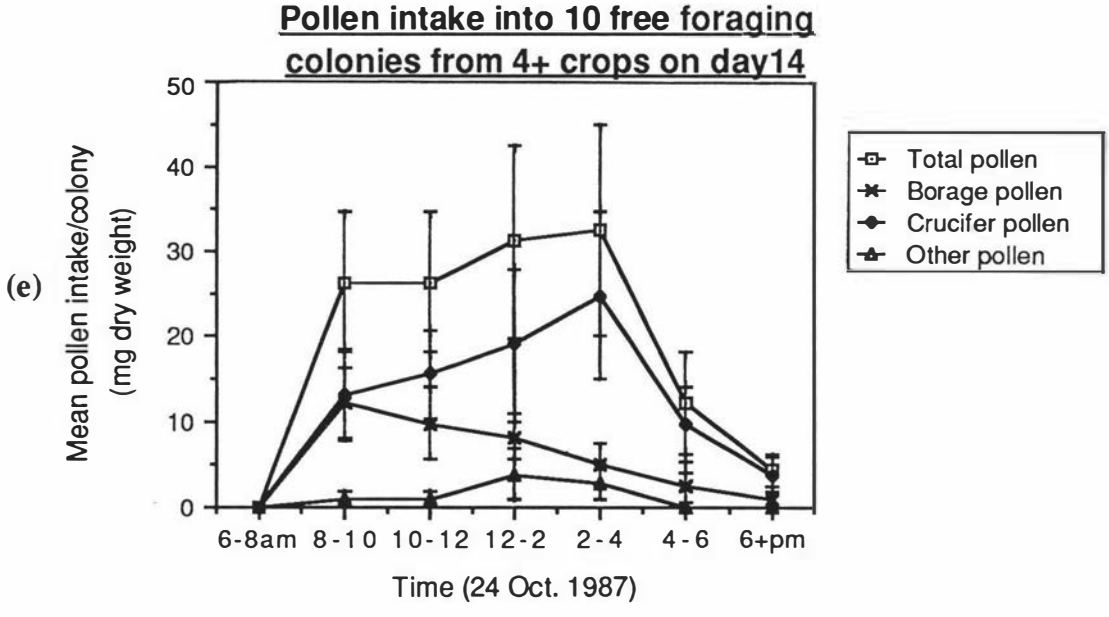
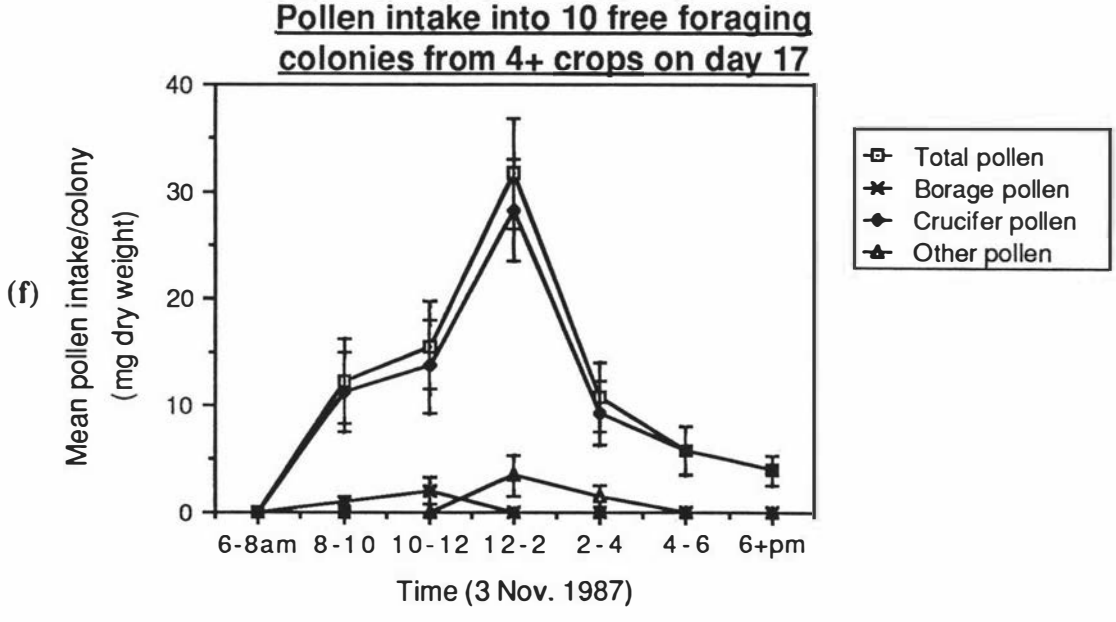


Figure 6.7. Pollen intake into 10 free foraging colonies from 4 crops on day 11







65μEm^{-2}s^{-1} at 5pm. A total of one hour of sunshine was recorded with 0.5mm of rain at 3pm. Honey bee numbers increased to 110/borage plot from 12-2pm then declined rapidly in late afternoon (see chapter 5, figs. 5.2c,d,e). The number of pollen and nectar gatherers was higher early (8-10am) and later (12-4pm) in the day (fig. 6.7b). Total pollen intake was highest between 8am-4pm with no decline in pollen intake as a result of high honey bee numbers (fig. 6.7e). Borage pollen was collected earlier in the day (8am-12noon) with crucifer pollen collected later in the day (10am-4pm).

On 3 Nov. (day 17), the maximum temperature was 19 C with no rainfall and 6.7 hours of sunshine. Light intensity was highest at 1pm (2100) declining to 1285μEm^{-2}s^{-1} at 5pm with wind increasing from 1.2ms^{-1} (9am) to 6.6ms^{-1} (5pm). Honey bee numbers were high on swede (100/plot) with fewer on borage (38/plot) (see chapter 5, figs. 5.3c,d,e). Nectar gatherers returning to hives increased later in the day (12-6pm) with pollen gatherers peaking between 12-2pm (fig. 6.7c). Total pollen intake also peaked between 12-2pm at 31.7mg dry weight/2 hours (fig. 6.7f). Crucifer pollen was the main pollen collected. Borage pollen was collected in small amounts early in the day, and white clover was collected from midday to 6pm.

6.2 Colony nectar intake

The aim was to identify which crop(s) supplied most of the nectar to the colonies and to determine the total nectar (energy) intake of one colony in order to compare with indoor reared colonies.

6.2.1 Methods

6.2.1.1 Sugar concentration in workers and crop flowers

Sugar concentrations of nectar from foragers and flowers were compared among the four forage crops at five time intervals throughout the day (chapter 4). At the end of each recording day, sugar concentrations of nectar in recently constructed nectar pots on the periphery of the comb (pots used for storing nectar from the day's foraging) were also measured by discharging 2μl samples onto a refractometer slide.

6.2.1.2 Total colony nectar (energy) intake

Foragers leaving and returning from one free foraging colony were monitored throughout the day twice weekly for seven weeks.

A number of methods of marking bees have been used e.g. using radioactive isotopes, spraying bees with powder at the entrance, walking bees through fluorescent markers which are left on flowers (Free 1970a). The use of numbered plastic discs, however, was most suitable for bumble bees, although some difficulty in reading numbers covered in wax or pollen occured and the presence of discs may have reduced pollen collection. Workers were refrigerated prior to applying the discs rather than being anaesthetised with CO_2, as this may cause changes in bee behaviour and physiology (Pomeroy and Plowright 1979; Roseler 1985).

Two-thirds (10-40) of the workers from colony one (and later colony 9) were removed twice weekly, refrigerated at 6 C for 30 minutes, marked with correction fluid, dabbed with a drop of 'Super glue', and labelled with a numbered plastic disc (as used in honey bee marking). Each bee was weighed and returned to it's original colony. Bees were marked the evening before a recording day. The number of bees marked fluctuated, depending on mortality from the previous marking. Small house bees were not marked as they did not forage. As all bees were weighed after marking, they were not weighed on leaving the hive.

During recording days, labelled foragers were monitored from 8am to 6pm exiting from and returning to the heated hive through the trapping system. Time of leaving and returning was recorded, and each bee weighed on returning. If a weight gain of more than 15mg was detected (apart from pollen loads which were removed and weighed, however very few labelled foragers returned with pollen), the worker was forced to regurgitate nectar from the honey stomach onto a refractometer slide by compressing it's abdomen. The 15mg cut-off was derived from testing 15-20 foragers showing weight increases of 1-15mg. These bees could not be forced to regurgitate nectar from the honey stomach. Above this weight, nectar was recorded from the honey stomach. The trap was cleared every 15-20 minutes (i.e. a 0-20 minute inaccuracy in foraging time) and the total number of foragers returning every two hours recorded. The number of foragers showing an increase in weight, and the mean volume and sugar concentration of nectar from the bee, were recorded (from increase in bee weight,see chapter 5.3) .

Sugar solution consumption for eight heated indoor colonies (1986) was then compared with nectar intake for one heated free foraging colony (1987). The weight of sugar solution (g) consumed for indoor colonies was converted to volume (Iscotables 1974) assuming a temperature of 20 C and mean sugar concentration of 53.5% (52-55%, chapter 2). Weekly energy (kilojoules) consumption, for each of the eight indoor colonies was calculated from weekly sugar volume (ml) consumption and sugar concentration using the formula from chapter 4 (Prys-Jones and Corbet 1987). The mean number of workers/colony for each week was also recorded. Statistical comparisons between indoor sugar consumption and

free foraging colony nectar intake were not undertaken because nectar consumption was only recorded for one free foraging colony.

6.2.2 Results

6.2.2.1 Sugar concentration in workers and crop flowers

The maximum and mean sugar concentration of nectar from foragers was correlated with the amount of sugar in borage nectar during the 14 recording days (table 6.1). Sugar content of swede was also correlated with forager sugar levels. However, 63% of the values were missing due to the short flowering period of swede. Sugar contents of swede and borage were positively correlated, but the sugar content of swede was higher than borage.

Because of the daily and diurnal changes in foraging strategy (chapter 5), a correlation between the amount of sugar returning in foragers and sugar content of the most preferred forage crop for each two hour period was determined. The sugar content of returning foragers was highly correlated with the mean sugar content of the most preferred crop (borage and fodder radish) at that time (table 6.1). The maximum and minimum sugar concentrations of foragers were also correlated with sugar content of the preferred crop.

Returning foragers discharged their contents of nectar into peripheral honey pots. The minimum sugar concentration of this nectar sampled at the completion of the day's foraging was found to be positively correlated with the range and mean sugar concentrations returning in the honey stomach of foragers (table 6.2).

6.2.2.2 Total colony nectar (energy) intake

Weekly energy intake was derived from the mean daily intake of colony 1 for weeks 1-4 and colony 9 for weeks 5-8. From week 1-4 (1987) weekly energy intake increased from one to 29 kilojoules (fig. 6.8a) for colony 1. From weeks 5-8, energy intake oscillated between one to 16 kilojoules for colony 9. Weekly nectar intake followed a similar trend to energy (fig. 6.8b); any differences were attributed to the variation in nectar sugar concentration resulting in higher or lower energy intake. Worker numbers/colony increased from 15 to 52 during the eight weeks.

During a similar period of development for eight indoor colonies (1986), mean number of workers increased from 11 to a peak of 45 (fig. 6.8e) while mean weekly colony energy consumption increased from 200 to 1330 kilojoules (fig. 6.8c). Weekly colony sugar volume consumption followed an identical trend (fig. 6.8d) to energy consumption because

Table 6.1. Pearson correlation coefficient between the nectar sugar concentration of 4 crops and the most preferred crop (borage or fodder radish) with the nectar sugar concentration of free foraging *B. terrestris* workers returning to hives at 5 times during 14 days (Oct.-Nov.1987).

Crop		Fodder radish	Swede	Broccoli	Borage	Most preferred crop
	No. cases	37	21	28	36	41
Mean nectar	r value	0.247	0.412	0.259	0.432	0.542
conc. from	Probabil.	0.071	0.032	0.091	0.004	0.000
foragers	Signific.	n.s.	*	n.s.	**	***
Max. nectar	r value	0.102	0.401	0.195	0.399	0.470
conc. from	Probabil.	0.275	0.036	0.159	0.008	0.001
foragers	Signific.	n.s.	*	n.s.	**	**
Min. nectar	r value	0.201	0.136	0.122	0.219	0.355
conc. from	Probabil.	0.116	0.279	0.268	0.100	0.011
foragers	Signific.	n.s.	n.s.	n.s.	n.s.	*

$r_{0.05(1)[19]}=0.369$ $r_{0.05(1)[39]}=0.261$
$r_{0.01(1)[34]}=0.386$ $r_{0.01(1)[39]}=0.362$
$r_{0.001(1)[39]}=0.474$

Table 6.2. Pearson correlation coefficient of nectar sugar concentration of free foraging *B. terrestris* workers returning to hives with the minimum sugar concentration of nectar from peripheral nectar pots within the hive sampled at the completion of the day's foraging (Oct.-Nov. 1987);n=13.

		Forager sugar concentration		
		Mean	Maximum	Minimum
Minimum sugar concentration from nectar pots	r value	0.720	0.732	0.641
	Probabil.	0.003	0.002	0.009
	Signific.	**	**	**

$r_{0.01(1)[11]}=0.634$

Figure 6.8. **Nectar energy consumption for 1 free foraging colony**

(a)

(b)

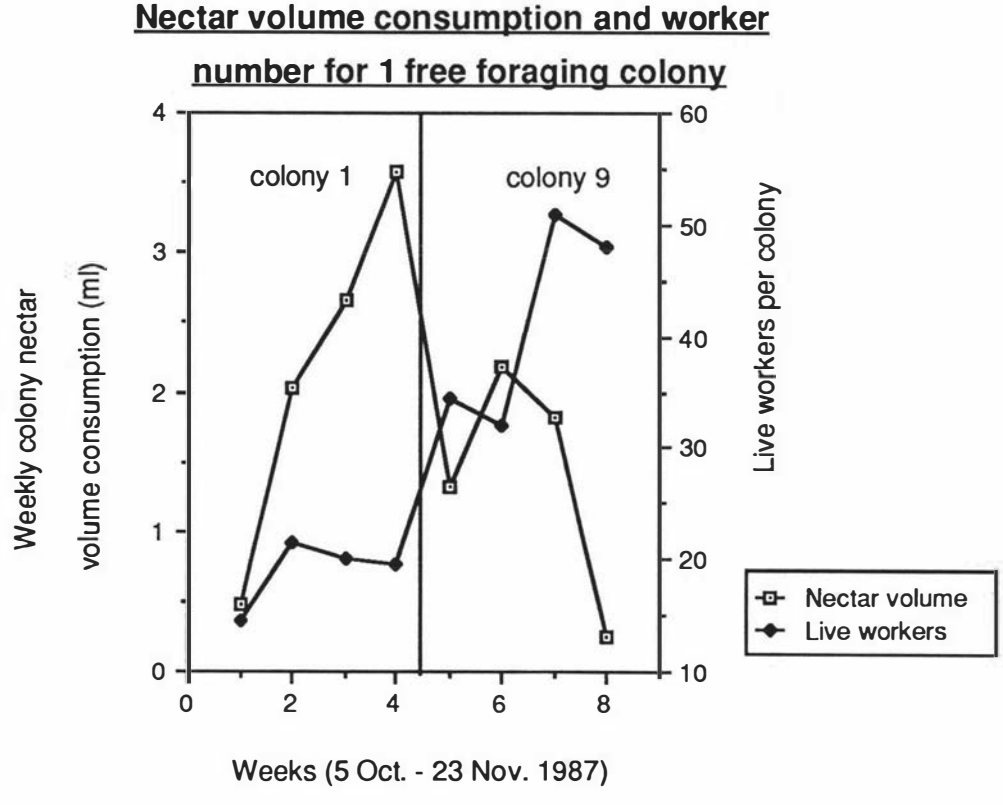
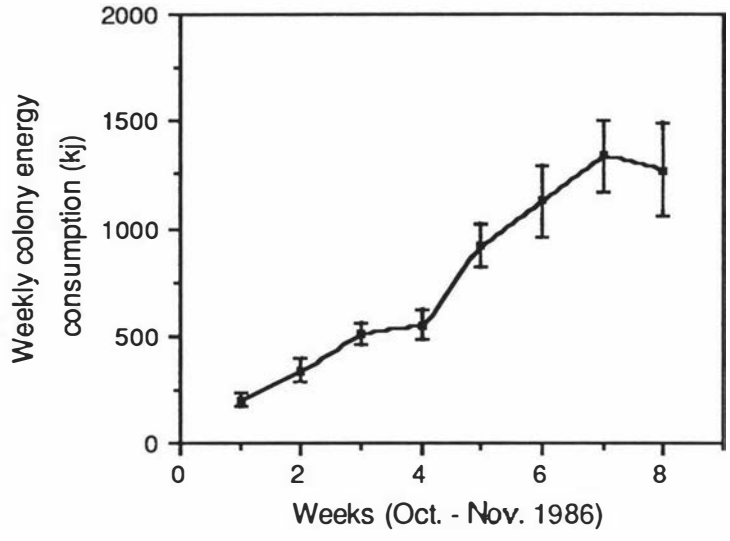


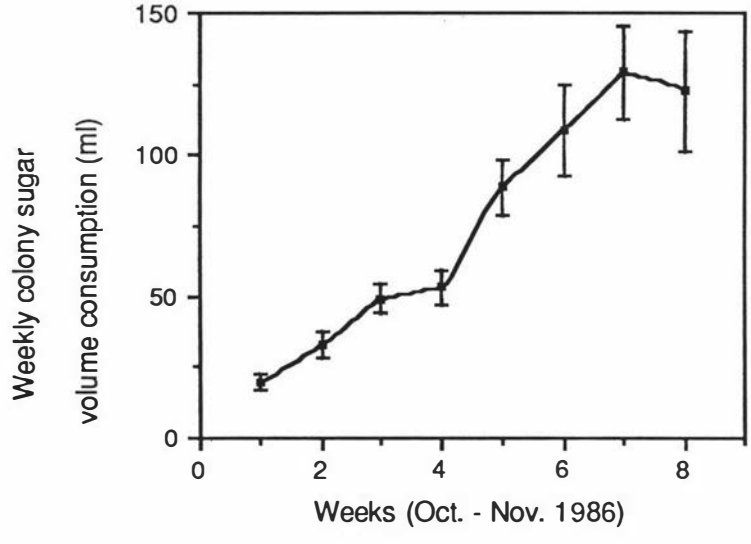
Figure 6.8. Sugar energy consumption for 8 indoor colonies

(c)



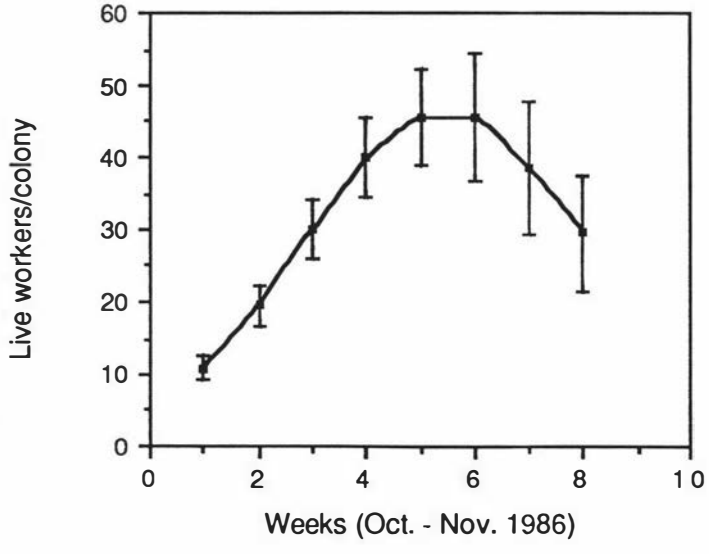
Sugar volume consumption for 8 indoor colonies

(d)



Number of live workers for 8 indoor colonies

(e)



sugar concentration was assumed to be a constant 52.5% sugar. In reality it was probably 52.5±1.5%. Energy consumption for indoor colonies continued to increase even after worker numbers declined. The indoor colonies were consuming between 38-50 times the quantity of nectar that outdoor colonies consumed and between 45-200 times the amount of energy. Indoor colonies had a mean of 50 half-full honey pots at the termination of the indoor trial while free foraging colonies 1 and 9 had no half-full honey pots.

6.3 Nectar foraging efficiency in relation to weather conditions, pollen and nectar availability and foraging competition

The aim was to determine which factors were most important in explaining colony nectar (energy) intake from nectar gatherers.

6.3.1 Methods

Two parameters were calculated for bumble bee foraging:
(1) Nectar energy per bee (joules/foraging trip), calculated from volume and sugar concentration of nectar collected by foragers returning to colony 1 (and later colony 9) using the formula from Prys-Jones and Corbet (1987) (chapter 4).
(2) Energy harvest rate (joules/minute), calculated from nectar energy collected/bee divided by time foraging.

The mean nectar energy per worker bee and energy harvest rate over each two hour period for five time intervals throughout 13 recording days from 10 Oct. - 21 Nov. was compared (using multiple regression analysis) with:
1. Weather variables e.g. temperature, wind speed, light intensity, R.H. and rainfall.
2. Pollen and nectar (energy) available from exposed flowers.
3. Pollen availability and nectar production from bagged flowers.
4. Mean number of *B. terrestris* nectar gatherers, pollen gatherers and honey bees on all crops.

Initially all parameters from 1-4 were regressed against nectar energy/bee and energy harvest rate. Because pollen availability and nectar production from bagged flowers had a number of missing values reducing the degrees of freedom to 19, the analysis was repeated without bagged pollen and nectar production (45 df). A correlation matrix between all variables was also analysed.

6.3.2 Results

As the amount of pollen available in exposed flowers increased and rainfall deminished, the quantity of nectar energy collected/bee, returning to hives, increased (appendix tables A6.3, A6.4). This analysis accounted for only 31.3% of the variation.

Energy harvest rate was not significantly affected by any of the variables tested (appendix table A6.3). Although honey bees numbers increased with an increase in energy harvest rate, the ANOVA was not significant.

6.4 Pollen harvesting in relation to weather conditions, pollen and nectar availability and foraging competition

The aim was to determine which factors were most important in explaining colony pollen intake from pollen gatherers.

6.4.1 Methods

The total pollen collected by workers returning to ten colonies (every two hours for five time intervals throughout 13 recording days; 10 Oct. - 21 Nov.) was determined from the trapping of workers every 15-20 minutes. Multiple regression analysis compared total pollen dry weight from pollen gatherers returning to colonies 1-10 with:

1. Weather variables.
2. Pollen and nectar (energy) from exposed flowers.
3. Pollen availability and nectar production from bagged flowers.
4. Mean number of *B. terrestris* nectar gatherers, pollen gatherers and honey bees on all crops.

Bagged pollen and nectar production were then dropped from the analysis, and the regression repeated for each colony. To determine if pollen intake into each colony was correlated with that of other colonies, a correlation matrix was tabulated (appendix table A6.5). As only 47% of the correlations between colonies were significant, regression analysis for each colony was undertaken rather than grouping all colonies together.

6.4.2 Results

With an increase in temperature, light intensity and wind speed and a decrease in R.H., more pollen was collected by workers. This was accompanied by an increase in nectar and pollen gatherers and honey bees on the crops (appendix table A6.6). Conditions favouring

foraging for pollen and nectar also favoured pollen collection and, hence, intake into colonies. There was no decrease in pollen from exposed flowers. The order of influence of main effects on pollen intake was: weather e.g. temperature, wind, rain > nectar gatherers = exposed nectar > honey bees on crops. This analysis excluded bagged food. The increase in pollen intake as nectar in exposed flowers decreased suggested that times of favourable pollen harvesting were also suitable nectar harvesting periods. The order of influence of main effects on pollen intake when harvested food was included was: weather > pollen gatherers on crops > honey bees = nectar production (appendix table A6.7). An improvement in weather with more pollen and higher nectar production attracted more pollen and nectar gatherers and honey bees to the crop.

The former regression analysis excluding bagged food had a total of 64 observations compared with 38 for the latter analysis which included bagged food. The order of main effects was therefore probably more accurate for the former analysis. While weather, foragers and nectar influenced pollen intake, the amount of pollen on crops was not important. This suggests that pollen intake into colonies was not measurable directly from the loss of pollen in the field in this trial.

6.5 Intra-colony factors affecting foraging

The aim was to determine which colony factors were most important for the daily foraging of workers leaving the colony and which factors, if any, influenced the nectar volume and energy collected by returning foragers.

6.5.1 Methods

Larval area, total bee numbers/colony, maximum number of foragers and maximum number of pollen gatherers foraging during each recording day from 6 Oct.-8 Dec. were determined. At the end of each recording day, the number of at least half-full nectar and pollen pots was also recorded for each colony. Pearson correlation coefficients were determined between the 6 parameters for each of the ten colonies. The number of significant correlations ($p< 0.05$) between the different variables is presented as a percentage of ten colonies. The six parameters were compared with the daily nectar volume and energy of nectar returning to the colony recorded from foragers (see 6.2.2). These correlations were calculated from 10 Oct. - 8 Dec. for nectar gatherers rather than pollen gatherers used initially.

6.5.2 Results

The maximum foraging force of free foraging colonies was correlated with the larval area and number of live bees/colony in seven and eight out of ten colonies respectively (appendix tables A6.8, A6.9). The number of pollen gatherers was correlated in more colonies with the number of bees in the colony (90%) than with the larval area (50% of colonies). The maximum number of pollen gatherers was correlated with the number of pollen pots in only 40% of the colonies. The total number of bees in the colony was correlated with the number of nectar pots in only 40% of colonies. Results suggested the factors influencing bees to forage may not always be within the colony.

Total daily nectar volume and energy intake into colony 1, and later colony 9, was not correlated with larval area, live bees, or foragers (appendix table A6.10). The number of pollen and nectar pots increased with increasing nectar intake. However, the range of values for pollen and nectar pots was small (0-3), making the correlation more of an aberration of the data. Results of daily nectar intake indicated more colonies would need to be monitored for meaningful correlations. The lack of definite trends in pollen and nectar intake with intra-colony factors may suggest that these factors are influenced more by weather.

6.6 Colony development and pollen consumption.

The aim of this section was to determine whether food intake into free foraging colonies supported development. This was determined by comparison of pollen consumption and colony development for indoor colonies.

6.6.1 Methods

Colony development

Records of newly emerged workers, total live workers, larval area, pupae and number of sexuals emerging were taken twice weekly. All emerging sexuals were removed from the parent colony. Larval area was measured with acetate sheets placed over the glass cover of the observation hive and viewed consistently from above the glass. An outline of the brood was traced with a felt pen. A parallax correction was included for the area traced, by recording the area of a 3 x 3cm square placed at different vertical distances beneath the glass and traced onto the acetate. The brood outline was coloured in, and the acetate pieces run through a Lambda leaf area meter (Li-cor Model LI 3000) to record total brood area with $\pm$0.1% accuracy. A correction was added depending on the depth of the brood from the glass lid. Comparison of this method and measurement of brood with dividers (chapter 2)

indicated that the former method gave a mean of +4% (range -14% to +28%) more than brood measured with dividers for nine colonies with larval area between 5-10cm^2. This was considered to be within the range of accuracy of both methods.

The timing of first male emergence was recorded, and the time at which the foundress queen switched to male oviposition was estimated (see chapter 2). Brood bionomic parameters, at the time of switch, were recorded for each free foraging colony and compared with the 1986 indoor reared colonies using Student's t test.

In three colonies, 5-15 additional workers were added to replace the original workers that had died or left the colony soon after transfer to free foraging hives.

Because one colony and another three foundress queens died between 11 October and 2 November, requeening and colony replacement techniques were used to maintain these hives with viable colonies.

All bees from colony 7 died suddenly on 14 October presumably from food shortage due to bad weather during the previous week (no insecticide sprays were applied). This colony was thus repopulated on 15 October with another indoor-reared colony, founded by a field captured queen. Colony 9 was also replaced with an indoor-reared colony and field queen, while colonies 2 and 8 were requeened with field captured queens, maintaining the original brood of the previous deceased queen. These new queens had initiated indoor colonies, but only the queen and workers were introduced. Requeening involved permanent removal of all 'house' bees from the original colony and temporarily trapping all returning foragers. This avoided any antagonism developing between dominant workers and the new queen. The new queen was first placed in a vial with several drops of vanilla essence to develop a new smell over her body (Rosemary Read pers. comm.). She was then introduced onto the brood. After 20 minutes, her own indoor workers were introduced, and after 30 minutes, the trap was opened and foragers from the original colony allowed to merge with the new bees. After a period of reorientation, both worker groups and queen cohabited successfully, and the colonies grew well.

Colony pollen consumption

The total pollen collected by foragers from each hive (throughout two recording days/week for seven weeks then once/week for a further two weeks) was estimated and converted to a dry weight value. A mean value for the two days/week of trapping was determined and multiplied by seven to give an estimated weekly intake. This weekly intake was then compared with indoor consumption (chapter 2) for colonies with comparable larval area (measured within 12 hours of pollen consumption) and total worker numbers.

6.6.2 Results

Colony development

The chronology of colony events is illustrated in figures 6.9a,b and 6.10a,b (and appendix figs. A6.1a,b-A6.8a,b).

Four free foraging colonies were requeened, and these kept growing for longer than non-requeened colonies, but the experiment was terminated, due to completion of flowering, before final P.I.s could be determined for requeened colonies. Non-requeened free foraging colonies had finished growing when the trial was terminated, and these colonies were smaller than indoor colonies (table 6.3). Comparison of other bionomic parameters (table 6.4) showed that the brood, workers and males produced were not significantly different between free foraging and indoor colonies (table 6.3).

P.I. for free foraging (non-requeened) colonies was correlated with maximum live workers only (table 6.5).

The timing of foundress queen switch to male production was not related to any brood bionomic or developmental parameters recorded (appendix table A6.11). The date of switch to male production ranged over 21 days compared to 34 days for indoor colonies from 1986, but the mean number of days from colony inception to oviposition of males was similar (51.3 days indoor vs. 50.5 days free foraging).

Colony pollen consumption

Pollen intake was significantly lower (one order of magnitude) in free foraging colonies than indoor pollen consumption (table 6.3). Possibly as a consequence of this, no free foraging colonies produced new queens.

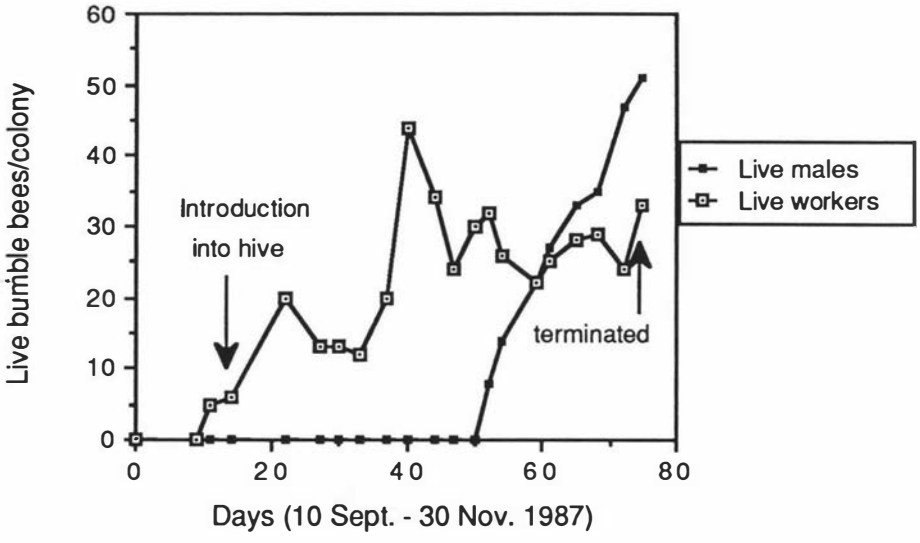
Weekly pollen intake for the ten free foraging colonies is illustrated in figures 6.9c and 6.10c (and appendix figs. A6.1c-A6.8c). Weekly pollen intake was significantly correlated to mean larval area in three out of ten colonies (table 6.6).

The predictability of weekly pollen consumption from larval area was compared independently for indoor and free foraging colonies using pooled data. The predictability of pollen consumption for indoor colonies was significantly more accurate ($r = 0.812$) than for free foraging colonies ($r = 0.437$; table 6.7).

To determine whether extrapolation of free foraging pollen intake from indoor pollen consumption using larval area was justified, the regression line for indoor consumption was plotted (fig. 6.11). Data were transformed $\ln(x + 1)$ to stabilise the variance, and a formula calculated (appendix table A6.12) to predict pollen intake for free foraging colonies. Plotting

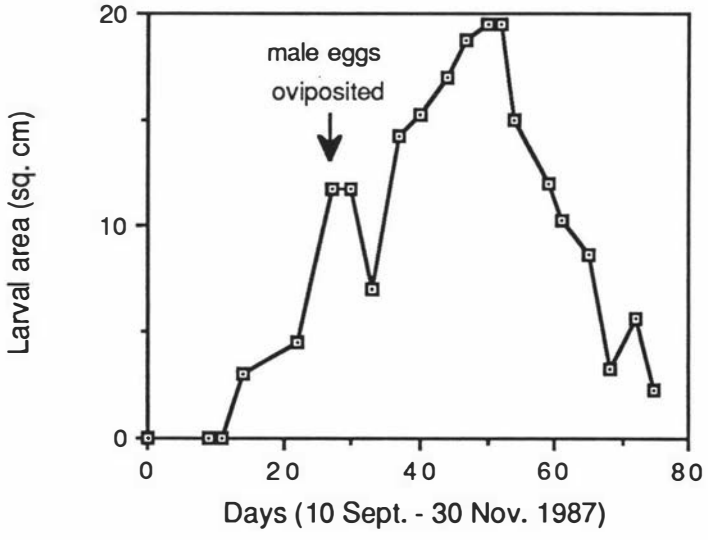
Figure 6.9. Bumble bees for free foraging hive 4

(a)



Larval area for free foraging hive 4

(b)



Weekly pollen returning to free foraging hive 4

(c)

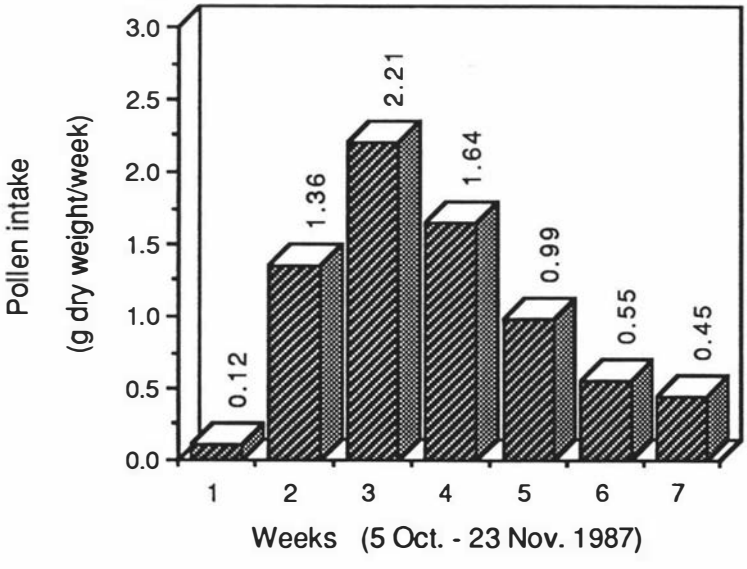
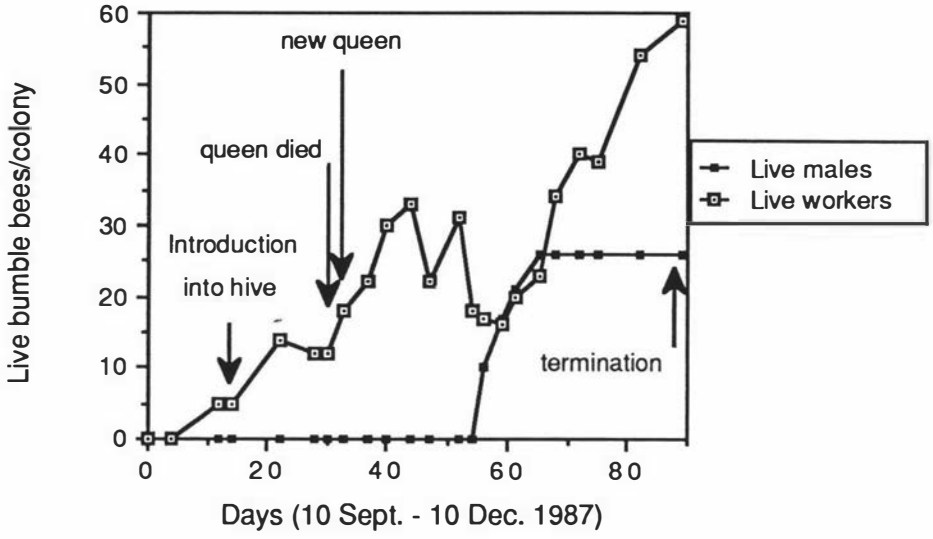


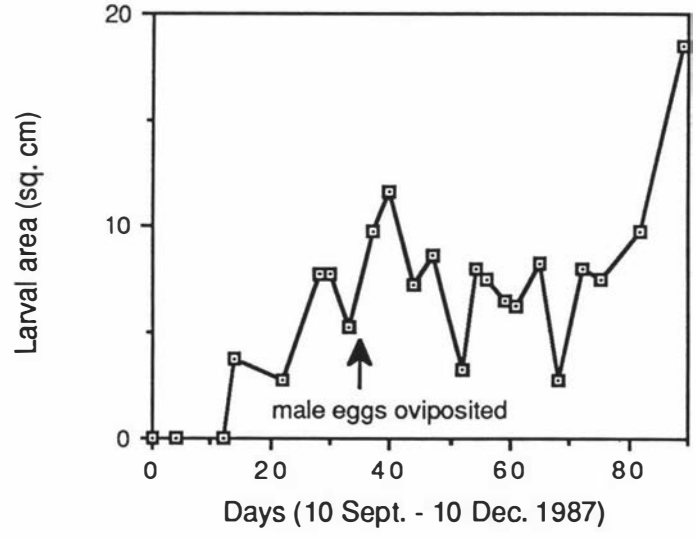
Figure 6.10. Bumble bees for free foraging hive 8

(a)



Larval area for free foraging hive 8

(b)



Weekly pollen returning to free foraging hive 8

(c)

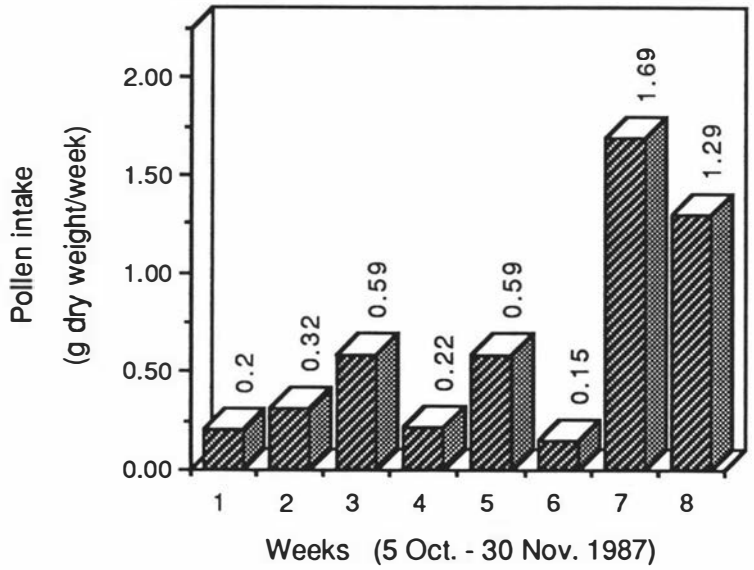


Table 6.3. Comparison of colony development for indoor reared 1986 colonies and non-requeened free foraging 1987 colonies.

	Colony mean (± S.E). indoor	free foraging	df	Number of reps	t test T value	Two tail prob.	Significance
P.I.	291.1±45.6	155.7±10.4	7.7	8,6	-2.90	0.021	*
Total males emerging	113.4±34.1	49.5±10.5	12	8,6	-1.57	0.143	n.s.
Total workers emerging	112.3±18.5	106.2± 9.8	12	8,6	-0.26	0.797	n.s.
Max.live workers	57.0±10.7	38.2± 3.5	8.4	8,6	-1.68	0.130	n.s.
Max. larval area (cm^2)	26.1± 4.4	17.5± 1.9	12	8,6	-1.59	0.137	n.s.
Max.weekly P.D.W.C.(g)	20.1± 3.2	1.7± 0.4	7.2	8,6	-5.64	0.001	**

Table 6.4. Brood bionomic parameters for 10 free foraging colonies from 1987 season.

Colony No.	8*	9*	4	5	3	2*	6	10	1	7*
P.I.	326	239	178	174	171	164	164	128	119	119
Max.live workers	59	57	45	37	50	38	39	30	28	45
Max.larval area (cm^2)	18.7	18.9	19.5	15.4	15.4	14.3	18.1	25.4	11.4	13.4
Total workers	300	235	127	121	128	149	71	84	106	104
Total males[@]	26	4	51	53	43	15	93	44	13	15
Max.weekly P.D.W.C.(g)	1.69	1.68	2.22	0.85	2.25	1.72	2.92	1.23	0.50	1.11
Days from inception to worker emergence of	21	32	19	19	19	21	21	21	20	22
male first:	71	71	59	78	70	80	79	61	80	81
P.D.W.C./cm^2/day at max.larval area (mg)	1.5	37.3	7.8	12.2	4.7	21.6	1.0	9.0	15.7	14.7

P.D.W.C. = Pollen dry weight consumption [@] = no queens emerged
* = requeened colonies (still growing at end of trial).

Table 6.5. Pearson correlation coefficient of P.I. for non-requeened free foraging colonies with maximum workers, larval area and pollen dry weight consumption (g/week), n=6.

		Max.larval area (cm^2)	Max.live workers	Max.weekly P.D.W.C.
P.I.	r value	-0.026	0.851	0.597
	Probabil.	0.480	0.016	0.106
	Signific.	n.s.	*	n.s.

$r_{0.05(1)[4]}=0.729$

Table 6.6. Pearson correlation coefficient of mean weekly pollen trapped (grams dry weight) with mean larval area (cm^2) for 10 free foraging colonies.

Colony No.	1	2	3	4	5	6	7	8	9	10
Larval area versus pollen harvested.										
r value	0.384	0.577	0.576	0.682	0.178	0.668	0.222	-0.181	0.747	0.592
No. cases	6	8	7	7	7	8	8	8	8	6
Probabil.	0.227	0.067	0.088	0.046	0.351	0.035	0.299	0.334	0.017	0.107
Signific.	n.s.	n.s.	n.s.	*	n.s.	*	n.s.	n.s.	*	n.s.

$r_{0.05(1)[4]}=0.729$
$r_{0.05(1)[5]}=0.669$
$r_{0.05(1)[6]}=0.622$

Table 6.7. Comparison of pooled data for colony pollen consumption (g/week dry weight) versus larval area (cm^2) for 8 indoor colonies (1986) and 10 free foraging colonies (1987).

Colonies	Indoor	Free foraging
r value	0.812	0.437
Probabil.	0.000	0.000
z value	1.133	0.469
No. cases	70	73
$Z_{(lab,free\ foraging)}$	3.888***	

$z_{0.001(2)}=3.291$ $p<0.001$ $r_{lab} \neq r_{free\ foraging}$

Figure 6.11. Pollen consumption vs. larval area (laboratory colonies 1986)

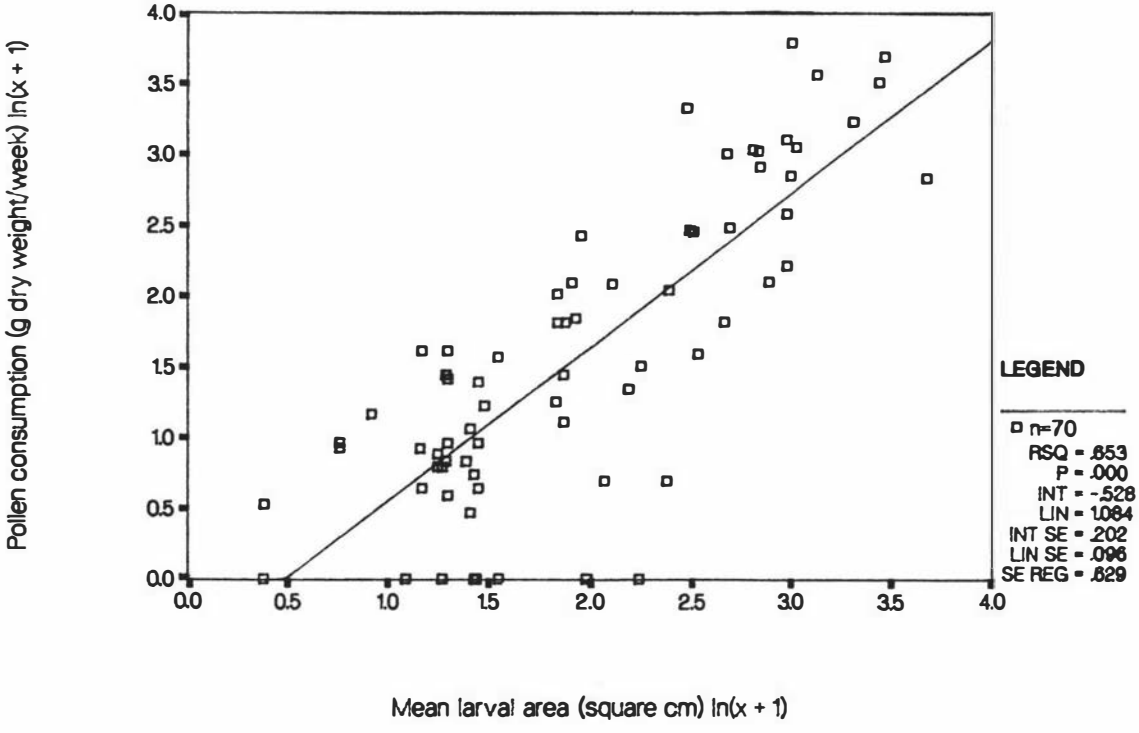
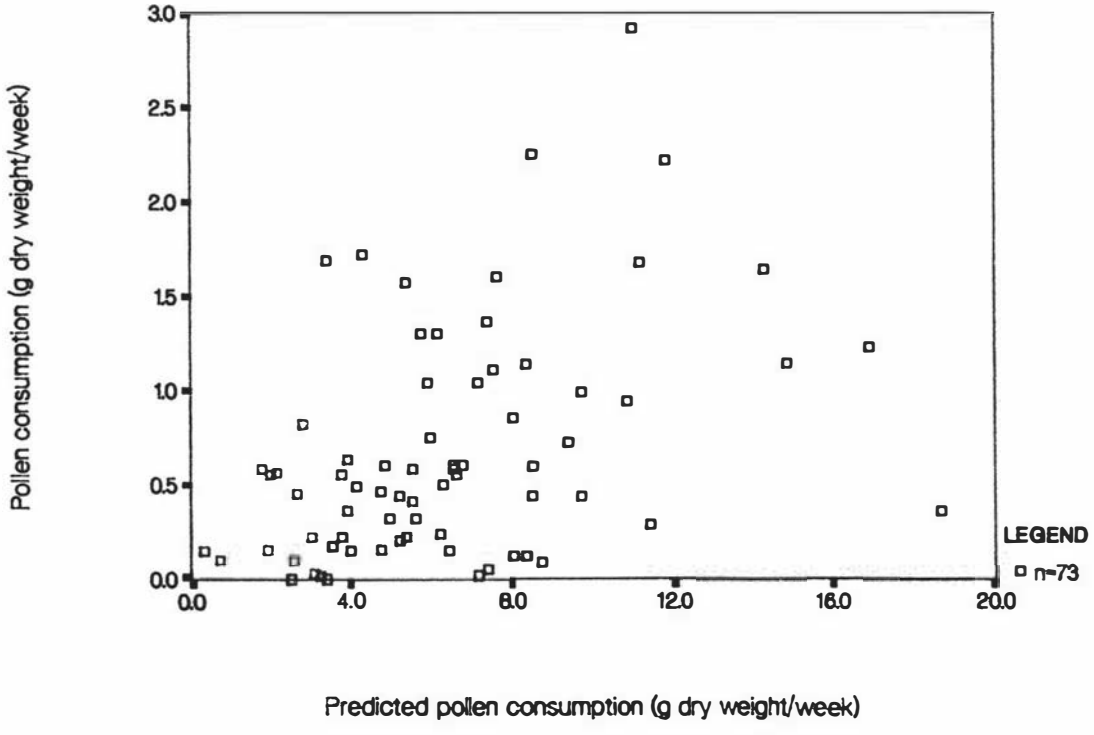


Figure 6.12. Pollen consumption (field colonies) vs. Predicted pollen consumption (laboratory colonies)

(1987 field colonies vs. 1986 laboratory colonies)



pollen intake (free foraging field colonies) versus predicted pollen consumption (indoor colonies) graphically demonstrated the poor correlation (fig. 6.12).

Extrapolation to field pollen intake from indoor colonies clearly gives the wrong result because the indoor regression equation gives ten times more pollen consumption/cm^2 of larvae than field results.

6.7 Discussion

Early in the season, *B. terrestris* workers collected borage pollen in the middle of the day (10am-2pm). Later in the season, collection of borage pollen was confined to the morning (8am-12noon), and afternoon activity was directed onto cruciferous flowers, possibly because honey bees displaced *B. terrestris* from borage during the warmest parts of the day. Honey bee numbers were low early in the season probably due to low temperatures, strong wind and rain. Later in the season, with increasing numbers of honey bees, more borage pollen was removed; consequently *B. terrestris* pollen gatherers diversified onto other crops. While these might not have been preferred, there was apparently plenty of pollen available from cruciferous crops, and later still, white clover provided a pollen source.

The pollen preference trial suggested crucifer and borage pollen was readily consumed, and that crucifer pollen may be preferred over borage. Pollen loads collected by bees may contain certain amounts of nectar which may influence the result. If more pollen had been available, the pollen should have been dried, preweighed, introduced into pollen pots, then known amounts of water added before feeding began.

The concentration of sugar in nectar pots was correlated with the sugar concentration returning in the honey stomach of nectar gatherers which was correlated to the sugar content of the most preferred crop(s) (borage and fodder radish) foraged upon. These preferred crops, recorded by bee counts in chapter 5, had sugar concentrations approaching those of nectar gatherers returning to the hive. Therefore it may be possible to identify which crop is the major source of nectar, if crops have different sugar content, by analysing the sugar concentration of returning foragers. Also nectar quality and quantity within the colony may reflect availability on the crops.

Analysis of returning foragers suggested borage was used as a pollen and nectar source early in the season. Later in the season, all crucifers were harvested for pollen. Borage provided a pollen and nectar source early in the day while fodder radish was utilized as a nectar source from late morning onwards.

So what factors influenced pollen and nectar collection? Results indicated that pollen intake increased as the weather became fine with more pollen and nectar gatherers and honey

bees foraging on crops. These improved weather conditions (which were often accompanied by wind) also favoured anther dehiscence thus increasing pollen availability (chapter 4), and increasing nectar production. However, the actual nectar available in exposed flowers decreased, presumably due to the increased bee activity.

Nectar energy returning to colonies was diminished by rainfall. As weather became fine, nectar energy from returning foragers increased. Nectar energy intake increased as the amount of pollen available on crops decreased; hence conditions favouring nectar harvesting may also favour pollen collection.

Early in the season (Oct.), extended periods of bad weather may have played a part in reducing pollen and nectar intake. Although borage did produce nectar early in the season (chapter 4), the low sugar concentration and volume secreted may have made collection unprofitable. Later in the season, foraging strategies of workers enabled nectar acquisition even when the density of honey bees exceeded $2/m^2$ on borage (chapter 5). Free foraging colonies were unlikely to have suffered from a pollen shortage as early in the season workers collected borage pollen, and while the availability of this pollen declined during the day (chapter 4), it was probably not limiting. Pollen was still recorded in borage anthers later in the day. Later in the season, foragers diversified onto crucifer crops. Teras (1976), studying flower visits of nine *Bombus* species in southern Finland, found flight activity decreased during heavy rain, high wind, low light intensity and temperatures below 10 C, with no foraging below 6 C. Foraging was most favoured when the sky was partly cloudy with light wind, temperatures of 15 C and R.H. of 71-80%. Synge (1947) and Percival (1965) also consider light intensity, rain and R.H. important factors in pollen collection, but they suggest it was difficult to evaluate the effect of one of these factors independent of the other. Brian (1952) found that *B. agrorum* collected pollen faster in damp than dry weather.

While *B. terrestris* was observed foraging in strong wind, light rain and low light intensity, the numbers were not great. Workers.often foraged on the leeward side of plots and preferred pendulous borage flowers during light rain. Rain has less effect on bumble bee foraging at the beginning of the season because the urgency to collect food is much greater (Free and Butler 1959). While low light due to excessive cloud cover may shorten the hours of foraging (Alford 1975), wind may shorten the life of bumble bees even though they are stronger fliers than honey bees (Kevan and Baker 1983). Barth (1985) reported that bumble bee workers generally fly between 10-30 C. Thus, although pollen and nectar gatherers were comparatively insensitive to weather conditions compared to honey bees (chapter 5), it seems likely that strong wind, heavy rain and possibly low light may have hampered both pollen and nectar acquisition early in the season. Weather also affected food availability and thus was a major factor influencing fluctuation in food intake into colonies.

Did any intra-colony factors affect colony food intake? Results of this study suggest the maximum number of foragers and maximum pollen gatherers are correlated in more colonies with the number of bees/colony than with the larval area. A reduction in the number of bees/colony may reduce the number of foragers with consequent reduction in food intake. Reduced food intake may, in turn, result in fewer workers emerging and as a consequence of this positive feedback, colonies may produce fewer sexuals later in colony development.

As the maximum number of foragers increased, nectar stores within the colony increased. There was no negative feedback which resulted in a reduction in pollen and nectar gathering with increased food storage. Owen (pers. comm. reported in Pendrel and Plowright 1981) found that altering the number of pollen pots in *B. terrestris* colonies affected the rate at which food was supplied to the larvae. Liu *et al.* (1975) found peak pollen collection coincided with the peak in colony development and suggested pollen gathering was a behavioural act distinct from nectar gathering. Brian (1954) found the amount of pollen collected was apparently not influenced by the number of larvae in the nest, but the amount of nectar in the nest did seem to influence foragers.

Was there any indication that the numbers of workers or larve were reduced in free foraging colonies? Comparison with indoor colonies may provide some clues.

Indoor colonies reached a peak in live workers after a mean of 44 days and peak larval area after 42 days while for free foraging colonies this was 61 and 57 days, respectively. Larval area was comparable during the first 30 days after first worker emergence between indoor and free foraging colonies. By 40 days, indoor colonies were, on average, $6cm^2$ larger. However, considerable differences were found in worker numbers. After 30 days, indoor colonies had an average of ten more workers than free foraging colonies. After 40 days, this difference increased to 17 workers.

So did the effect of weather on food availability and foraging, and the reduction in workers/colony, result in any reduction in food intake? The rate of pollen and nectar intake for free foraging colonies was one order of magnitude lower for pollen and 1-2 orders of magnitude lower for nectar than consumption for indoor colonies.

However, it is necessary to consider the different methods of recording pollen and nectar consumption and the frequency of data collection for indoor and free foraging colonies before conclusions can be drawn. Indoor pollen consumption was recorded continuously from eight colonies as the amount of pollen removed from vials offered every 2-3 days, then calculated on a per week basis. Indoor nectar consumption was recorded continuously from eight colonies as the total sugar solution (g) removed from feeding bottles. By contrast, pollen intake of free foraging colonies was recorded by observing the number and size of pollen loads returning on forager corbiculae from dawn to dusk on two days/week. These

figures were then converted to total dry weight intake/day and a mean calculated for the two days. Weekly pollen intake was extrapolated from this mean value. Nectar intake of free foraging colonies was recorded from returning foragers showing an increase in bee weight (>15mg) and from sugar concentration of regurgitated nectar throughout two recording days/week. Weekly nectar volume and energy consumption for one free foraging colony was extrapolated. Also, larval areas were recorded differently. For indoor colonies dividers were lowered onto the brood. For free foraging colonies, the brood outline was traced onto acetate, coloured in and run through a leaf area meter. A correction was made for a parallax error. Larval area was recorded within 12 hours of recording pollen consumption for indoor and free foraging colonies.

Indoor colonies did not store pollen in pollen pots, so all pollen removed from vials was consumed by larvae, sexuals etc. By contrast, pollen intake for free foraging colonies involved temporary storage in pollen pots. Early in the season all pollen was consumed overnight. Later in the season, prior to sexual emergence, free foraging colonies had 1-8 surplus pollen pots filled with pollen. This seasonal increase in surplus pollen was also recorded by Hasselrot (1960) and Webb (1961). So in reality, these colonies were consuming even less pollen later in the season than was indicated by pollen intake from workers. Surplus pollen and nectar stores were not used until the emergence of sexuals. Indoor colonies stored nectar in nectar pots, with a mean of 50/colony at termination. Free foraging colonies had few nectar stores early in the season; later in the season, one colony had up to 35 nectar pots. The remaining colonies had 1-12 full nectar pots.

The vestibule traps may have slowed the food intake by increasing the turn-around time of pollen gatherers. However, foragers could respond by foraging for longer on each trip collecting larger pollen loads or by foraging for a longer period of the day. If the colony had sufficient workers, more could be mobilised to forage; however, this was less likely if the number of workers was reduced. Also traps were only set for two days/week.

Even taking the different methods of recording pollen and nectar consumption into account and the different number of colonies assessed, the pollen and nectar intake of free foraging colonies does appear to be significantly less than pollen and sugar consumption of indoor colonies. Indoor colonies collected and stored excess sugar solution in nectar pots which may account for a 2-10 times higher increase but would be unlikely to account for the 100 times higher increase observed.

So what effect did the reduced food intake in free foraging colonies have on colony development?

There were no significant differences between maximum larval area and maximum live worker numbers or total male production between indoor and free foraging colonies. The

mean time of male production from first oviposition to the switch to oviposition of males by the foundress was the same (51 days) for indoor and free foraging colonies; suggesting some 'innate clock' may be operating in the foundress queen as indicated by Duchateau and Velthuis (1988).

No new queens were produced in free foraging colonies, only males. The higher consumption for indoor colonies may therefore partly reflect greater pollen investment required to produce queens (approximately 3.5 times that of males and workers) in 50% of the indoor colonies. However, greater pollen consumption in indoor colonies was evident well before queen production, probably as a result of more rapid development of brood and higher numbers of workers emerging. Owen and Plowright (1982) suggested wild colonies deprived of food by inclement weather, at a critical period (in development), may produce workers from female larvae destined to become queens.

So were there any early warning signs to indicate food deprivation? Early in the season, sampling of nectar and pollen pots suggested that periods of poor weather resulted not only in lower concentrations of sugar in nectar pots, but also complete depletion of nectar and pollen stores.

The effect of pollen deprivation may be to suspend brood development (Plowright and Pendrel 1977). However the effect of nectar deprivation means that colony maintenance, including temperature regulation and brood rearing, ceases. This often results in stunted growth, developmental defects (Heinrich 1979a) and in some cases death of workers or the entire colony. This was dramatically illustrated when one apparently healthy free foraging colony died overnight on 13-14 October 1987. This death may have been accelerated by the maintenance of observation hives at 30 C. During the previous seven days, sustained poor weather meant all ten colonies showed signs of nectar depletion i.e. empty nectar pots. Webb (1961) and Macfarlane (1974) observed that larval mortality occurred in developing nests when food intake dwindled. Macfarlane also found dwindling worker populations during food deprivation which resulted in the last brood of larvae dying due to neglect. Larval mortality would restrict growth of brood by reducing rates of eclosion of new workers and restricting the rate of egg production by the foundress queen, because egg laying was closely related to pupation (Webb 1961). Macfarlane (1974) suggests that restricted food intake due to adverse weather such as rain or drought (Plath 1934; Brian 1951) or a discontinuous supply of food (Cumber 1953a; Gurr 1957a) will reduce colony size causing newly emerged queens to die due to insufficient stores or result in a failure of nests to mature. While non-requeened free foraging colony size was smaller than final indoor colony size, requeened colonies continued to develop. These colonies were generally increasing in size when the trial was terminated. Requeening appeared to result in greater

colony stability and increased egg laying. This resulted in an increase in larval area, worker emergence and weekly pollen intake. Voveikov (1953) suggested natural queen-replacement in bumble bee colonies in Russia increased colony size, delayed sexual production and produced more queens. Where natural queen replacement did not occur, colonies often perished during early stages of development. Fisher and Pomeroy (1989), working with *B. terrestris* in New Zealand, found no improvement in colony size between requeened and non-requeened colonies. However, this was performed early in colony development.

Dwindling worker numbers in free foraging colonies may have resulted from drifting, as a number of individually marked bees from one colony were located in other colonies from time to time, apparently foraging for the new colony. Eshelman and Plowright (1972) found bumble bees are better able to recognise end members of a series of identical colony entrances than are honey bees. Strong wind at the tunnel entrance may hamper the orientation flight of bees leaving the entrance holes, while drifting may also be caused by social facilitation i.e. foragers following other bees into the nest entrance (Pomeroy 1977).

6.8 Summary

1) Early in the season, *B. terrestris* pollen gatherers collected pollen throughout the day. Later in the season as honey bee numbers increased on borage, pollen gatherers collected borage pollen early in the day and foraged on the remaining crops during the rest of the day.
2) Pollen intake into colonies increased with an improvement in weather conditions which favoured food harvesting and increased food availability. High honey bee numbers on borage did not reduce pollen intake.
3) Sugar concentration of nectar returning to the colony in the honey stomachs of foragers were correlated with the most preferred crop foraged upon at that time.
4) Free foraging colonies had ten times less pollen and 10 -100 times less nectar energy intake than indoor colonies.
5) Free foraging colonies grew more slowly than indoor colonies, although maximum larval area and worker numbers were equivalent. No queens emerged in free foraging colonies.

CHAPTER 7

GENERAL DISCUSSION

The main objectives of the thesis, namely to determine colony food consumption and factors affecting consumption, to evaluate a limited number of bee forage crops for colony development, to determine floral preferences of *B. terrestris* on these crops and factors influencing food harvesting, have been pursued. Although indoor colony consumption and development varied, it was possible to estimate food consumption based on brood bionomic parameters. However, for free foraging colonies, the consumption and development, were less predictable. When evaluating bee forage crops for colony development it is important to consider the whole ecological interaction between the crop and the bee rather than selecting crops simply on their botanical characteristics. In this study, food availability and harvesting by *B. terrestris* were significantly influenced by weather patterns; while bumble bee crop preference was related to food availability and competition from honey bees which, in turn, was weather dependent. Development of free foraging colony was influenced as much by intra-colony factors (e.g. foundress queen fecundity and worker emergence), and external factors (e.g. weather), as it was by the forage crops in question.

Pollen and sugar consumption by a colony were determined under laboratory conditions (chapter 2), and the pattern of colony development influencing consumption, final colony size and sexual production were also considered.

The peak in colony food consumption suggested the optimum period for achieving maximum pollination efficiency from indoor colonies would be from one week prior to the peak in larval area to two weeks after peak larval area or ten days after sexuals first emerged. One week prior to peak brood, worker numbers were relatively high; while larval area was rapidly increasing. Introduction prior to peak larval area would favour pollen collection e.g. for kiwifruit, while introduction as sexuals are emerging would favour nectar collection e.g. for melons.

Regression equations developed from colony food consumption for indoor hives (chapter 2) can be applied to *B. terrestris* management where colonies of a minimum size are required. For example, if the aim is to produce colonies with a final productivity index of 200 or more, the equations predict that colonies with a minimum larval area of $10cm^2$ with 31 live workers would be required. Weekly colony food consumption should be at least 13g dry weight of pollen and 130g of sugar solution. For a minimum P.I. of 300, these values increase to $27cm^2$ of brood, 60 live workers, 21g of pollen and

194g of sugar, respectively. These equations may be useful for colonies reared completely indoors, but for free foraging colonies, the food consumption parameters and larval area are unlikely to be applicable.

Sugar and pollen consumption and colony productivity (P.I.) could also be used to determine the total biomass (but not sex ratio) of sexuals produced i.e. males + (3.5 x queens), where 3.5 represents the greater pollen investment required for queen rearing compared to workers and males (Pomeroy 1977; Tod 1986). There was no indication that larger colonies invested a greater proportion of food into sexuals than smaller colonies. It was not possible to make predictions of final colony size from very small indoor colonies prior to removal to the field.

So what developmental factors affected colony consumption? Considerable variation in food consumption was recorded for colonies reared indoors in stable laboratory conditions at 30 C with surplus food always available. Consumption was influenced by larval area, live worker numbers and the production of sexuals. Any variation in these three parameters was likely to affect the P.I. Possible factors that may affect these bionomic parameters would be: the timing of sexual production; the rate of colony growth (i.e. workers emerging/unit time); and fecundity of the foundress queen. These may all be interrelated.

Pomeroy (1979) found a correlation between P.I. and the timing of male emergence for *B. ruderatus*, although, in this case, males always emerged before queens. However, in this study, no significant correlation between P.I. and timing of male or queen emergence was identified. No other brood bionomic or environmental factors were found which correlated with male production. Possibly some 'innate clock' may operate within the foundress queen (Duchateau and Velthuis 1988) which may be completely independent of external factors, or unfertilised egg laying may be genetically coded (Plowright and Laverty 1984).

The rate of colony growth, measured by the rate of new workers emerging every ten days during the growth phase, was higher for larger colonies. With more workers emerging, food demand is likely to increase as more workers are available to feed more brood. However, higher worker numbers did not necessarily result in more biomass of sexuals.

Foundress queen fecundity may also influence colony growth as egg shortage would limit larval area and worker emergence. Variation in fecundity may result from the earlier history of the queen (prior to capture) being uncontrolled. The fecundity of founding queens may reflect their 'health' or vigour which could be influenced by pre-hibernation conditions such as food availability and parasitism.

Criteria were established (chapter 3) to evaluate four bee forage crops for *B. terrestris* colony development during the spring dearth of flowering. The main objective of the 1986 season was to determine the relative preference of *B. terrestris* on six crops. Results indicated four crops may meet the criteria. Data of the first season's field work failed to conclusively show significant differences in crop preference mainly because of differences in crop areas and lack of diurnal monitoring of bee distribution. Results from this season suggested more detailed diurnal evaluation of food availability, bee preference and weather was required. Also flower density and flower production should be measured fortnightly; while a new trapping system for monitoring foragers returning to the hive and differentiation between feral and laboratory reared workers was required. Some data implied honey bees may be significant competitors on some crops. The suitability of *B. terrestris* for nectar removal from the four preferred crops was examined by determining tongue length and observing behaviour on the crops. Workers robbed nectar from fodder radish by perforating the base of the calyx and by probing between the calcyes on kale but foraged legitimately from borage and broccoli.

During 1987, detailed monitoring of four crops evaluated their suitability for *B. terrestris* colony growth on the basis of seasonal flowering time, flower duration, flower density, flower morphology, food availability relative to weather conditions and the standing crop of pollen and nectar (chapter 4). Data suggested fodder radish was probably the most suitable crop for *B. terrestris*. This was based on a higher density and rate of production of flowers, with the crop flowering over an extended period (ten weeks) and with ample pollen and nectar available. The long corolla tube was not a barrier to *B. terrestris* workers with the ability to bite holes in the base of the corolla. The disadvantage of this crop was the lack of nectar early in the season.

Borage was considered to be the second most suitable crop with a long flowering period and a high standing crop of pollen and nectar available throughout the season. The dry weight of pollen per borage flower was 2-3 times more than fodder radish and six times more than swede. Although borage had a shallow corolla (2mm), suggesting nectar production may be affected by changing weather conditions, the concealment of the nectar may have buffered against this and may explain why nectar production was not associated with weather parameters. However, flower production and density were comparatively low. Broccoli had high flower density and production, but pollen and nectar availability was low especially early in the season. Swede was unsuitable because of a short flowering period.

The most suitable fodder crop on the basis of bee food yield per hectare per season may not necessarily be the most attractive, as the cost (energy expended) of flight between wider spaced flowers is not great. This reinforces the need to test the preference

of the forager in question in order to verify the suitability of the anticipated preferred crop.

The suitability of these four crops was then compared with their attractiveness to *B. terrestris*, especially workers (chapter 5). This would help to indicate whether criteria used to assess suitability were justified. Crop preference of *B. terrestris* was considered in relation to food availability, weather conditions and foraging competition.

During the 1987 field trial, far more data were collected than could be presented in the course of this thesis; therefore, only the main trends were selected.

Borage was attractive to nectar gatherers as nectar was secreted during adverse conditions and the nectar sugar concentration range (16-55%) was probably within the limits that could be collected and used by bumble bees (Heinrich 1979a; Kevan and Baker 1983). Nectar energy yields also increased with an improvement in weather conditions. On very warm days, high sugar concentrations may have inhibited nectar removal, but depletion of nectar by honey bees was more likely a major obstacle to energy uptake by *B. terrestris* on borage. However, because of the foraging strategy of bumble bees which 'major' on one crop while having 'minor' crops which are periodically 'sampled' (Heinrich 1976, 1979a, 1979b), *B. terrestris* was capable of 'switching' to an alternative nectar source that secreted nectar from late morning on mild days.

As honey bee numbers increased on calm warm days, nectar gathering *B. terrestris* workers utilised nectar from fodder radish by biting holes at the base of the corolla tube. This was because *B. terrestris* workers, with a tongue length of 5.5mm, were unable to reach the nectar available by approaching flowers legitimately from the front. Honey bees, with less powerful mandibles, were not observed biting holes in fodder radish. Nectar exploitation of fodder radish by honey bees was also inhibited because their proboscis was too short (5.5mm) for the length of the fodder radish corolla tube (9.9mm) However, honey bees could rob nectar from holes already perforated by bumble bees or from aging fodder radish flowers with separating calyces.

Bumble bees would be at an adaptive advantage to harvest food early in the season before honey bee competition increased with warmer weather,.because bumble bees were more tolerant of bad weather than honey bees and appeared to forage at lower temperatures, during light rain and in strong winds.

Nectar gatherers on fodder radish increased as nectar gatherers on borage increased (although the correlation was not significant; chapter 5), while nectar gatherers on borage were not significantly negatively correlated with honey bees on borage. Both results could be used as evidence against the existence of 'competition' between honey bees and *B. terrestris* nectar gatherers on borage. To the contrary however, a build up of nectar

gatherers on borage would seem likely to precede any increase of honey bees on this crop, and at a certain threshold density of honey bees on borage, *B. terrestris* workers could collect more nectar on fodder radish as the standing crop of nectar became depleted on borage. *B. terrestris* workers, conditioned to foraging on borage, may continue to forage on that crop while newly recruited workers would find fodder radish more attractive. The only real way of proving 'competition' would be to control the influx of honey bees either by caging the entire crop or by removing all honey bee hives (managed and feral) from the area and determining whether *B. terrestris* remained on borage.

Bumble bees generally forage on zygomorphic flowers with deep corollas rather than actinomorphic flowers with shallow corollas. However, features of the actinomorphic borage flower, especially colour and scent, may have provided attraction at a distance. The colour and scent of borage may have been relatively strongly distinguishable from the three cruciferous crops. Bees are generally more attracted to blue compared to yellow flowers, with their colour vision being more sensitive to the former (Menzel and Erber 1978). Borage flowers are darker towards the centre, and this may have increased their attractiveness. *B. terrestris* prefers nectar with a combination of sucrose, fructose and glucose sugars or sucrose dominant nectar rather than fructose and glucose dominant (Pouvreau 1974). These three sugars are readily found in varying proportions in borage (Percival 1961). This may explain the attractiveness of *B. terrestris* and honey bees to this crop. Honey bees also prefer a combination of these three sugars (Heinrich 1975). Inversion of sucrose to glucose and fructose approximately doubles the osmolarity, thus the resulting two sugars will be in equilibrium with drier air than sucrose solution of the same percentage concentration by weight (Corbet 1978). Highly inverted nectars, such as those found in Brassicaceae (fructose and glucose), undergo less rapid evaporative concentration than nectar of borage containing sucrose. Higher sugar concentration in borage than crucifers may therefore stimulate foragers to preferentially collect nectar from this crop.

Another reason for the preference of borage may lie in the history of previous contacts between *B. terrestris* and members of the family Boraginaceae. *B. terrestris* originated from eastern and central Europe where at least ten subspecies and seven sister species exist (Rasmont 1983). *Borago officinalis* is also of European origin. While it is difficult to generalise about European flora, the remnant flora of the Canary Islands, which may epitomise parts of the original European flora, is well endowed with Boraginaceae. In particular the genus *Echium*, to which *Borago* is very closely related, is particularly diverse with over 20 species represented (Bramwell and Bramwell 1974). Also *Echium* is a favoured pollen source by bumble bees in Ontario, Canada, even though it is not overly abundant (Liu *et al.* 1975). Such innate predilection for Boraginaceae may have

originated from coevolution of this plant family with the sub genus *Bombus* Latreille *sensu stricto.*

Although borage was the 'major' crop utilised by *B. terrestris* workers with fodder radish as a 'minor' alternative crop, workers could still make energy profits on less favoured crop species. Comparison between the individual foraging performance of workers on borage with the less favoured broccoli, from caged trials, indicated that the rate of nectar energy harvested was comparable on both crops. Workers adopted certain energy saving strategies e.g. robbing nectar, walking between flowers on less rewarding broccoli, while workers flew between the higher rewarding borage flowers. Robbing of broccoli flowers by *B. terrestris* nectar gatherers had not been identified during the previous season (1986). Results of individual bees foraging in confinement were hampered by inclement weather, destruction of cages by wind, uncooperative bees and the large variation in foraging behaviour as a result of previous contact with the crop the bees were released on. No comparison between caged trials and free foraging nectar gatherers was conducted because of the difficulty in monitoring individual free foraging workers.

The poricidal-like dehiscence of borage anthers may have increased the attractiveness of this crop to *B. terrestris* pollen gatherers. This enabled workers to harvest pollen by vibration of the anthers, giving them an adaptive advantage in pollen removal over honey bees which could not vibrate anther locules. This pollen harvesting often occurred early in the day (matinal foraging) before pollen was depleted either by weather conditions e.g. strong wind, or by competition from honey bees. Also the pendulous nature of the flowers would assist in pollen removal and allow pollen harvesting during light rain as occurred for *B. terrestris* early in the season. Removal of borage pollen by honey bees appeared to be by incidental dusting while nectar collecting; this resulted in small pollen loads/bee. Exactly how the pollen was transferred to the honey bee without vibration would require further investigation. The overall effect of a large number of honey bees collecting nectar on borage was a depletion in both nectar and pollen.

The criteria used to assess the suitability of the four crops for *B. terrestris* (chapter 4) appears to have been partially justified. However, factors such as bee adaptations for nectar and pollen removal from crops were seen to be important, as well as physical features of the flower providing the initial attraction. The degree of previous evolutionary contact between the bee and host plant may also be significant. Once foraging began, the continual availability of food seemed to be the overiding factor influencing crop preference.

On warm sunny days, many small marked workers that would not normally forage were noted on the fodder radish plot immediately adjacent to the hives. This may be an example of polyethism with smaller workers foraging closer to the nest (Waddington

1981). Few workers as small as these were observed from feral populations as possibly these workers would have been disadvantaged to return nett energy profits due to their higher surface area to volume ratio which may increase their thermoregulation needs and their flight drag. This could have advantaged marked workers during fine weather by enabling a greater proportion of workers from the hive to forage on nearby crops. This hypothesis would require testing to validate as no records of feral worker weight were taken.

The aim of chapter 6 was to determine which crops were foraged upon by analysing returning foragers at the hive entrance, what factors influenced food returning to colonies and the consequent effect of food intake on colony growth. Early in the season, workers collected borage pollen in the middle of the day (10am-2pm). Later in the season, collection of borage pollen was confined to the morning (8am-12noon) and afternoon activity was directed to the cruciferous crops, possibly because honey bees displaced *B. terrestris* from borage during the warmer parts of the day. The high density of honey bees on borage did not reduce the pollen and nectar intake into free foraging colonies. Near the end of the season white clover provided a pollen source.

As competition intensified later in the season, pollen gatherers were forced to forage on a wider variety of crops. Flowers of borage, swede and broccoli showed decreases in pollen availability during the day, but this was not so apparent in fodder radish. Fodder radish had a very large standing crop of pollen, and yet very little of this pollen appeared to be harvested. Possibly this pollen does not have an attractive phagostimulant or is nutritionally unsuitable for larval development. Pollen preference trials were inconclusive mainly because of the difficulties in obtaining sufficient pure lines of pollen.

Food availability was affected by the weather and number of bees foraging. Weather conditions were the main factor affecting fluctuations of food intake into colonies. However, intra-colony factors may also play a role in food intake. The maximum number of foragers and pollen gatherers were correlated in more colonies with the total number of bees/colony than the larval area. A reduction in bees/colony, as a result of forager mortality or a decline in worker emergence, may reduce food intake. Food reduction may result in fewer workers emerging, and as a consequence of this positive feedback, colony growth and sexual production could be impaired. Free foraging colony growth was considerably slower than indoor colonies with 17 fewer workers having emerged after 40 days. Poor weather conditions may have reduced worker life expectancy to less than the 13.2 days suggested by Owen and Plowright (1982) for temperate bumble bees.

The combined effects of weather on food availability, food harvesting and possibly forager mortality with fewer workers emerging/colony could potentially reduce total food

intake. Food intake of free foraging colonies was significantly lower than pollen and nectar consumption of indoor colonies. Pollen intake was correlated with larval area for three of the ten free foraging colonies. However, pooling the data produced a highly significant correlation. This agrees with Tod (1986) who found a linear correlation between daily pollen income and area of brood for *B. terrestris* colonies free foraging on Massey University flora from indoor observation hives during the 1984/85 summer. Pomeroy (1977) also found a linear correlation between daily food input and larval biomass for *B. ruderatus* colonies.

The mean pollen consumption of larvae for indoor colonies in this study was 0.76g/cm^2/day (0.62g dry weight, 23% water). Pomeroy and Plowright (1982) estimated that the pollen consumption for *B. perplexus*, reared indoors in heated observation hives, was 0.12 and 0.22g/cm^2/day (fresh pollen) for two and eight workers/colony. The mean pollen intake for free foraging colonies for this study was 13.5mg/cm^2/day (11mg dry weight, 18.8% water) This compares with 295mg/cm^2/day from Tod's (1986) data for *B. terrestris* free foraging during the summer. The pollen intake for this study was recorded during spring (Sept.-Nov.) and may explain the much lower pollen intake compared to Tod's summer results. However, for these comparisons, moisture levels may vary. Pomeroy and Plowright (1982) moistened pollen with honey.

Difficulties in recording larval area with dividers resulted in the alternative method of tracing brood onto acetate sheets. Retrospectively, more comparisons could have been made when comparing brood measured using these two methods. This would not alter the range in variation of the data but should decrease the standard error of the difference (S.E.D.) between measures for dividers versus acetate sheets, giving more confidence for comparisons of the data. Discrepancies in measures may have resulted from the three-dimensional formation of brood area with some larvae obscured from view.

Further research would be required to verify whether the ten-fold reduction in pollen intake (10-100 fold for nectar energy) for free foraging colonies, compared to indoor colonies, was simply an artifact of the trapping system employed or whether very low food intake is consistently recorded for colonies foraging under adverse weather conditions. The 15mg cut-off point for recording nectar from free foraging nectar gatherers arose from a lack of nectar detected after regurgitation. This weight gain may have resulted from a build up of body fluid prior to excretion or the presence of ungroomed pollen on body hair. However, to be certain that no nectar was present, a few workers could have been dissected, and the stomach contents analysed.

Indoor colonies had an abundant food source; while by comparison, free foraging colonies acquired food under considerable hardship. Indoor colonies stored excess sugar solution in nectar pots which may account for a higher indoor sugar consumption.

In retrospect, energy stored in nectar pots could have been analysed to determine if differences in energy intake between indoor and free foraging colonies could be accounted for by the sugar stored in indoor colonies. Pollen was not stored in indoor colonies but was stored in free foraging colonies. These differences would be unlikely to explain the dissimilarity in food intake recorded between indoor and free foraging colonies for these trials.

If lower food intake for free foraging colonies is supported in future research, this would be an argument for rearing colonies outdoors on crops, providing crop cultivation costs are not excessive. Determining the threshold level of food intake required for queen production from free foraging colonies would be the next step in a complete management programme.

Only workers and males emerged in free foraging colonies, no new queens were produced. This may reflect the lower food supply to larvae in these colonies; whereas, greater pollen consumption for indoor colonies may have resulted in greater queen production. Production of queens, which are fed more than workers or males during early larval development, may be dependent on levels of food consumption more in line with indoor colonies. Indoor colony development suggested new queens were produced from fertilised eggs laid prior to the oviposition of non-fertilised male eggs. Possibly, colonies fed ample food during the growth phase may produce more queens; while colonies fed more during nest maturity may produce more males. However, indoor results suggested that colonies producing more queens did not have higher total or weekly colony pollen or nectar consumption (chapter 2). Discovery of large feral colonies with hundreds of queens each season suggests that some feral colonies are well supplied with food, but these colonies may be the exception rather than the rule.

Because requeened free foraging colonies were still growing when the trial was terminated, reduced food intake does not directly appear to have reduced colony size compared to indoor colonies. Possibly, new queens introduced during requeening, had higher fecundity resulting in a higher rate of new workers emerging, prolonging the growth phase. With a small bee population, more energy/bee must be spent incubating, feeding and maintaining brood. As more bees emerge, economies of scale result from the presence of a much larger population of workers maintaining brood with less energy expenditure/worker.

A number of assumptions were made when determining the area of borage and fodder radish required to support one *B. terrestris* colony during development. Firstly, all pollen and nectar/flower was available to *B. terrestris* foragers, and secondly, all pollen and nectar was harvested and returned to the colony. Because of the large difference in food consumption between indoor and free foraging colonies, both sets of data were

used. Indoor food consumption probably reflected the upper limits of consumption for colonies of this size; while food consumption of free foraging colonies in adverse weather conditions probably reflected the lower limits of consumption.

For indoor colonies, the maximum energy (of sugar solution) consumption/colony/day was 190.71kj; while the maximum pollen (dry weight) consumption/colony/day was 2.88g. These were mean values from eight colonies. For free foraging colonies, the maximum nectar intake/colony/day was 4.07kj and the maximum pollen intake/colony/day was 0.23g. The energy intake was recorded from one colony; while pollen intake was the mean from ten colonies.

From chapter 4, the production of nectar was 111joules/m^2/day for borage and 278joules for fodder radish. The production of pollen was 35mg/m^2/day for borage and 150mg for fodder radish. Hence, the area (m^2) of borage and fodder radish required to feed one colony on pollen and nectar was:

		Indoor colony (maximum)	Free foraging colony (minimum)
Borage	nectar	1718.1	36.7
	pollen	82.3	6.6
Fodder radish	nectar	686.0	14.6
	pollen	19.2	1.5

The assumption that all nectar and pollen produced from borage was available to *B. terrestris* workers may be reasonable early in the season when competition was minimal. Later in the season, when honey bee competition increased, some of the standing crop of borage pollen may still be available to *B. terrestris* workers, while the nectar in fodder radish would also be available. The nectar in borage, however, for the sake of calculation, could be expected to be unavailable to *B. terrestris* except during cool (<15 C), wet, windy (> 2.0ms^{-1}) weather (chapter 3).

The most unpredictable factor influencing food availability would be the removal of food by feral *B. terrestris* workers. During the 1987, trial on average, there were 1.1 times more feral nectar gatherers and 2.8 times more feral pollen gatherers than marked workers. This would vary from season to season, but with more artificial colonies and larger areas of forage crop, the proportion of feral workers could possibly be reduced significantly. This feral population may continue to remain an enigma, and hence to compensate, a greater rather than a lesser area of forage crop should be grown.

Employment of heated observation hives (Pomeroy and Plowright 1980) in free foraging trials, apart from maintaining consistency in rearing conditions between seasons, eliminated variables such as colony temperature and insulation which could influence the results. However, it should be noted that colony energy consumption would be considerably higher in unheated hives lacking insulation because more energy would be required to maintain a consistently high temperature for brood development. Larval area and live bee counts could be undertaken without disturbing the colony in heated hives as workers refrained from constructing wax canopies over the brood; while numbers of pollen pots and samples from nectar pots could be quickly taken. Rapid removal, marking, weighing and replacement of workers was also possible. Early signs of possible colony decline (e.g. the death of foundress, worker egg laying, depletion of food stores and low worker numbers) could be counteracted by requeening, worker supplementation, supplementary feeding and even complete brood replacement. The disadvantages of heated hives were the cost of initial installation, the cost of heating and the design of colonies ducted to the exterior.

For successful management, the preferred crops for *B. terrestris* should be identified both diurnally and seasonally. These crops should be regularly monitored for food availability, especially during poor weather or heavy competition, together with recording the number of days when weather prevented or reduced foraging and food harvesting. It is pointless monitoring food availability on crops not used by workers. Alternatively, daily observations of the colony to determine the number of full pollen and nectar pots or sampling of the nectar pot sugar concentration would be useful for determining when food became depleted. During periods of poor weather, supplementary feeding with sugar solution and pre-frozen pollen would prevent slow brood development and colony starvation. Identifying the direction of the prevailing wind during bee foraging may also be useful. Colonies can then be sited downwind of forage crops. Flying upwind will assist in attraction to crops by the presence of odour plumes from flowers. Flowers and inflorescences will be more visible when approached into the prevailing wind, flight can be regulated and the approach and landing on small pendulous flowers more controlled. Bees with full pollen and nectar loads will then be carried back to the hive with the prevailing wind.

B. terrestris has an adaptive plasticity which enables the insect to respond to an ever-changing environment, guaranteeing survival of the species in this country. To successfully manage this extremely useful pollinator, bombiculturalists need to be equally adaptable and provide suitable forage crops for colony development and rearing facilities which are acceptable to the bee, while allowing the opportunity for close observation and manipulation.

RECOMMENDATIONS

1). Borage and fodder radish complement each other as suitable food sources for *B. terrestris* and therefore they should be grown together.

2). The possibility of other crops (e.g. kale) providing suitable bee forage should not be discounted. Such crops should be individually tested against borage in the future.

3). Borage should not be grown in areas adjacent to honey bee apiaries as competition on borage may reduce the standing crop of available food for bumble bee colonies. By sowing two crops of borage, six weeks apart in autumn, the flowering in spring should be spread over at least three months. Sowing borage in areas adjacent to white clover would be advantageous as this may provide an early summer food source for *B. terrestris* after borage finished.

4). If bee forage is provided as a monoculture, poor weather or competition from other species could significantly change the attractiveness of the crop as a food source to *B. terrestris*. In such cases of low reward, bees may forage further afield, this could reduce the rate of food intake to the colony and increase the risk of forager mortality. To counter this, growing an alternative crop, which provides food for *B. terrestris* either in poor weather or when honey bees are numerous, would be sound management.

5). The most suitable time for transferring colonies to orchards for pollination is when the foraging force and food demand peaks. This period of colony development extended from approximately one week prior to first sexual emergence to two weeks after sexuals first emerged.

6). Because colony dynamics, food supply and foraging strategy are closely related to the 'major' forage crop, monitoring this crop can provide information on the health of and food supplied to colonies. Alternatively, monitoring colonies can provide information about food shortages, and by supplementary feeding, loss of colonies can be avoided during periods of bad weather.

7). Mass rearing of colonies in heated wooden observation hives,which are ducted to the exterior and sited adjacent to crops grown as bee forage, may suffice to provide an alternative to management methods presently in use. Mature colonies could be removed from the hive, transferred to insulated vestibules and relocated into orchards for pollination.

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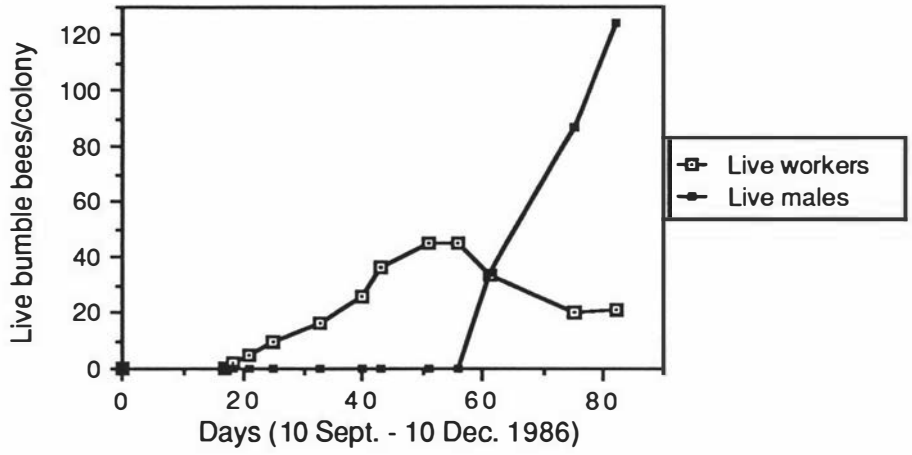
Jai Guru Dev

APPENDIX I FIGURES

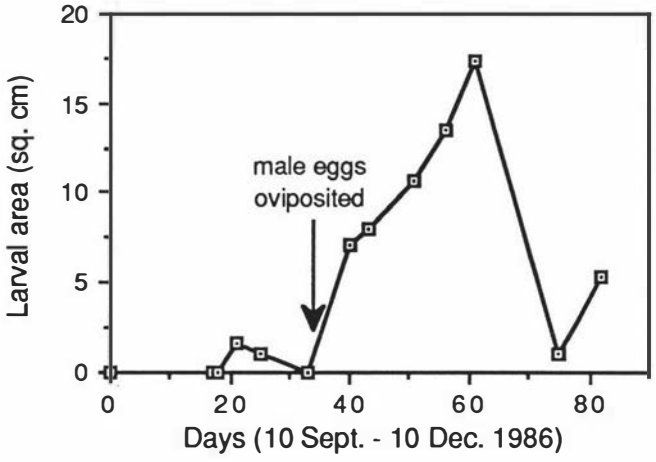
Figure A2.1. Bumble bees for indoor hive 1

(a)



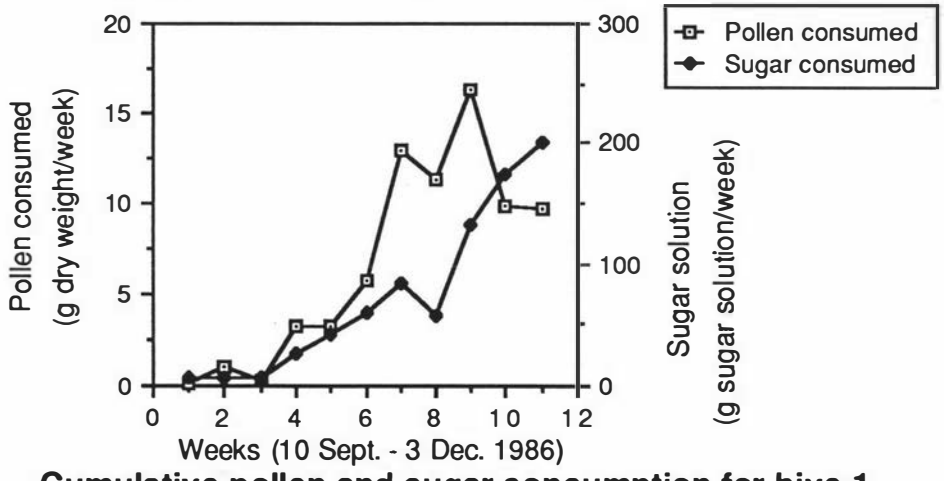
Larval area for indoor hive 1

(b)



Weekly pollen and sugar consumption for hive 1

(c)



Cumulative pollen and sugar consumption for hive 1

(d)

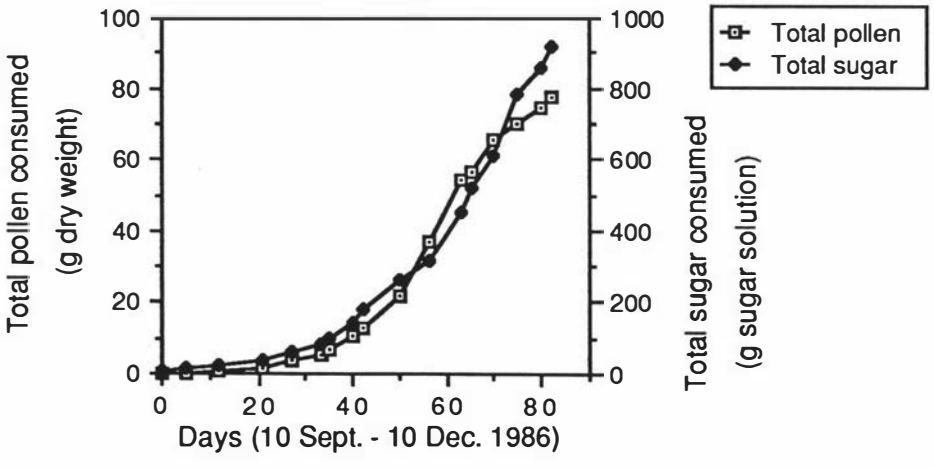
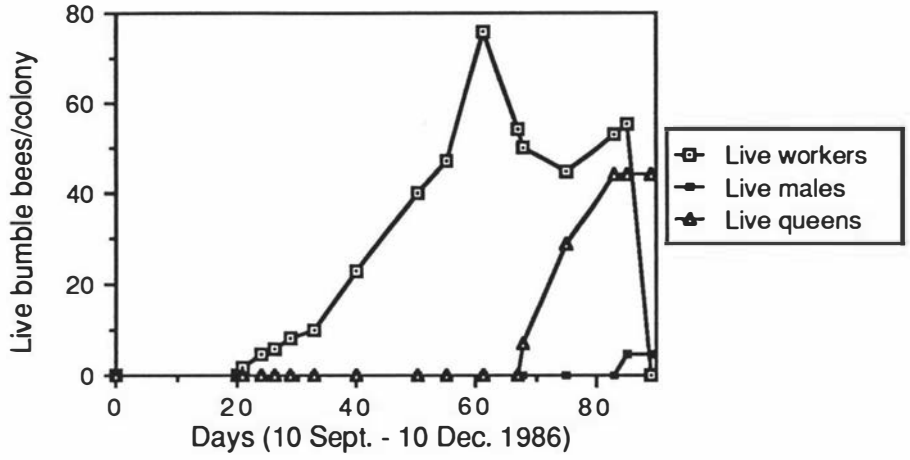


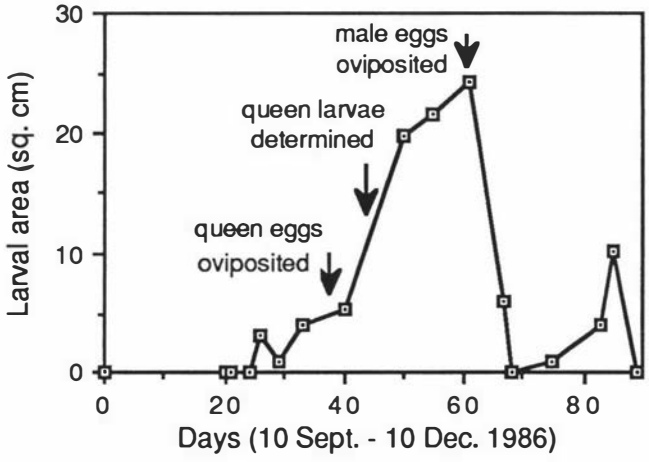
Figure A2.2. Bumble bees for indoor hive 3

(a)



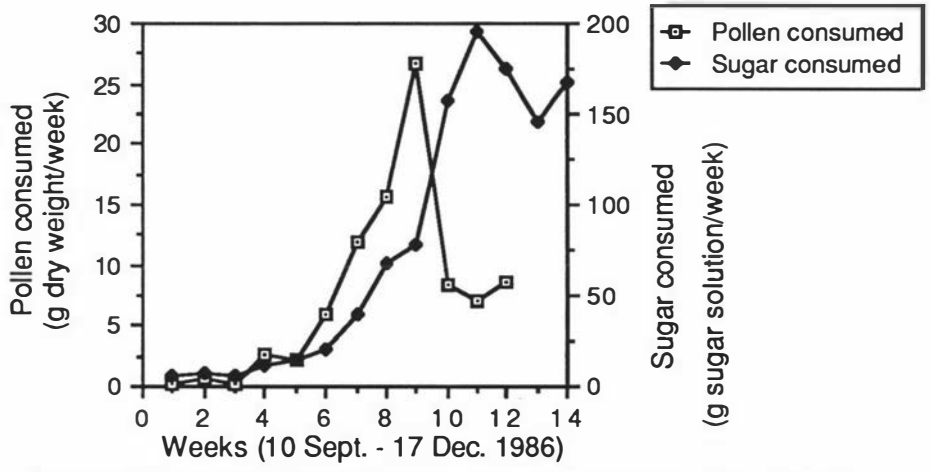
Larval area for indoor hive 3

(b)



Weekly pollen and sugar consumption for hive 3

(c)



Cumulative pollen and sugar consumption for hive 3

(d)

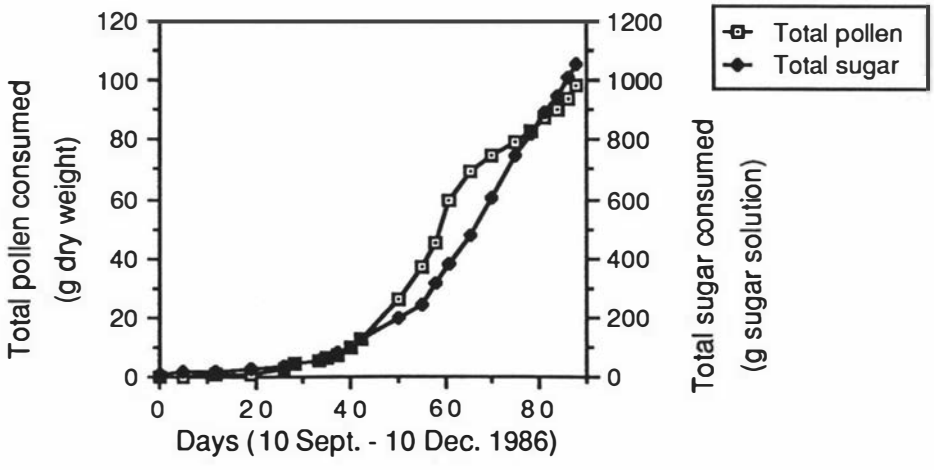
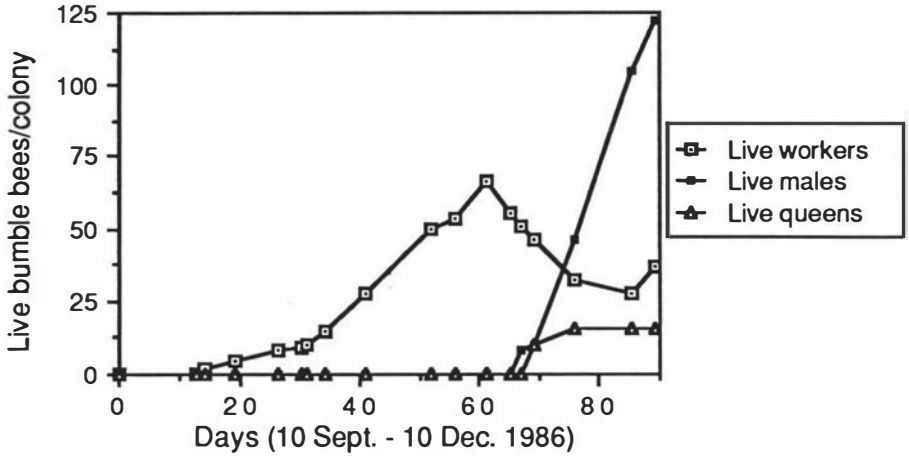


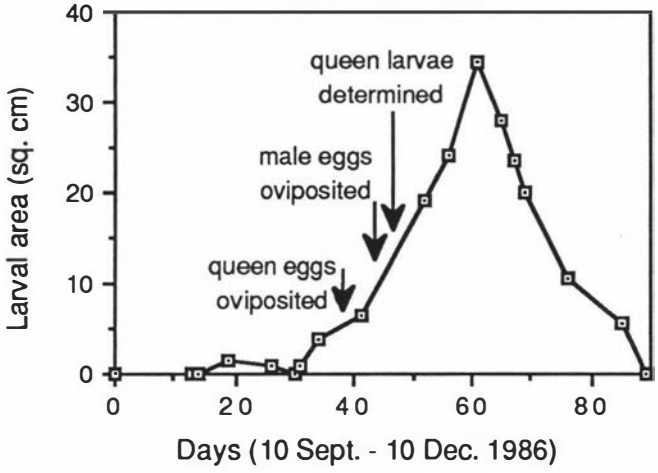
Figure A2.3. Bumble bees for indoor hive 4

(a)



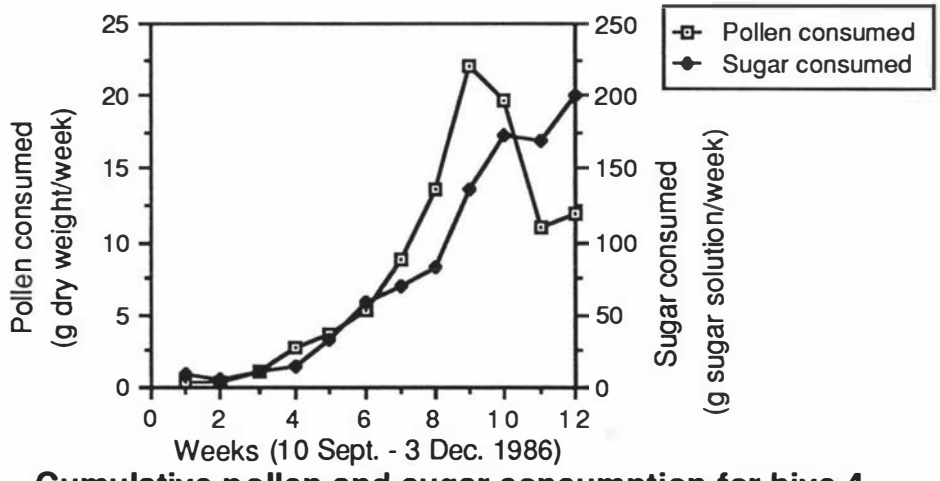
Larval area for indoor hive 4

(b)



Weekly pollen and sugar consumption for hive 4

(c)



Cumulative pollen and sugar consumption for hive 4

(d)

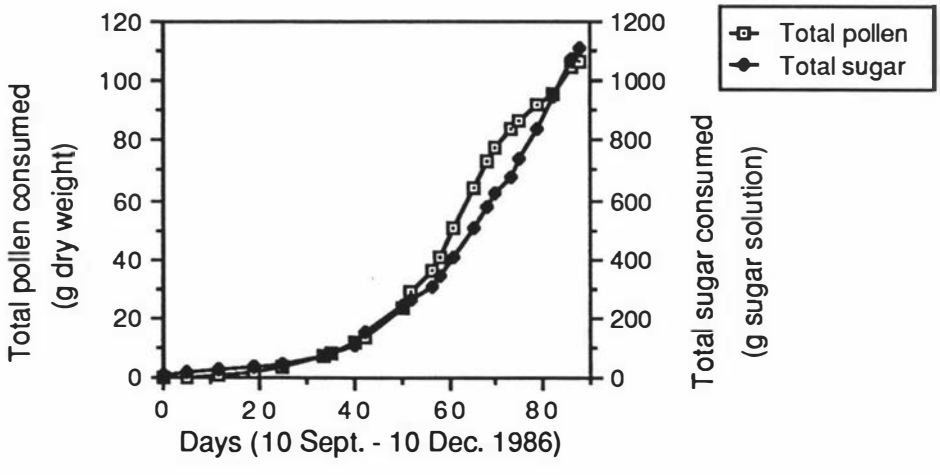
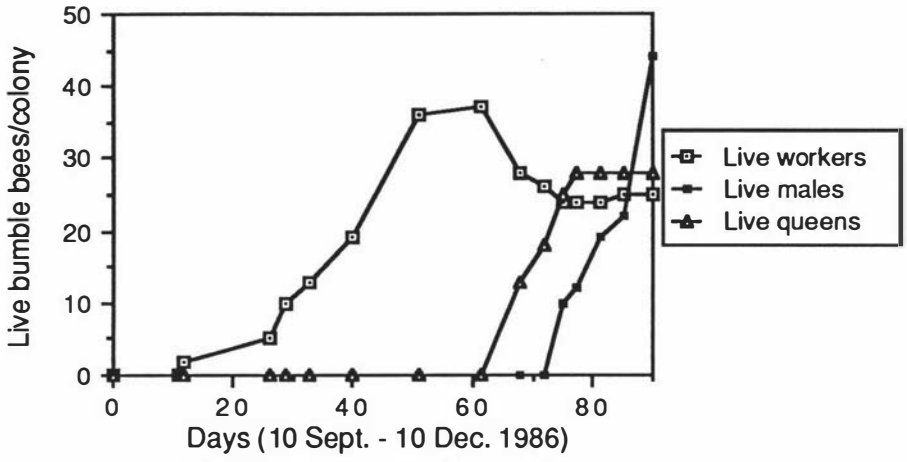


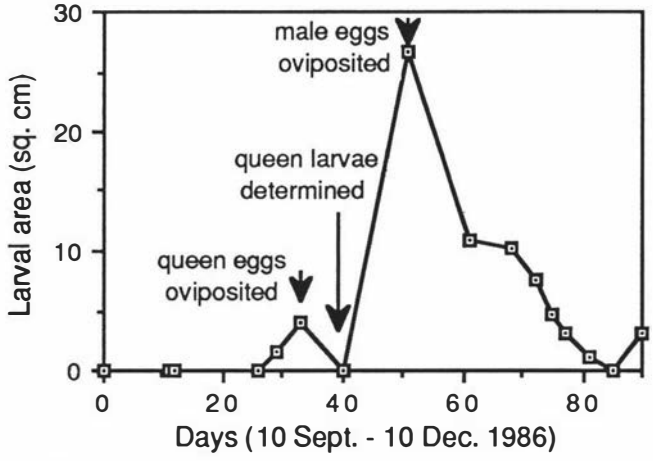
Figure A2.4. Bumble bees for indoor hive 6

(a)



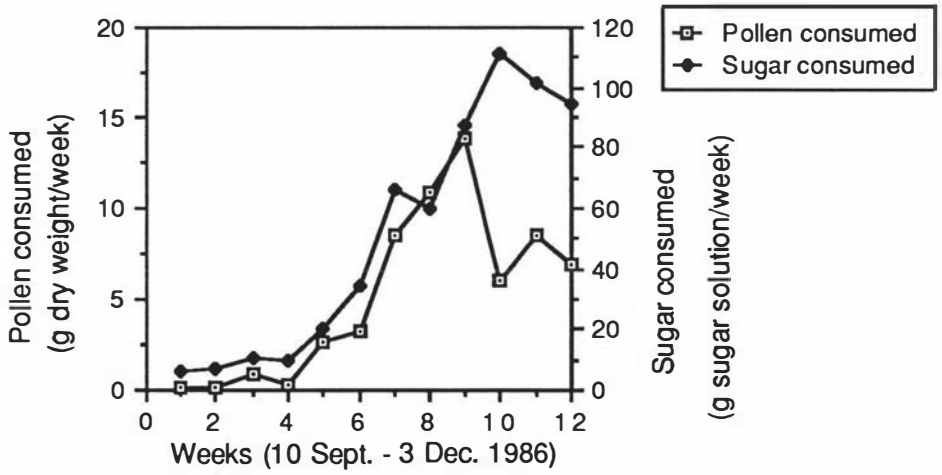
Larval area for indoor hive 6

(b)



Weekly pollen and sugar consumption for hive 6

(c)



Cumulative pollen and nectar consumption for hive 6

(d)

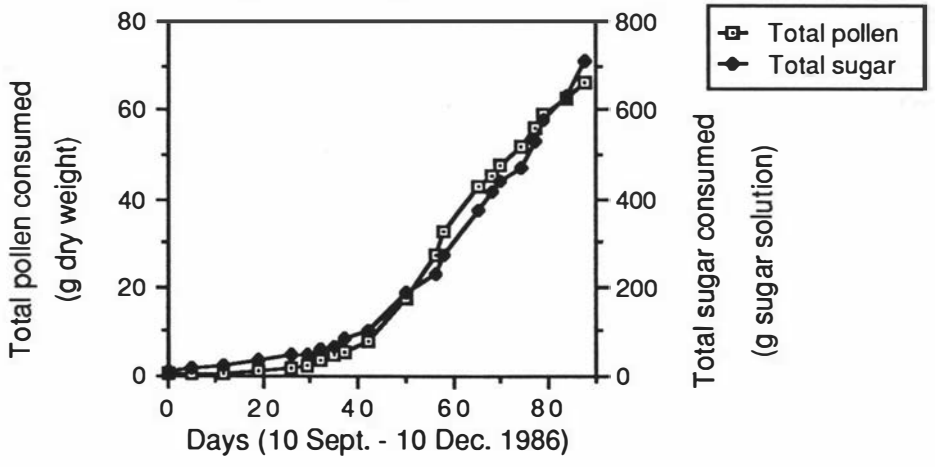
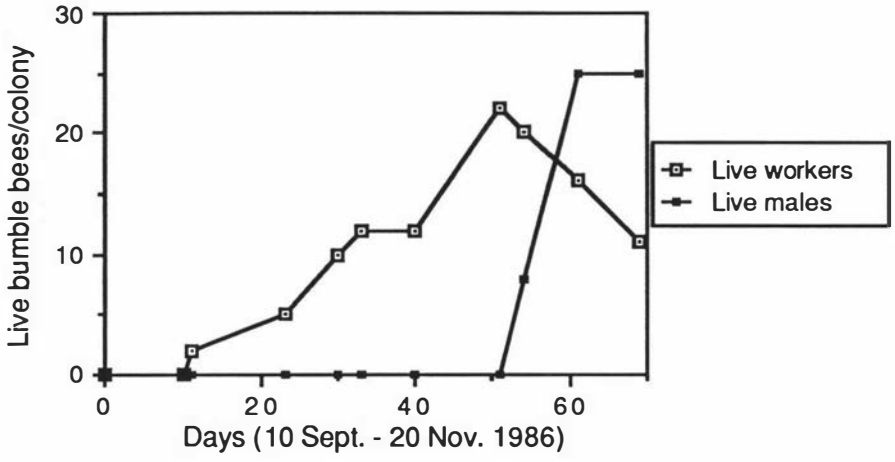


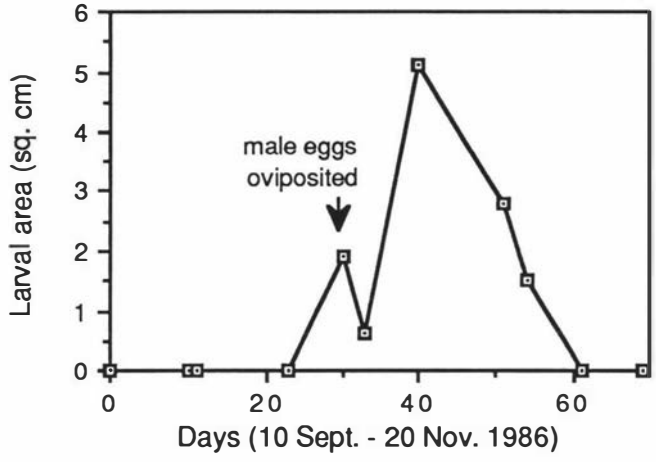
Figure A2.5. Bumble bees for indoor hive 7

(a)



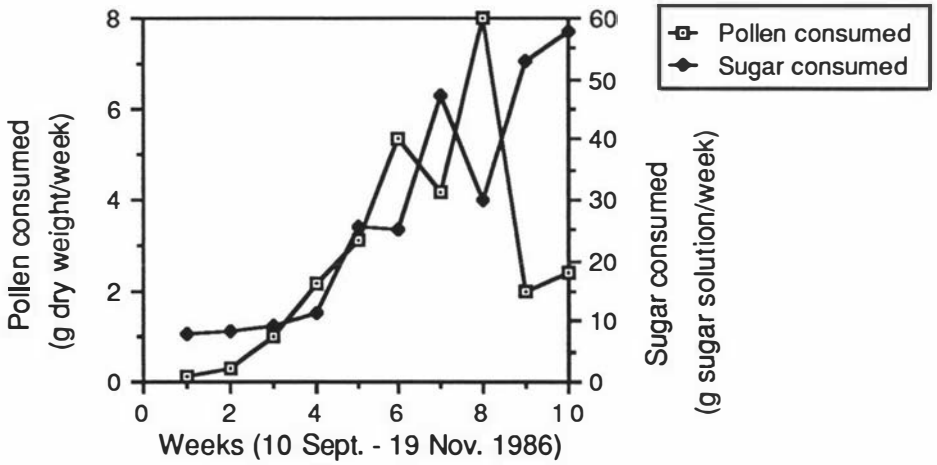
Larval area for indoor hive 7

(b)



Weekly pollen and sugar consumption for hive 7

(c)



Cumulative pollen and sugar consumption for hive 7

(d)

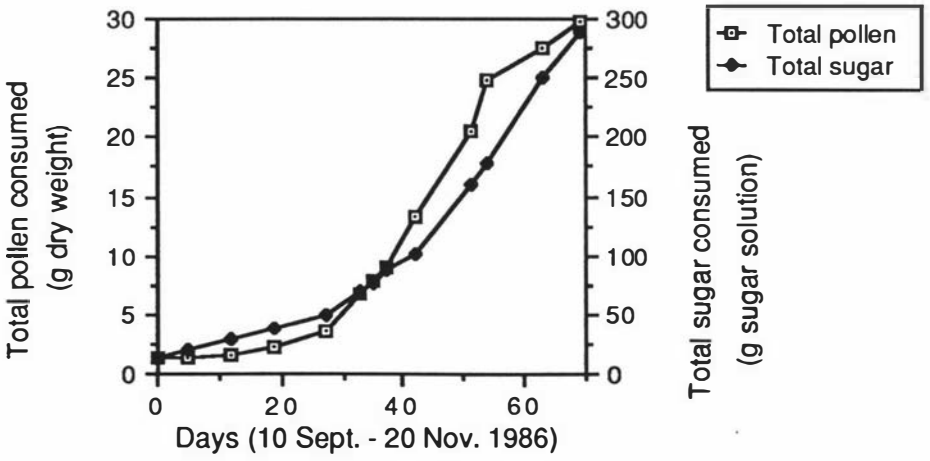
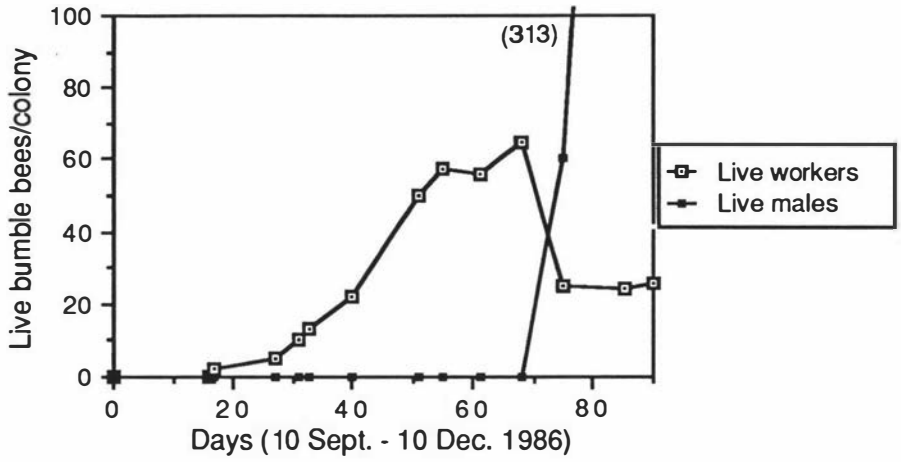


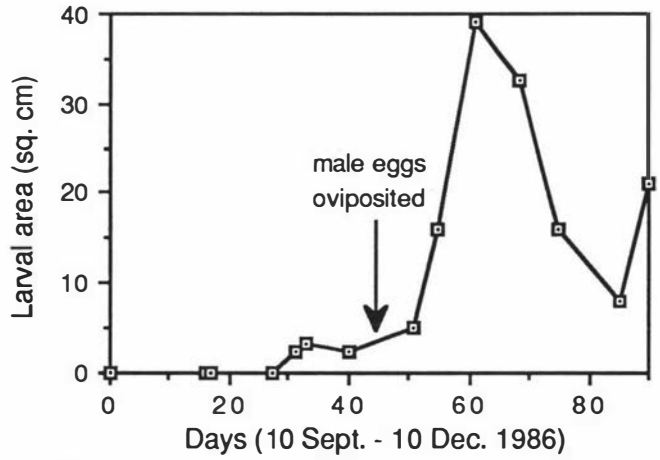
Figure A2.6. Bumble bees for indoor hive 8

(a)



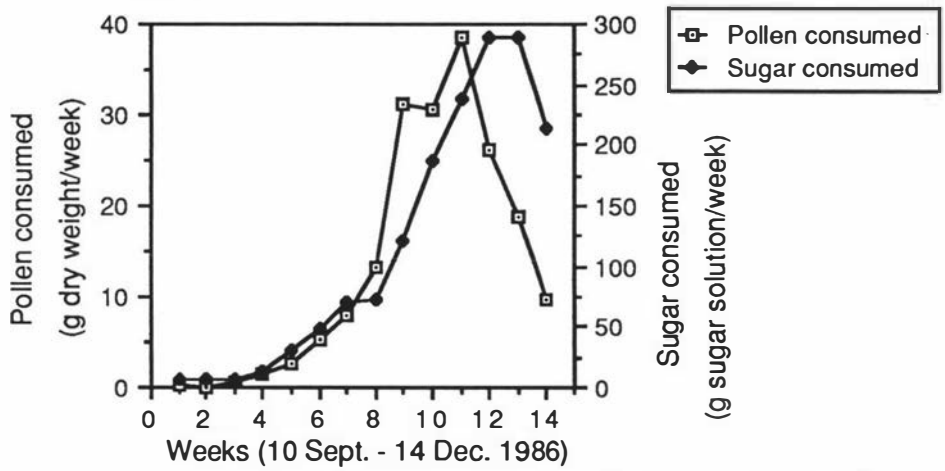
Larval area for indoor hive 8

(b)



Weekly pollen and sugar consumption for hive 8

(c)



Cumulative pollen and sugar consumption for hive 8

(d)

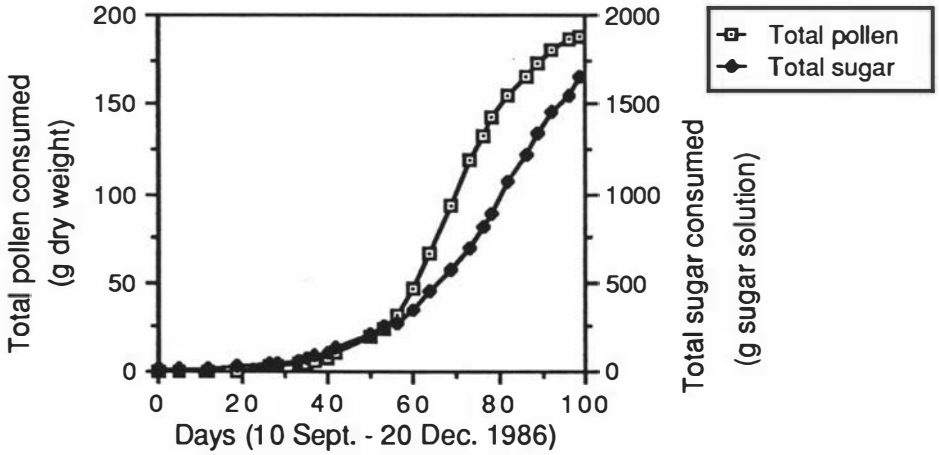
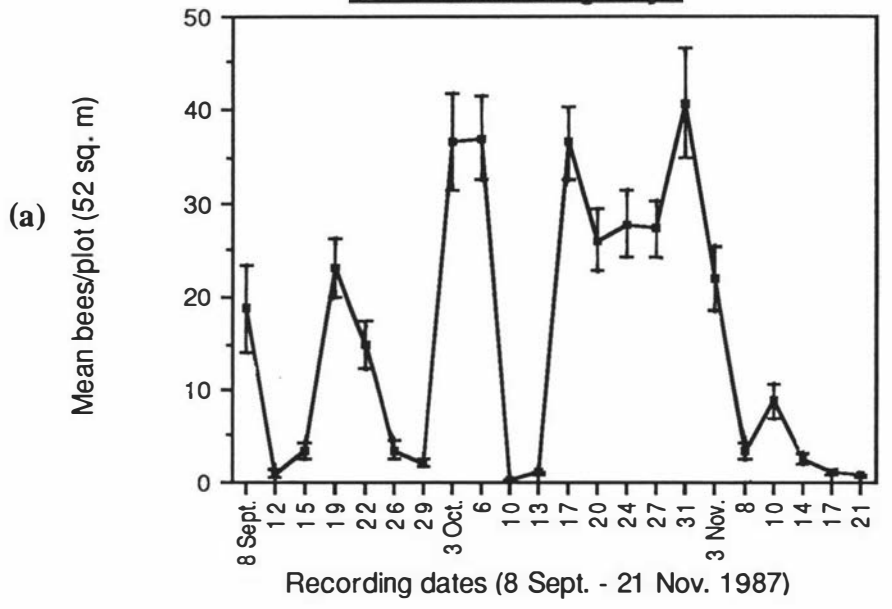
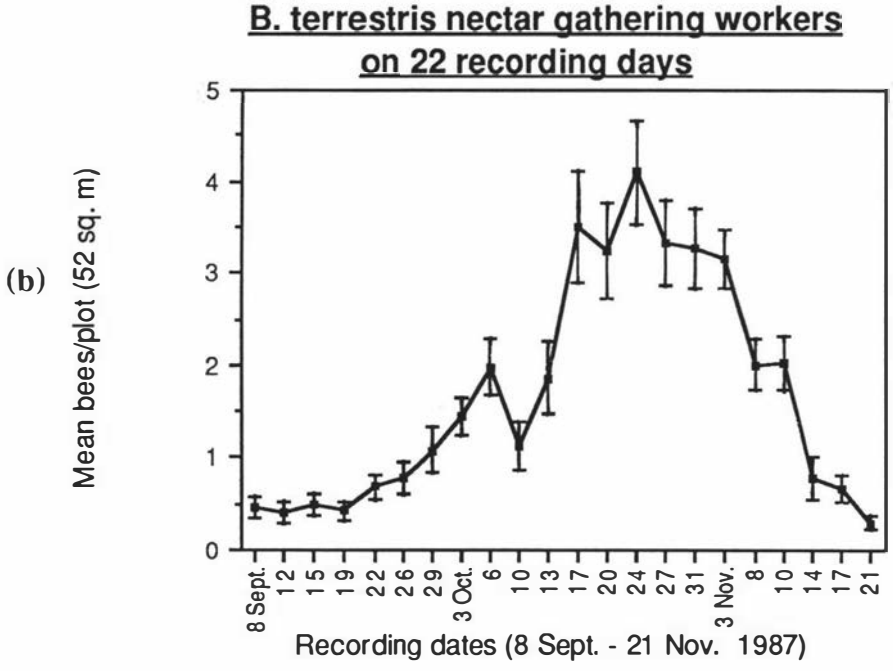


Figure A5.1. Number of honey bees on 22 recording days





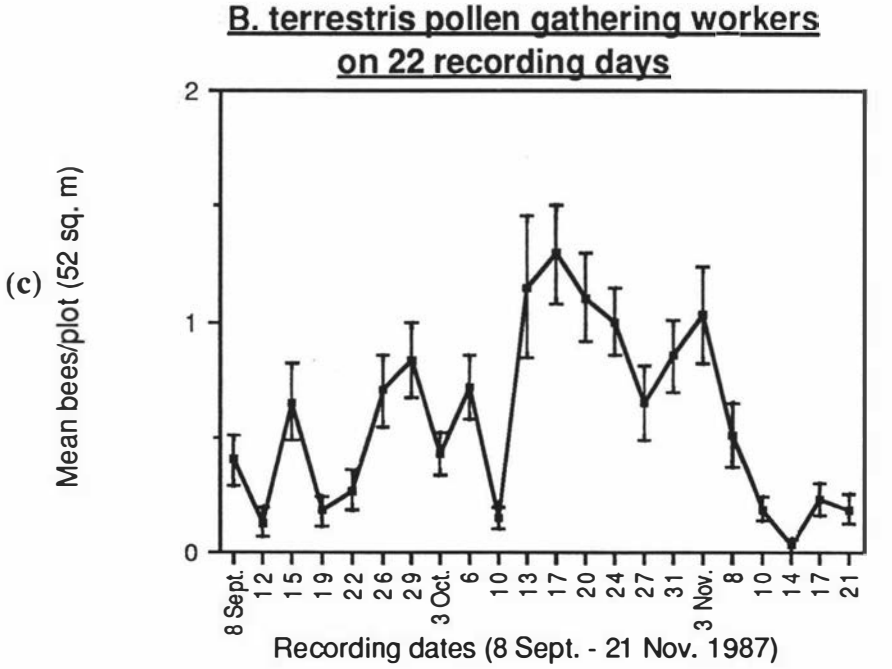
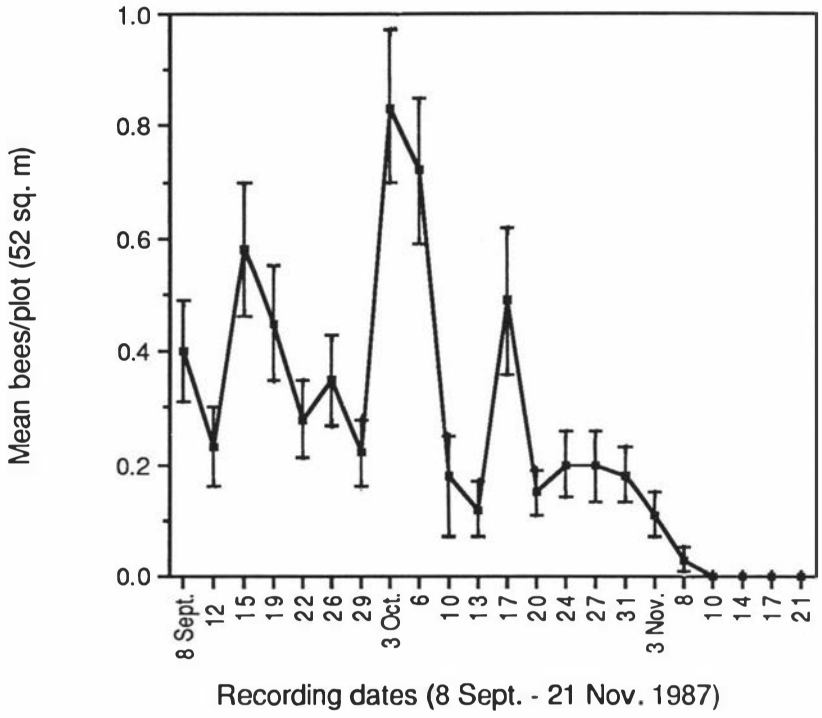


Figure A5.1. B. terrestris queens on 22 recording days

(d)



B. terrestris males on 22 recording days

(e)

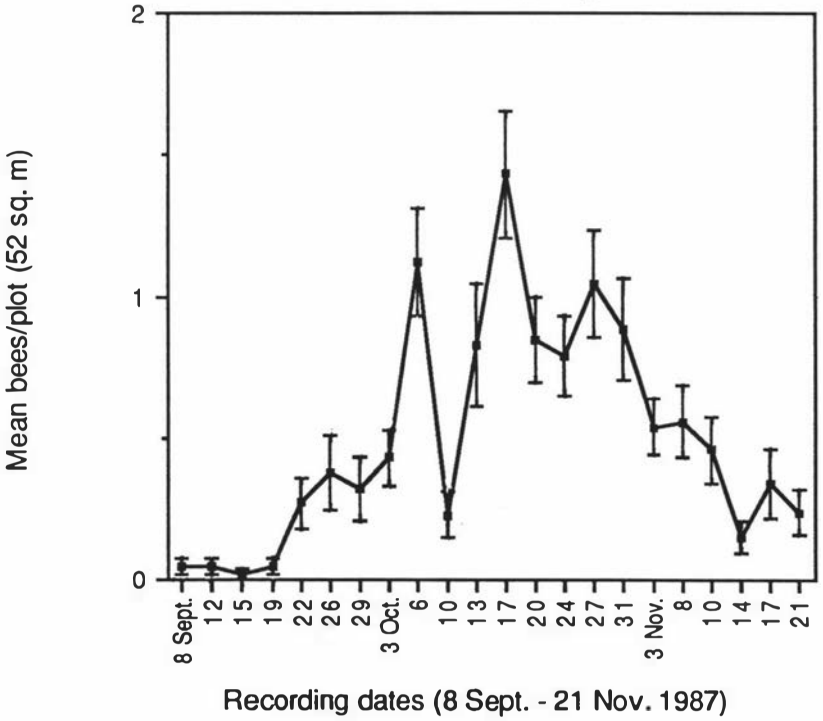
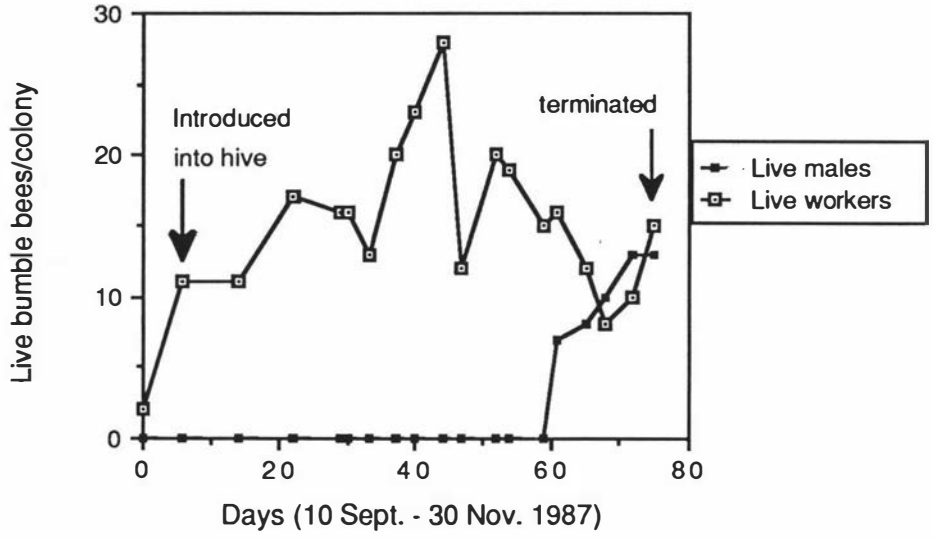


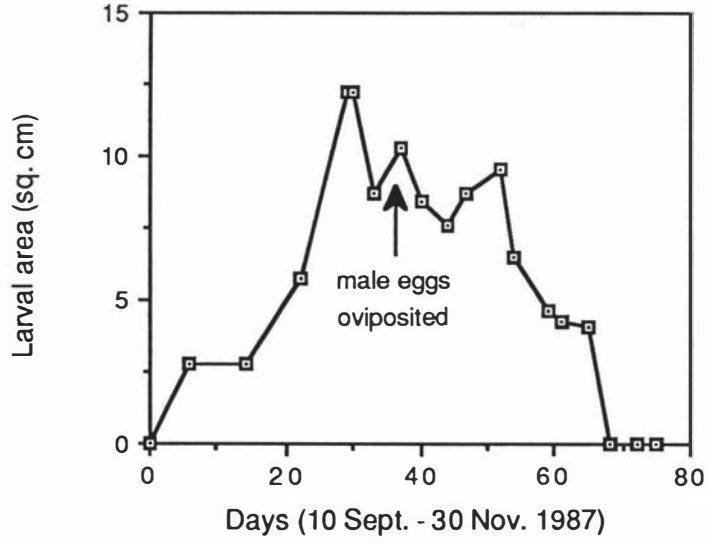
Figure A6.1. Bumble bees for free foraging hive 1

(a)



Larval area for free foraging hive 1

(b)



Weekly pollen returning to free foraging hive 1

(c)

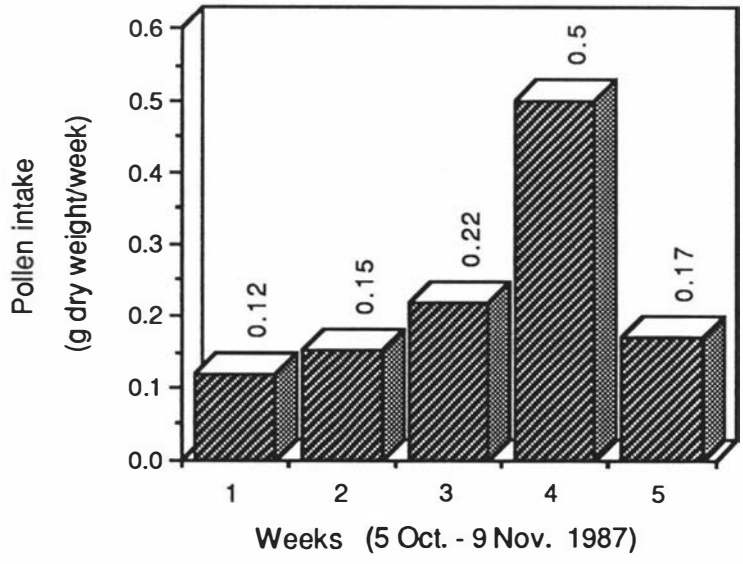
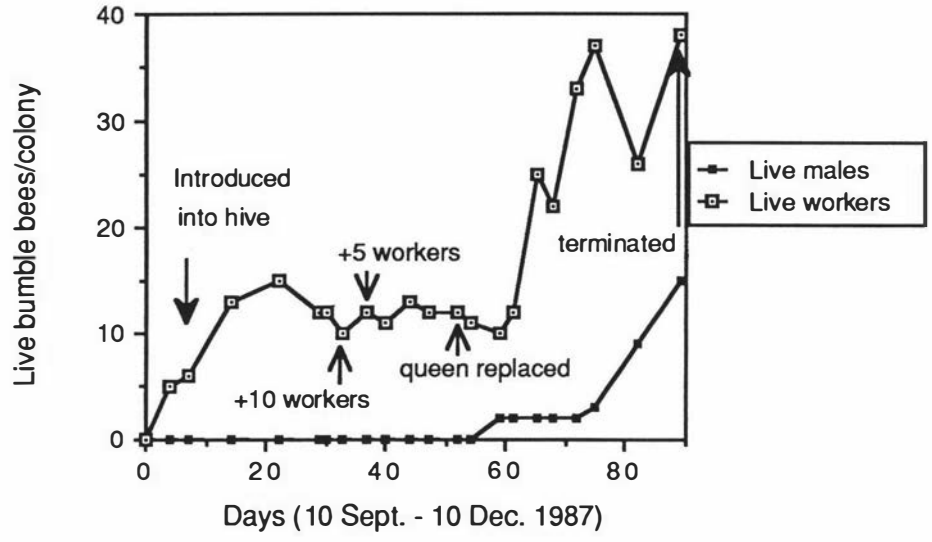


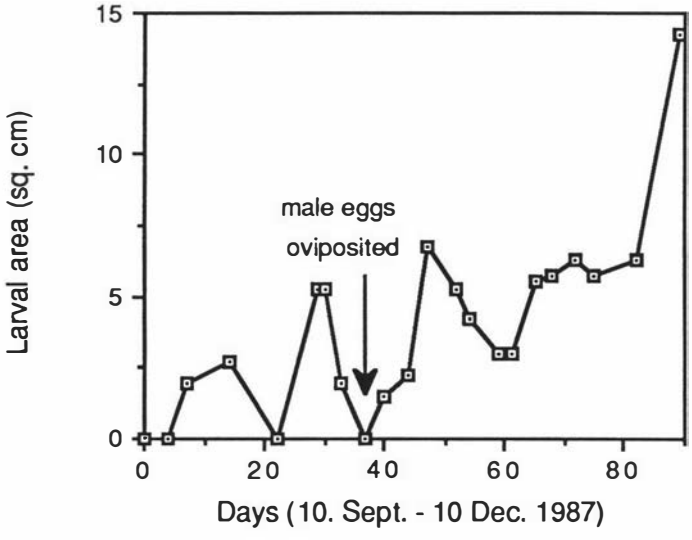
Figure A6.2. Bumble bees for free foraging hive 2

(a)



Larval area for free foraging hive 2

(b)



Weekly pollen returning to free foraging hive 2

(c)

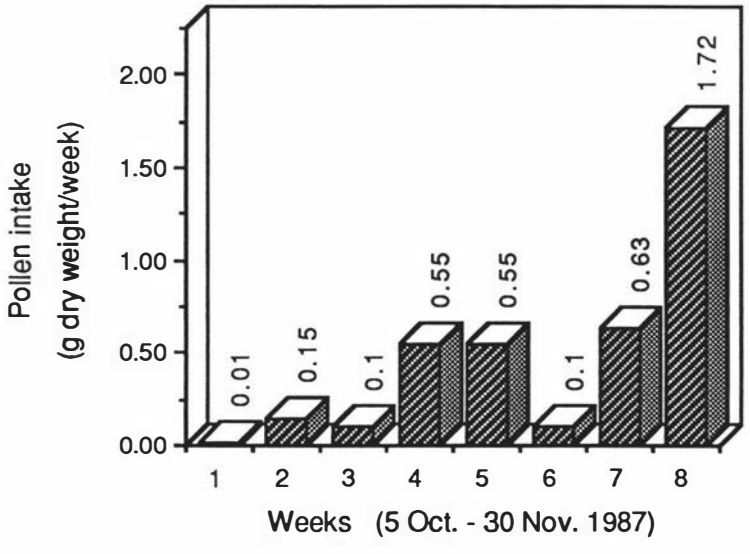
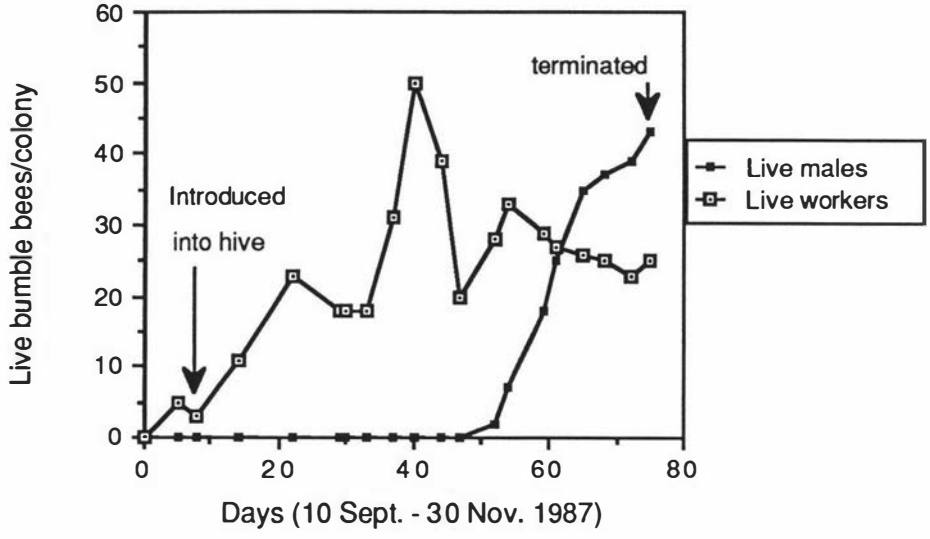


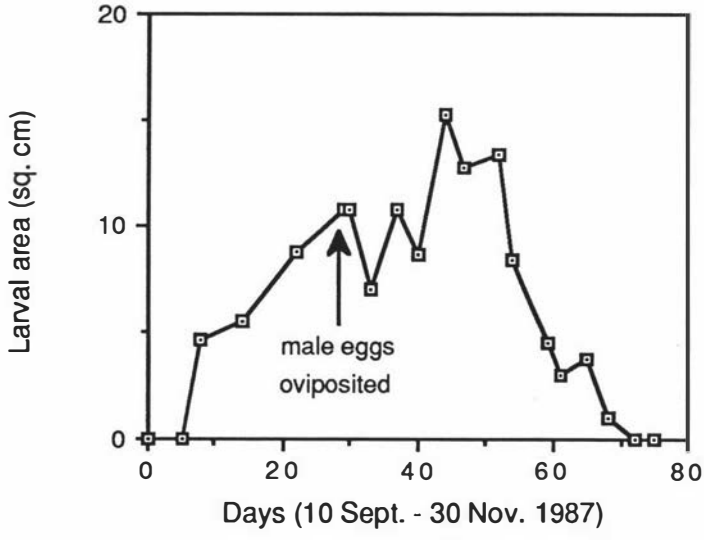
Figure A6.3. Bumble bees for free foraging hive 3

(a)



Larval area for free foraging hive 3

(b)



Weekly pollen returning to free foraging hive 3

(c)

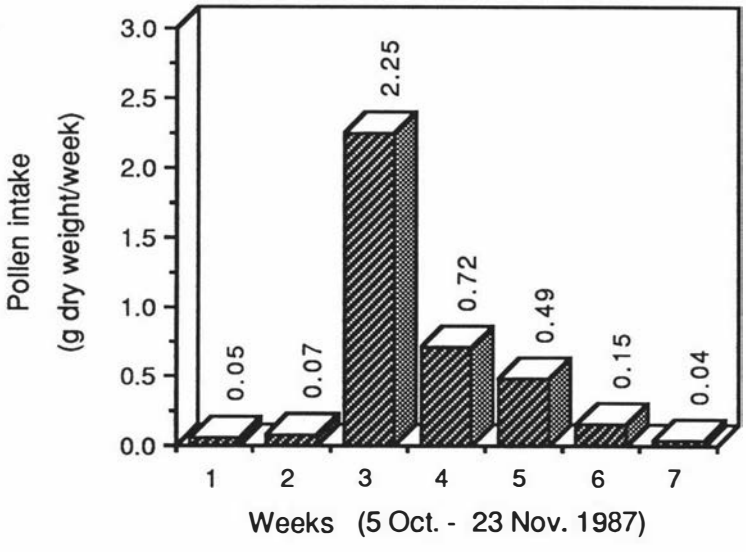
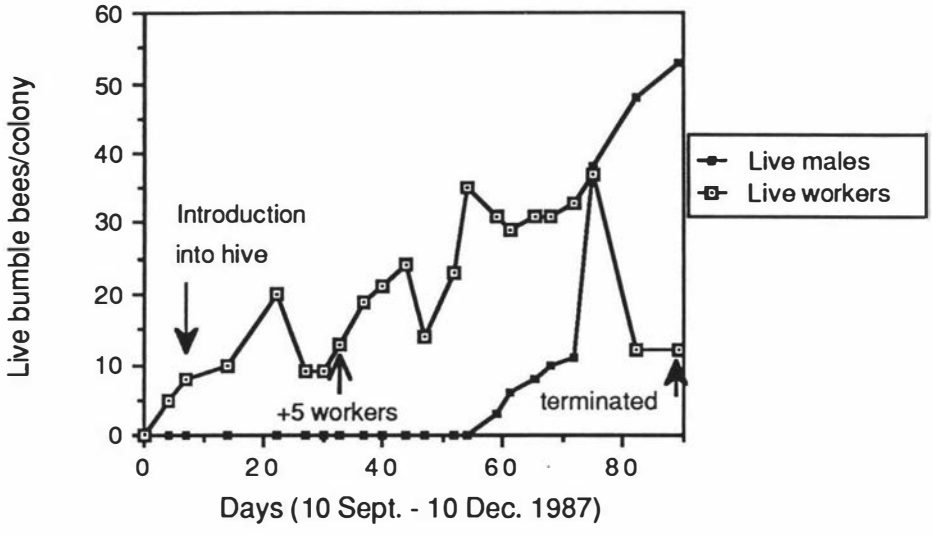
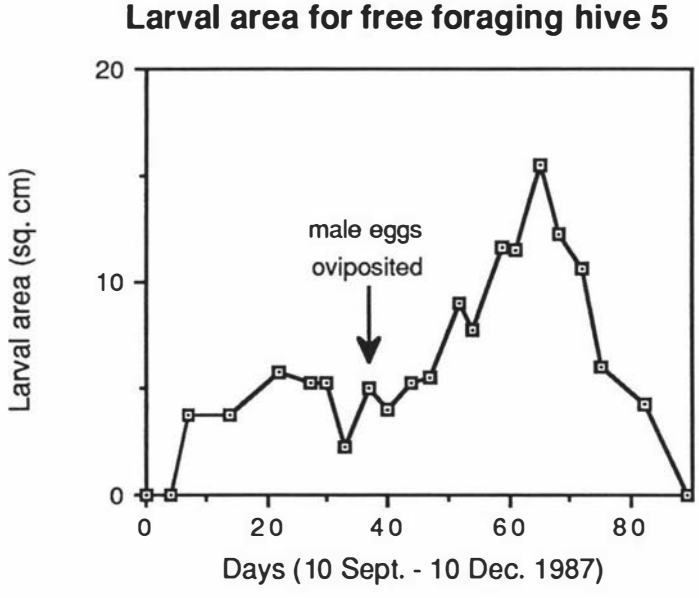


Figure A6.4. Bumble bees for free foraging hive 5

(a)



(b)



(c)

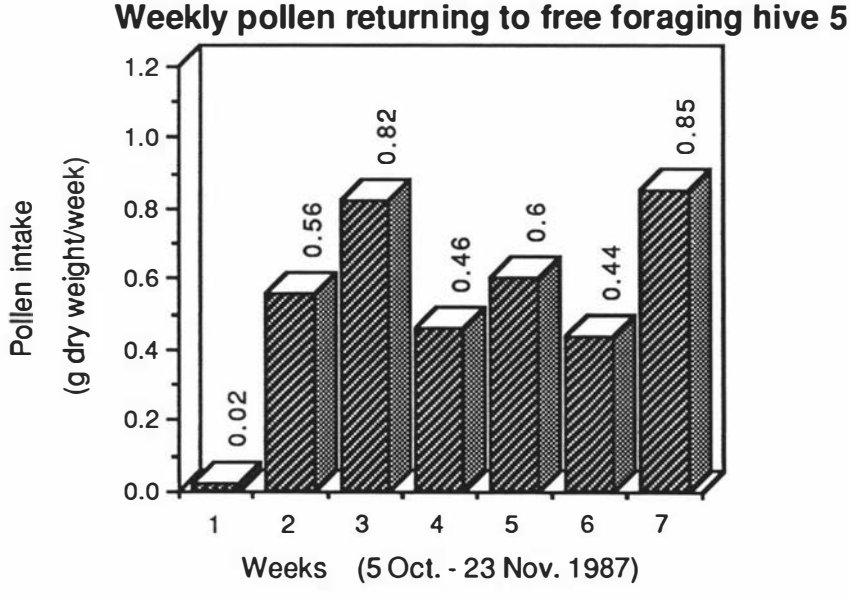
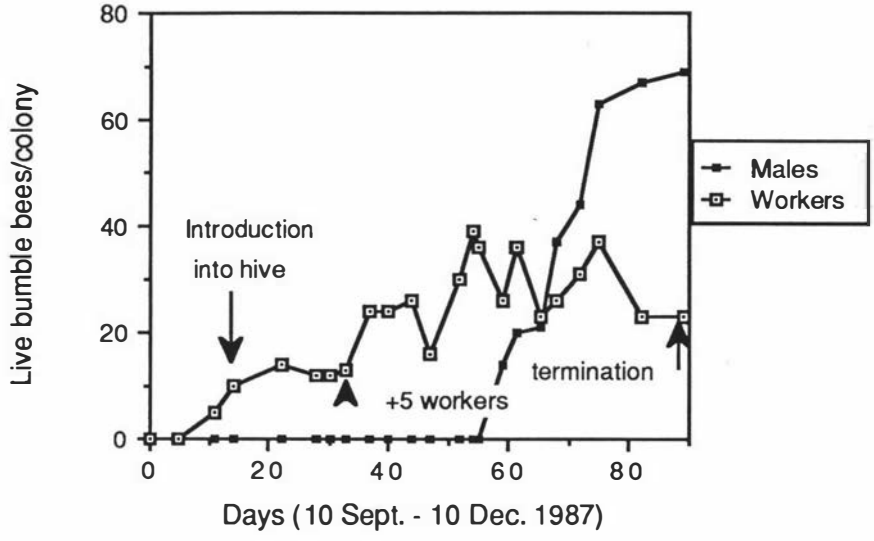


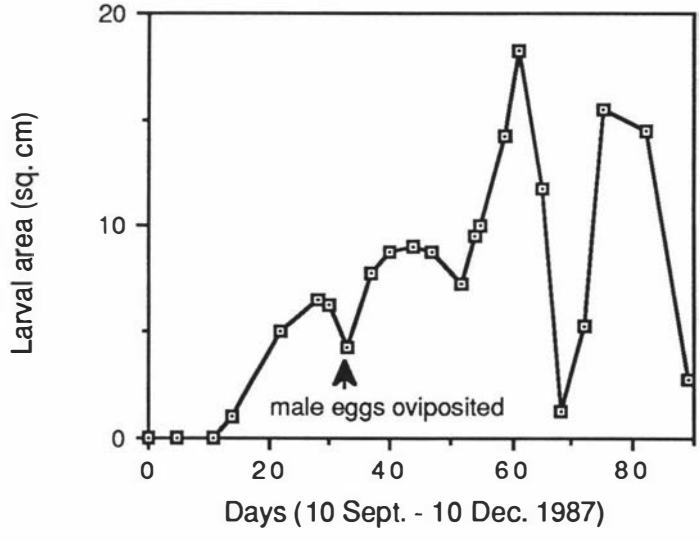
Figure A6.5. Bumble bees for free foraging hive 6

(a)



Larval area for free foraging hive 6

(b)



Weekly pollen returning to free foraging hive 6

(c)

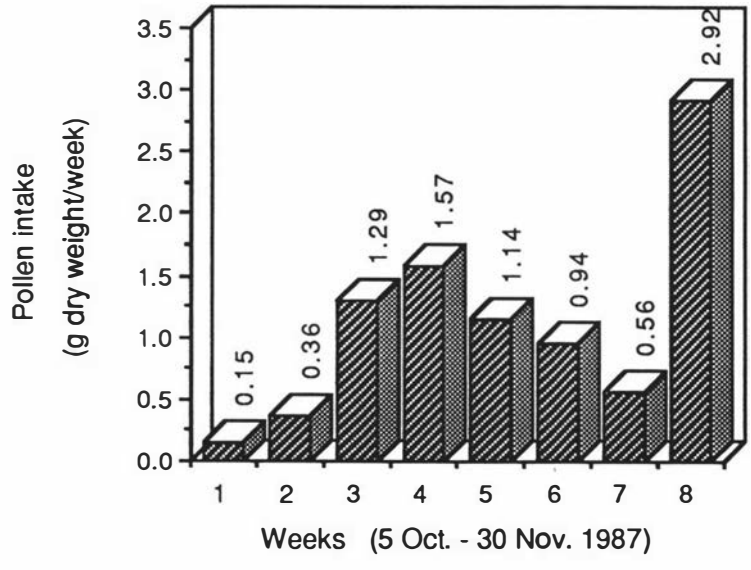
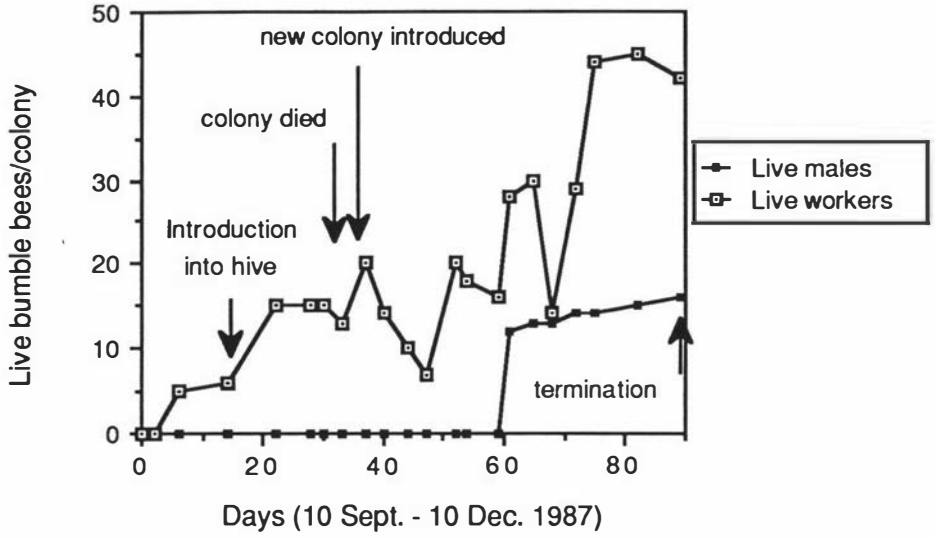


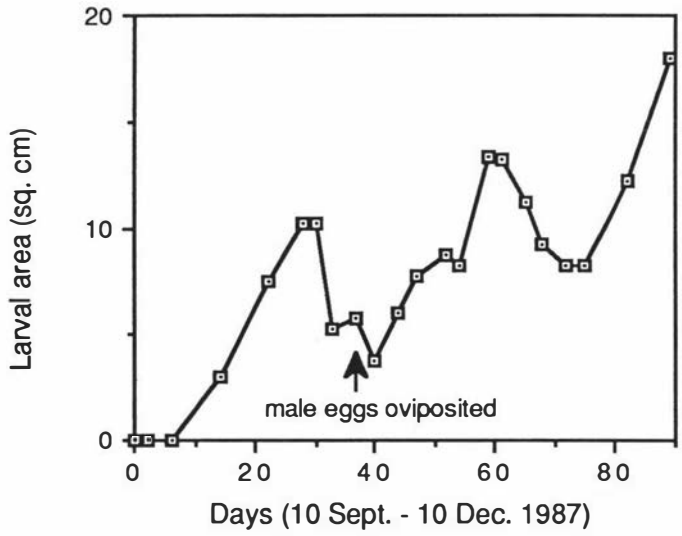
Figure A6.6. Bumble bees for free foraging hive 7

(a)



Larval area for free foraging hive 7

(b)



Weekly pollen returning to free foraging hive 7

(c)

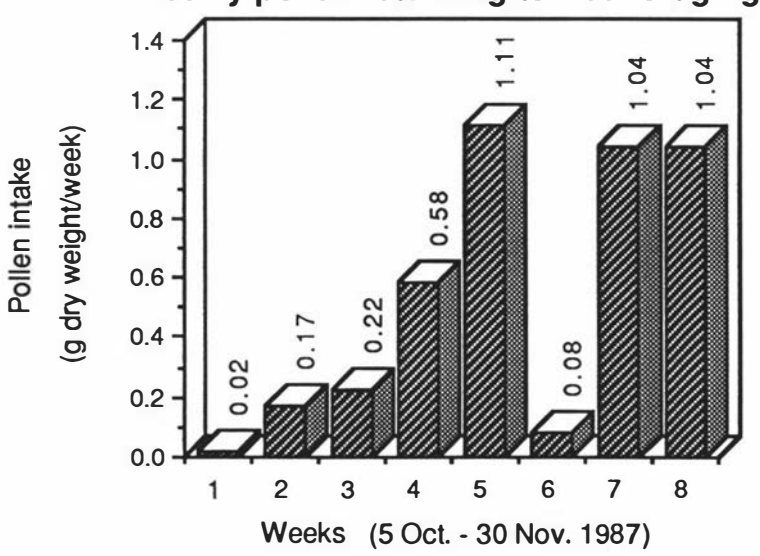
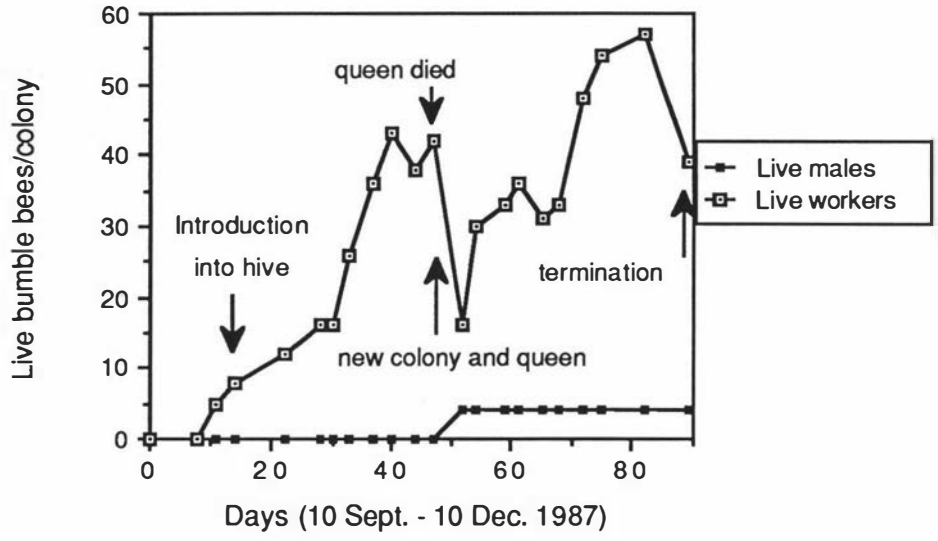


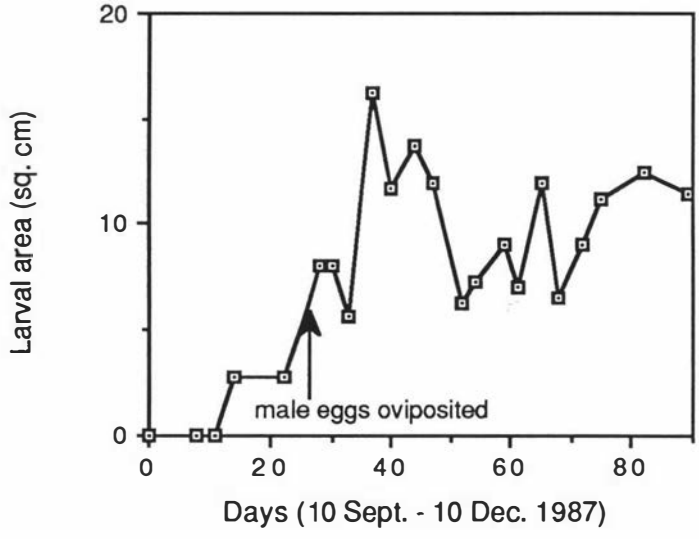
Figure A6.7. Bumble bees for free foraging hive 9

(a)



Larval area for free foraging hive 9

(b)



Weekly pollen returning to free foraging hive 9

(c)

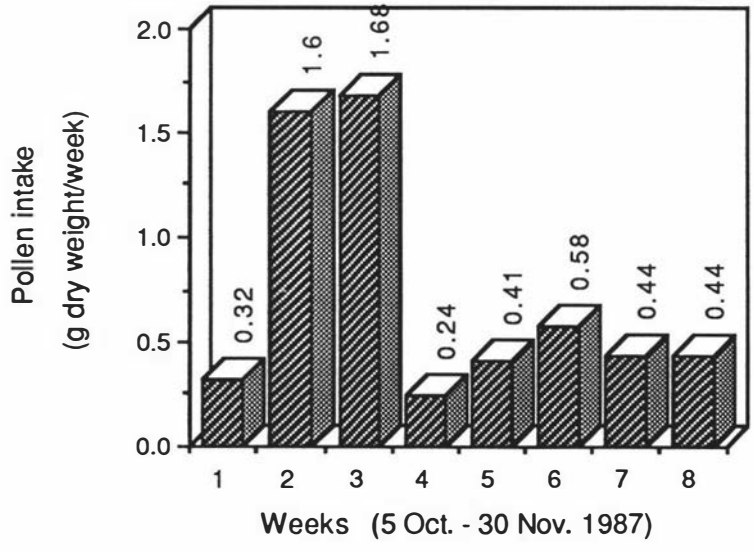
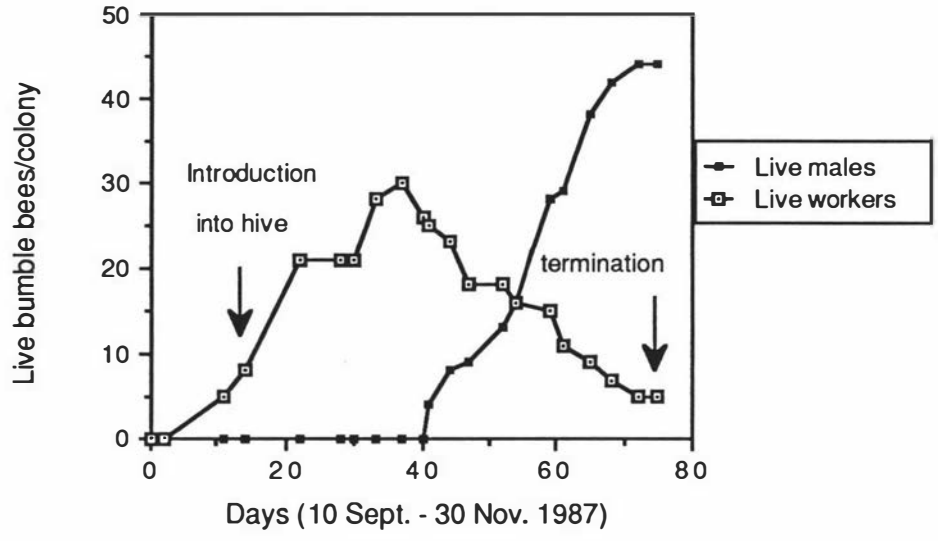


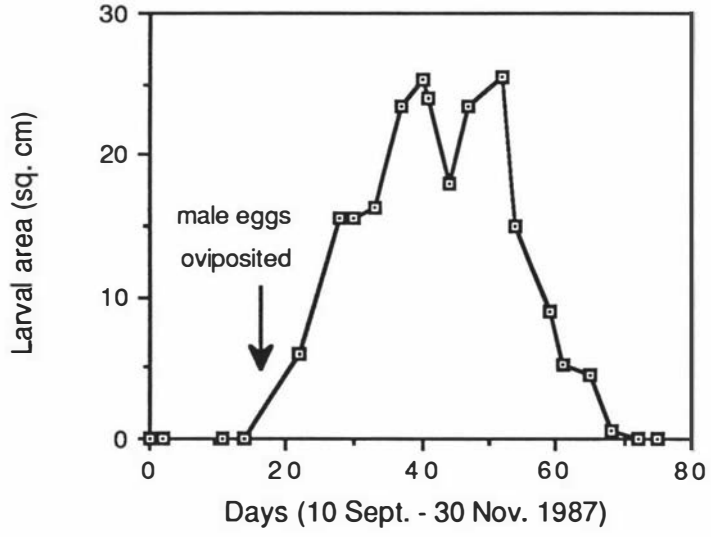
Figure A6.8 Bumble bees for free foraging hive 10

(a)



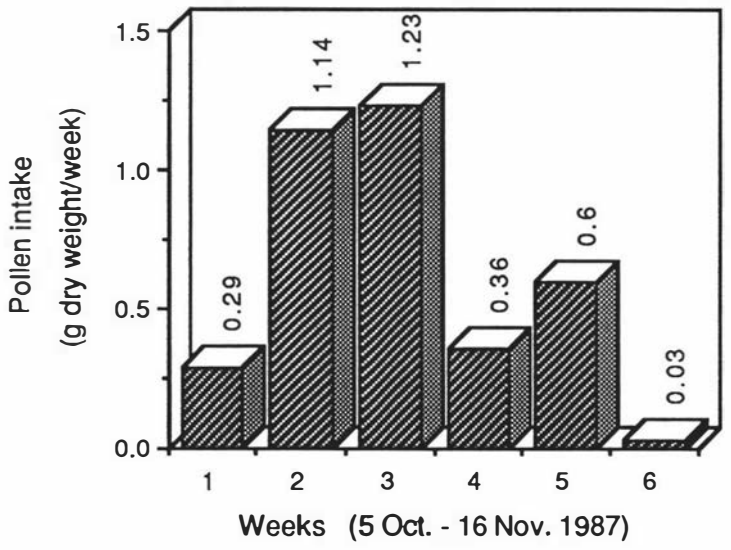
Larval area for free foraging hive 10

(b)



Weekly pollen returning to free foraging hive 10

(c)



APPENDIX II TABLES

Table A2.1. Brood bionomic and consumption parameters during switch to male production by foundress queen. Ranked from highest to lowest Productivity Index (P.I.). Assumed that males took 21-23 days from oviposition to emergence.

	Colony							
	8	5	4	3	1	6	2	7
Productivity Index	465	412	351	349	248	235	207	62
Date of switch to males (day and month)	22-27 Oct	2-4 Nov	22-24 Oct	9-11 Nov	13-15 Oct	30-1 Oc/Nov	13-15 Oct	8-10 Oct
Days from colony inception to switch to male production	50-52	66-68	52-54	60-62	34-36	61-63	38-40	41-43
Live workers present	35-40	72-83	32-36	71-72	16-19	25-26	11-16	8-10
Queens emerged	0	9	16	44	0	28	0	0
Larval area (cm^2)	3.5-4	7.5-16.5	8.5-11.0	24-21.5	0-2	12-13	1.5-2.5	1.5
Worker:larval area (cm^2) ratio	10:1	5.0-9.6:1	3.3-3.8:1	3.0-3.3:1	9.5-+10:1	2.0-2.1:1	6.4-7.3:1	5.3-6.7:1
Pollen consumed/week(g)	8.05	3.28	8.76	26.62	3.20	10.95	2.55	3.11
Sugar consumed/week (g)	70.58	103.51	69.27	77.34	59.78	60.10	21.65-47.77	25.57
Total pollen consumed at time of switch(g)	13.9-16.2	32.7-33.5	13.8-16.3	54.6-64.7	6.7-8.1	17.6-21.1	5.4-6.9	4.8-5.4
Total sugar consumed at time of switch(g)	161-181	360-380	153-165	355-404	92-105	189-213	72-78	54-62

Table A2.2. Brood bionomic parameters at time of switch to queen production by foundress queen via worker-larval feeding. Ranked highest to lowest P.I. Assumption that new queens took 27-29 days from oviposition to emergence.

	Colony			
	5	4	3	6
Productivity Index	412	351	349	235
First queen emergence	30 Nov	16 Nov	16 Nov	10 Nov
First eggs laid by queen(estimate)	1-3Nov	18-20Oct	18-20Oct	12-14Oct
Probable queen determination date	6-11Nov	23-28Oct	23-28Oct	17-22Oct
Live workers present	93-110	34-44	28-36	16-20
Larval area (cm^2)	25-40	10-15.5	9.5-15.5	1-2
worker:larval area (cm^2) ratio	3.7-2.8:1	3.4-2.8:1	2.9-2.3:1	16-10:1
Pollen consumed/week (g)	19.31	8.76	11.97	3.22
Sugar consumed/week (g)	127.20	69.27	39.10	34.38-66.50
Total pollen consumed at time of queen determination (g)	34.2-50.8	15.1-21.3	13.9-22.5	5.7-7.9
Total sugar consumed at time of queen determination (g)	412-507	159-208	130-170	80-107
Number of queens produced	9	16	44	28
Number of males produced	143	122	5	48

Table A4.1.ANOVAs (analysis of variance) of pollen availability and energy from nectar of bagged and exposed flowers by 22 days by 4 crops by either 5 (exposed) or 3 (bagged) times.

Food type
1=pollen availability from bagged flowers
2=energy of nectar from bagged flowers
3=pollen availability from exposed flowers
4=energy of nectar from exposed flowers

			CROP			TIME			TIME BY CROP	
Day	Food type	%SS	F_S	F.prob	%SS	F_S	F.prob	%SS	F_S	F.prob
1	1	84.0	91.362	0.000	0.2	0.143	0.870	1.2	0.676	0.617
	2	23.3	37.137	0.000	23.3	41.766	0.000	46.6	37.145	0.000
	3	47.4	25.000	0.000	2.9	0.855	0.518	9.5	1.253	0.304
	4	3.2	2.750	0.083	55.8	16.410	0.000	24.8	5.296	0.000
2	1	0.0	0.017	0.984	97.5	364.677	0.000	0.7	3.469	0.029
	2	0.0	0.000	1.000	0.0	0.000	0.999	0.0	0.000	1.000
	3	1.0	9.025	0.000	94.1	332.355	0.000	2.3	5.156	0.000
	4	41.8	24.514	0.000	13.9	4.999	0.026	29.2	5.705	0.000
3	1	41.8	35.320	0.000	23.8	21.774	0.002	19.3	8.169	0.000
	2	1.0	0.344	0.714	0.4	0.064	0.939	43.2	7.200	0.001
	3	54.7	91.435	0.000	17.5	18.188	0.000	15.2	6.370	0.000
	4	7.0	3.907	0.031	1.2	0.185	0.942	40.0	5.591	0.000
4	1	66.7	24.464	0.000	0.1	0.062	0.940	0.3	0.062	0.992
	2	1.0	0.543	0.590	16.9	1.166	0.373	7.6	2.117	0.121
	3	74.8	67.276	0.000	0.4	0.214	0.926	1.7	0.381	0.923
	4	7.6	1.854	0.106	21.6	1.395	0.294	0.6	0.543	0.587
5	1	58.7	49.314	0.000	9.8	8.223	0.019	16.0	6.707	0.002
	2	27.1	6.147	0.009	6.8	1.468	0.303	7.1	0.801	0.540
	3	12.6	3.606	0.005	7.1	2.588	0.090	58.7	67.103	0.000
	4	11.7	4.238	0.024	5.0	0.653	0.636	17.9	1.623	0.160
6	1	72.1	41.208	0.000	0.1	0.056	0.946	0.9	0.266	0.896
	2	44.5	19.275	0.000	7.4	2.622	0.152	6.8	1.470	0.253
	3	69.7	61.382	0.000	1.6	0.511	0.729	2.0	0.436	0.890
	4	17.8	8.094	0.002	5.3	1.094	0.403	23.2	2.643	0.025
7	1	72.7	65.215	0.000	4.1	3.881	0.083	8.4	3.751	0.022
	2	52.9	18.337	0.000	2.4	0.464	0.650	1.5	0.255	0.903
	3	62.8	59.437	0.000	4.6	2.138	0.139	9.0	2.125	0.065
	4	54.5	29.210	0.000	3.2	0.880	0.504	2.4	0.316	0.954
8	1	35.9	7.293	0.005	6.3	25.125	0.001	11.7	1.191	0.349
	2	11.7	1.997	0.165	3.0	0.430	0.669	5.9	0.502	0.735
	3	49.5	24.881	0.000	3.6	6.190	0.006	13.9	1.741	0.129
	4	17.6	5.601	0.009	3.9	0.788	0.555	7.9	0.625	0.750
9	1	58.9	59.462	0.000	7.2	5.645	0.042	20.5	10.341	0.000
	2	3.7	0.653	0.532	1.8	0.243	0.792	13.0	1.155	0.363
	3	62.9	111.349	0.000	6.9	5.784	0.008	17.9	7.944	0.000
	4	17.6	9.484	0.000	22.2	6.616	0.005	17.0	2.280	0.049
10	1	52.2	81.261	0.000	6.1	5.384	0.046	29.7	23.083	0.000
	2	47.5	11.878	0.000	1.2	0.633	0.563	4.2	0.529	0.716
	3	48.5	84.086	0.000	14.4	8.215	0.002	22.1	9.577	0.000
	4	47.3	24.332	0.000	4.9	2.456	0.102	5.8	0.752	0.647
11	1	42.4	9.635	0.001	1.9	0.557	0.600	4.0	0.456	0.767
	2	42.8	20.678	0.000	6.2	2.885	0.132	18.4	4.443	0.011
	3	35.8	17.902	0.000	17.6	6.953	0.004	8.9	1.113	0.383
	4	36.6	20.716	0.000	6.4	1.685	0.218	15.8	2.232	0.053

12	1	65.6	34.308	0.000	3.8	2.597	0.154	4.0	1.046	0.418
	2	13.3	2.433	0.087	2.8	0.539	0.609	11.2	1.020	0.433
	3	60.8	47.524	0.000	9.0	4.128	0.025	3.3	0.643	0.795
	4	13.5	4.190	0.011	2.6	0.570	0.690	15.1	1.174	0.330
13	1	61.7	31.850	0.000	7.0	13.170	0.006	9.9	2.556	0.043
	2	18.5	3.955	0.018	6.3	2.582	0.155	19.0	2.029	0.096
	3	68.2	67.856	0.000	6.4	8.618	0.002	7.0	1.743	0.089
	4	9.6	3.242	0.031	4.3	1.305	0.323	26.6	2.241	0.025
14	1	62.1	40.049	0.000	4.3	4.998	0.053	10.8	3.467	0.011
	2	27.2	5.962	0.003	4.5	1.417	0.313	13.6	1.491	0.219
	3	61.6	64.048	0.000	5.0	2.378	0.110	8.2	2.137	0.033
	4	24.1	7.430	0.000	2.7	0.584	0.681	8.2	0.631	0.804
15	1	29.1	13.150	0.000	12.1	6.171	0.035	29.8	6.726	0.000
	2	7.4	2.178	0.114	27.0	6.299	0.034	14.5	2.125	0.083
	3	31.7	13.510	0.000	8.2	3.700	0.035	17.9	1.900	0.060
	4	6.4	2.932	0.044	24.5	5.978	0.007	17.9	2.054	0.041
16	1	51.2	41.719	0.000	21.6	190.676	0.000	15.3	6.232	0.000
	2	14.6	2.575	0.075	1.2	0.293	0.756	15.9	1.401	0.250
	3	53.2	65.701	0.000	22.0	39.116	0.000	10.7	3.298	0.002
	4	12.2	3.507	0.023	2.7	0.684	0.617	15.8	1.137	0.356
17	1	38.7	12.538	0.000	9.4	5.934	0.038	18.6	3.005	0.022
	2	18.7	3.464	0.030	8.4	3.524	0.097	9.8	0.905	0.506
	3	32.9	37.693	0.000	31.1	34.749	0.000	19.9	5.691	0.000
	4	21.7	5.976	0.002	6.2	3.986	0.028	8.3	0.571	0.853
18	1	52.2	16.118	0.000	1.4	0.499	0.630	4.2	0.644	0.694
	2	3.7	0.543	0.657	0.5	0.122	0.887	15.0	1.092	0.392
	3	39.6	22.893	0.000	10.6	3.912	0.029	11.4	1.646	0.113
	4	9.8	5.487	0.003	6.4	2.052	0.151	47.5	6.680	0.000
19	1	29.8	6.898	0.001	12.8	8.536	0.018	8.9	1.031	0.427
	2	7.3	1.311	0.291	0.5	0.078	0.926	16.4	1.467	0.227
	3	24.8	18.167	0.000	22.7	13.493	0.000	24.5	4.494	0.000
	4	9.8	3.218	0.031	1.3	0.252	0.903	26.6	2.198	0.028
20	1	9.8	3.339	0.096	20.0	4.494	0.064	13.3	1.597	0.186
	2	41.5	31.794	0.000	10.7	11.444	0.009	32.2	12.323	0.000
	3	8.6	3.135	0.035	15.0	3.159	0.054	18.0	1.644	0.113
	4	23.6	31.794	0.000	15.4	14.992	0.000	46.1	15.568	0.000
21	1	60.4	22.151	0.000	0.7	0.194	0.828	2.2	0.404	0.870
	2	8.4	1.172	0.339	4.4	0.974	0.430	7.3	0.508	0.797
	3	43.4	32.620	0.000	11.8	6.300	0.006	18.0	3.385	0.001
	4	8.1	1.953	0.135	4.5	0.978	0.456	8.4	0.506	0.900
22	1	82.9	138.712	0.000	2.4	5.941	0.038	7.4	6.183	0.000
	2	6.4	1.000	0.408	4.3	1.000	0.422	12.8	1.000	0.446
	3	84.8	291.530	0.000	2.0	7.331	0.003	7.3	6.309	0.000
	4	3.8	1.000	0.402	5.1	1.000	0.445	15.2	1.000	0.464

Table A4.2. ANOVA of energy from exposed flowers.
VARIATE: ENERGY (NORMALISED)

SOURCE OF VARIATION	DF(MV)	SS	SS%	MS	VR	F PR
UNITS STRATUM						
DAY	21	107.7865	15.18	5.1327	26.013	<.001
LIN	1	17.2408	2.43	17.2408	87.379	<.001
QUAD	1	4.2938	0.60	4.2938	21.762	<.001
CUB	1	5.3252	0.75	5.3252	26.989	<.001
QUART	1	4.9502	0.70	4.9502	25.088	<.001
DEVIATIONS	17	75.9765	10.70	4.4692	22.651	<.001
CROP	3	77.6196	10.93	25.8732	131.129	<.001
TIME	4	3.2473	0.46	0.8118	4.115	0.003
LIN	1	1.3934	0.20	1.3934	7.062	0.008
QUAD	1	1.7902	0.25	1.7902	9.073	0.003
DEVIATIONS	2	0.0638	0.01	0.0319	0.162	0.851
DAY.CROP	63	111.9083	15.76	1.7763	9.003	<.001
DAY.TIME	84	39.6529	5.59	0.4721	2.392	<.001
CROP.TIME	12	8.0308	1.13	0.6692	3.392	<.001
DAY.CROP.TIME	249(3)	106.9577	15.07	0.4295	2.177	<.001
DEVIATIONS	240(3)	98.6712	13.90	0.4111	2.084	<.001
RESIDUAL	1306(14)	257.6872	36.30	0.1973		
TOTAL	1742	712.8904	100.41	0.4092		
GRAND TOTAL	1742	712.8904	100.41			

ESTIMATED GRAND MEAN 0.051
TOTAL NUMBER OF OBSERVATIONS 1760 NUMBER OF MISSING VALUE (MV) 17

Table A4.3. ANOVA of energy from bagged flowers.
VARIATE: ENERGY (NORMALISED)

SOURCE OF VARIATION	DF(MV)	SS	SS%	MS	VR	F PR
UNITS STRATUM						
DAY	21	108.4969	9.09	5.1665	13.111	<.001
LIN	1	1.8233	0.15	1.8233	4.627	0.032
QUAD	1	32.4245	2.72	32.4245	82.284	<.001
CUB	1	14.8603	1.24	14.8603	37.711	<.001
QUART	1	3.5001	0.29	3.5001	8.882	0.003
DEVIATIONS	17	55.8888	4.68	3.2876	8.343	<.001
CROP	3	143.0872	11.99	47.6957	121.038	<.001
TIME	2	28.9667	2.43	14.4834	36.754	<.001
LIN	1	27.9453	2.34	27.9453	70.917	<.001
QUAD	1	1.0214	0.09	1.0214	2.592	0.108
DAY.CROP	63	103.9201	8.71	1.6495	4.186	<.001
DAY.TIME	42	24.5898	2.06	0.5855	1.486	0.024
CROP.TIME	6	4.3510	0.36	0.7252	1.840	0.088
DAY.CROP.TIME	126	61.3308	5.14	0.4868	1.235	0.044
RESIDUAL	1833(15)	722.3062	60.51	0.3941		
TOTAL	2096	1197.0488	100.28	0.5711		
GRAND TOTAL	2096	1197.0488	100.28			

ESTIMATED GRAND MEAN 0.055
TOTAL NUMBER OF OBSERVATIONS 2112 NUMBER OF MISSING VALUES (MV) 15

Table A4.4. ANOVA of pollen from exposed flowers.
VARIATE: POLLEN (NORMALISED)

SOURCE OF VARIATION	DF(MV)	SS	SS%	MS	VR	F PR
UNITS STRATUM						
DAY	21	162.6678	13.76	7.7461	69.664	<.001
LIN	1	31.9860	2.71	31.9860	287.663	<.001
QUAD	1	3.3045	0.28	3.3045	29.718	<.001
CUB	1	7.3575	0.62	7.3575	66.169	<.001
QUART	1	50.0446	4.23	50.0446	450.071	<.001
DEVIATIONS	17	69.9753	5.92	4.1162	37.019	<.001
CROP	3	534.2528	45.21	178.0843	1601.583	<.001
TIME	4	12.4366	1.05	3.1092	27.962	<.001
LIN	1	10.9715	0.93	10.9715	98.671	<.001
QUAD	1	0.6323	0.05	0.6323	5.687	0.017
DEVIATIONS	2	0.8328	0.07	0.4164	3.745	0.024
DAY.CROP	63	197.6366	16.72	3.1371	28.213	<.001
DAY.TIME	84	57.6119	4.87	0.6859	6.168	<.001
CROP.TIME	12	5.1976	0.44	0.4331	3.895	<.001
DAY.CROP.TIME	249(3)	71.0357	6.01	0.2853	2.566	<.001
RESIDUAL	1309(11)	145.5512	12.32	0.1112		
TOTAL	1745	1186.3904	100.39	0.6799		
GRAND TOTAL	1745	1186.3904	100.39			

ESTIMATED GRAND MEAN -0.0246
TOTAL NUMBER OF OBSERVATIONS 1760 NUMBER OF MISSING VALUE (MV) 14

Table A4.5. ANOVA of pollen from bagged flowers.
VARIATE: BAGGED POLLEN (NORMALISED)

SOURCE OF VARIATION	DF(MV)	SS	SS%	MS	VR	F PR
UNITS STRATUM						
DAY	21	226.1469	16.43	10.7689	75.717	<.001
LIN	1	57.7449	4.19	57.7449	406.011	<.001
QUAD	1	7.8780	0.57	7.8780	55.391	<.001
CUB	1	21.8756	1.59	21.8756	153.810	<.001
QUART	1	46.1454	3.35	46.1454	324.454	<.001
DEVIATIONS	17	92.5029	6.72	5.4413	38.259	<.001
CROP	3	523.6932	38.04	174.5644	1227.382	<.001
TIME	2	3.0239	0.22	1.5120	10.631	<.001
LIN	1	2.7333	0.20	2.7333	19.218	<.001
QUAD	1	0.2907	0.02	0.2907	2.044	0.153
DAY.CROP	63	256.9672	18.67	4.0788	28.679	<.001
DAY.TIME	42	53.0344	3.85	1.2627	8.878	<.001
CROP.TIME	6	7.2370	0.53	1.2062	8.481	<.001
DAY.CROP.TIME	126	51.7003	3.76	0.4103	2.885	<.001
RESIDUAL	1832(16)	260.5562	18.93	0.1422		
TOTAL	2095	1382.3591	100.41	0.6598		
GRAND TOTAL	2095	1382.3591	100.41			

ESTIMATED GRAND MEAN -0.0329
TOTAL NUMBER OF OBSERVATIONS 2112 NUMBER OF MISSING VALUES (MV) 16

Table A4.6. Multiple regressions and ANOVA of pollen and nectar energy from bagged and exposed flowers (transformed $\log_e (x + 1)$) with weather variables.

Food from flowers	ANOVA F ratio	df	Signif-icance	Regression coefficients 1st coef. t value Signifi.	2nd coef. t value Signifi.	% variance accounted for (R^2) R^2 for 1st cof.	R^2 for 2nd cof.	R^2 for total
Pollen bagged flowers	10.79	5,60	***	Temp. 4.96 ***	Rain -4.67 ***	22.8	19.3	42.9
Energy bagged flowers	1.94	5,60	n.s.	Temp. 2.18 *	Rain -1.64 n.s.	6.5	3.7	6.7
Pollen exposed flowers	2.11	5,103	n.s.	Rain -2.47 *	Wind -1.92 n.s.	2.3	1.8	4.9
Energy exposed flowers	8.82	5,104	***	Light -4.55 ***	Temp. -2.40 *	20.1	13.4	26.4

$t_{0.05(2)[60]}=2.000$ $t_{0.05(2)[103]}=1.983$ $F_{0.05(2)[5,60]}=2.79$
$t_{0.01(2)[60]}=2.660$ $t_{0.01(2)[103]}=2.624$ $F_{0.001(2)[5,60]}=5.20$
$t_{0.001(2)[60]}=3.460$ $t_{0.05(2)[107]}=1.983$ $F_{0.05(2)[5,103]}=2.70$
Temp.=temperature $t_{0.001(2)[104]}=3.386$ $F_{0.001(2)[5,104]}=4.85$
R.H.=relative humidity Wind=wind speed Light=light intensity Rain=rainfall

Table A4.7. Nectar production of bagged fodder radish and borage flowers in relation to weather parameters (Sept.-Nov.1987), n=66.

Nectar production of bagged:		Temp. (C)	R.H.	Wind (ms^{-1})	Light #	Rain (mm)
Borage flowers	r value	0.103	-0.051	-0.119	-0.101	-0.164
	Signif.	n.s.	n.s.	n.s.	n.s	n.s.
Fodder radish flowers	r value	0.196	-0.139	0.037	0.169	-0.205
	Signif.	n.s.	n.s.	n.s.	n.s.	n.s.

\# = ($\mu Em^{-2}s^{-1}$) $r_{0.05(2)[64]}=0.242$

Table A5.1. ANOVA of 5 bee classes by 22 recording days by 4 crops by 5 time intervals.

bee class 1 = *B. terrestris* nectar gatherers
bee class 2 = *B. terrestris* pollen gatherers
bee class 3 = *A. mellifera* nectar and pollen gatherers
bee class 4 = *B. terrestris* queens
bee class 5 = *B. terrestris* males

		CROP			TIME			TIME BY CROP		
Day	Bee class	%SS	F_s	F.prob	%SS	F_s	F.prob	%SS	F_s	F.prob
1	1	20.9	4.335	0.130	2.1	0.522	0.720	16.1	2.012	0.073
	2	12.4	5.680	0.102	23.7	7.444	0.000	24.9	3.906	0.002
	3	31.1	135.521	0.001	41.2	109.345	0.000	21.2	28.134	0.000
	4	5.7	4.948	0.112	8.0	1.588	0.198	32.3	3.201	0.008
	5	0.0	0.000	-	9.4	1.333	0.276	11.7	0.833	0.579
2	1	42.0	4.041	0.141	5.2	4.491	0.005	10.4	4.491	0.000
	2	17.1	15.393	0.026	8.3	1.423	0.246	16.6	1.423	0.221
	3	43.6	138.156	0.001	16.9	40.484	0.000	33.9	40.484	0.000
	4	38.2	22.147	0.016	7.7	2.864	0.037	12.6	2.340	0.039
	5	10.5	9.000	0.054	9.4	1.500	0.223	18.7	1.500	0.192
3	1	47.2	10.243	0.046	1.2	0.335	0.853	3.8	0.537	0.821
	2	39.8	65.859	0.003	10.6	4.760	0.003	16.5	3.702	0.003
	3	10.8	10.208	0.046	41.1	11.150	0.000	9.4	1.268	0.291
	4	38.2	21.229	0.017	12.4	3.589	0.015	5.3	0.761	0.639
	5	3.4	1.000	0.465	6.8	1.000	0.420	13.6	1.000	0.453
4	1	21.4	15.532	0.026	2.4	0.404	0.748	14.8	1.519	0.185
	2	17.6	5.898	0.091	6.5	1.773	0.156	19.1	2.594	0.024
	3	11.6	51.057	0.005	71.8	118.676	0.000	8.0	6.575	0.000
	4	21.8	8.734	0.056	9.4	2.205	0.088	23.5	2.761	0.017
	5	10.5	3.000	0.192	3.5	0.529	0.715	7.0	0.529	0.826
5	1	30.6	12.541	0.035	8.6	4.155	0.007	25.4	6.104	0.000
	2	12.7	2.992	0.193	11.6	1.893	0.133	9.4	0.766	0.634
	3	16.3	58.596	0.004	58.7	34.201	0.000	4.0	1.173	0.342
	4	11.2	2.560	0.225	3.3	0.682	0.609	18.3	1.907	0.089
	5	0.3	0.046	0.956	19.0	3.442	0.018	7.1	0.640	0.739
6	1	47.8	9.797	0.048	2.9	0.998	0.421	5.4	0.915	0.515
	2	44.1	12.887	0.034	15.9	9.781	0.000	16.6	5.115	0.000
	3	43.4	69.689	0.003	25.2	28.175	0.000	21.5	12.026	0.000
	4	4.5	1.441	0.364	13.3	1.928	0.127	8.6	0.626	0.750
	5	37.1	19.618	0.019	12.1	4.770	0.003	23.0	4.545	0.000
7	1	63.4	32.058	0.009	2.8	1.363	0.266	9.5	2.343	0.039
	2	25.0	34.363	0.009	12.0	2.356	0.072	7.1	0.696	0.692
	3	9.9	59.719	0.004	47.7	51.341	0.000	32.3	17.382	0.000
	4	17.0	6.051	0.089	5.9	0.928	0.459	9.2	0.725	0.668
	5	28.5	8.664	0.057	13.2	3.681	0.013	16.2	2.254	0.046
8	1	11.2	3.967	0.144	7.6	1.222	0.319	14.8	1.186	0.334
	2	0.7	0.256	0.790	8.5	1.320	0.281	22.8	1.770	0.116
	3	22.5	22.993	0.015	60.7	106.956	0.000	7.2	6.306	0.000
	4	9.3	16.681	0.024	7.2	1.217	0.320	18.2	1.539	0.179
	5	20.4	5.651	0.096	7.3	1.335	0.276	14.6	1.337	0.257
9	1	38.3	13.228	0.033	13.5	5.310	0.002	13.4	2.950	0.021
	2	14.0	3.632	0.158	14.5	3.018	0.030	20.6	2.147	0.056
	3	55.3	21.651	0.016	25.3	30.285	0.000	1.1	0.684	0.703
	4	10.0	6.850	0.076	10.1	1.890	0.133	26.4	2.470	0.030

	5	3.9	0.712	0.559	32.7	8.515	0.000	16.2	2.114	0.060
10	1	73.0	2986.704	0.000	6.8	9.126	0.000	13.5	9.126	0.000
	2	13.1	4.150	0.137	16.4	4.694	0.004	25.5	3.655	0.003
	3	7.0	1.169	0.421	5.3	0.885	0.483	15.7	1.318	0.266
	4	25.0	9.255	0.052	5.8	1.080	0.381	11.6	1.080	0.399
	5	28.9	12.893	0.034	9.1	2.406	0.067	17.0	2.236	0.047
11	1	57.8	71.971	0.003	13.9	10.600	0.000	12.9	4.883	0.000
	2	53.8	108.422	0.002	13.2	9.368	0.000	17.5	6.232	0.000
	3	27.5	38.698	0.007	28.4	10.155	0.000	16.6	2.962	0.012
	4	6.2	3.675	0.156	8.5	1.263	0.302	13.4	0.999	0.454
	5	59.8	1459.577	0.000	11.0	14.372	0.000	22.1	14.372	0.000
12	1	85.8	199.620	0.000	1.1	2.806	0.036	6.2	5.116	0.000
	2	44.9	49.880	0.000	2.6	1.605	0.188	27.2	5.544	0.000
	3	73.7	37.314	0.000	11.5	25.402	0.000	3.9	2.835	0.005
	4	18.5	8.379	0.014	6.2	1.210	0.319	3.5	0.228	0.996
	5	29.3	22.551	0.001	27.3	13.420	0.000	13.0	2.128	0.032
13	1	68.1	107.846	0.000	2.5	3.747	0.010	19.0	9.412	0.000
	2	45.8	24.506	0.000	6.0	3.309	0.018	20.7	3.830	0.000
	3	43.1	46.479	0.000	44.8	135.653	0.000	4.0	3.979	0.000
	4	9.8	1.667	0.272	8.1	1.980	0.113	13.5	1.100	0.382
	5	21.2	5.364	0.039	7.9	3.008	0.027	19.8	2.529	0.011
14	1	75.3	236.792	0.000	2.6	2.570	0.050	8.3	2.787	0.006
	2	15.3	3.877	0.074	1.9	0.547	0.702	26.1	2.491	0.013
	3	45.3	56.479	0.000	41.7	102.322	0.000	2.1	1.744	0.086
	4	14.8	7.940	0.016	17.6	4.746	0.003	10.2	0.919	0.536
	5	13.2	1.548	0.297	17.4	5.064	0.002	7.3	0.706	0.738
15	1	35.4	34.858	0.000	14.4	11.085	0.000	23.3	5.983	0.000
	2	5.2	1.921	0.227	20.1	5.510	0.000	18.3	1.679	0.102
	3	33.9	137.420	0.000	52.0	198.005	0.000	8.9	11.316	0.000
	4	6.2	1.015	0.449	6.3	1.179	0.332	7.3	0.457	0.930
	5	13.7	1.729	0.260	22.2	8.373	0.000	8.0	1.010	0.455
16	1	40.8	13.941	0.004	3.0	2.697	0.042	33.0	9.811	0.000
	2	11.4	1.662	0.273	1.3	0.467	0.760	36.2	4.230	0.000
	3	42.7	31.103	0.001	38.9	118.686	0.000	9.0	9.112	0.000
	4	1.9	0.791	0.541	16.3	3.623	0.012	8.9	0.655	0.785
	5	24.8	3.418	0.093	10.1	4.657	0.003	12.6	1.932	0.054
17	1	30.8	13.592	0.004	3.4	1.204	0.321	25.3	2.969	0.004
	2	11.9	3.047	0.114	9.7	4.528	0.003	40.6	6.343	0.000
	3	45.9	67.675	0.000	34.3	71.732	0.000	10.0	6.975	0.000
	4	3.1	0.778	0.548	7.5	1.314	0.278	6.3	0.372	0.967
	5	25.9	2.613	0.146	3.8	1.285	0.289	11.7	1.320	0.239
18	1	18.8	4.998	0.045	6.5	2.248	0.078	17.3	2.009	0.044
	2	14.2	3.015	0.116	2.5	0.834	0.511	24.9	2.808	0.006
	3	18.7	7.334	0.020	38.7	24.246	0.000	14.0	2.911	0.004
	4	7.7	3.000	0.117	3.9	0.692	0.601	11.5	0.692	0.751
	5	18.3	10.410	0.009	12.2	4.115	0.006	21.7	2.438	0.014
19	1	4.4	0.999	0.455	30.8	17.098	0.000	29.3	5.426	0.000
	2	6.7	1.672	0.271	9.0	2.224	0.080	14.9	1.235	0.288
	3	17.4	25.333	0.000	54.8	117.854	0.000	18.6	13.306	0.000
	4	-	-	-	-	-	-	-	-	-
	5	25.4	7.786	0.017	13.1	6.352	0.000	24.3	3.916	0.000
20	1	53.0	12.297	0.006	6.0	5.793	0.000	13.4	4.343	0.000
	2	3.8	1.000	0.455	5.1	1.000	0.417	15.2	1.000	0.463
	3	49.9	24.464	0.000	15.3	28.189	0.000	22.6	13.865	0.000
	4	-	-	-	-	-	-	-	-	-
	5	9.3	7.891	0.017	17.9	8.198	0.000	42.1	6.421	0.000
21	1	36.2	9.083	0.012	2.1	0.755	0.560	4.9	0.598	0.833
	2	16.5	4.223	0.063	3.0	0.661	0.622	9.2	0.671	0.770
	3	27.0	12.648	0.005	27.8	22.496	0.000	16.8	4.522	0.000
	4	-	-	-	-	-	-	-	-	-

	5	35.4	5.962	0.031	4.0	1.631	0.182	8.1	1.105	0.378
22	1	30.6	7.211	0.020	0.3	0.116	0.976	11.2	1.289	0.256
	2	36.4	6.089	0.030	1.4	0.494	0.740	4.2	0.494	0.908
	3	28.2	3.861	0.075	8.4	3.975	0.007	11.3	1.776	0.080
	4	-	-	-	-	-	-	-	-	-
	5	27.3	6.555	0.025	9.8	4.897	0.002	23.4	3.882	0.000

Table A5.2. ANOVAs of marked and feral pollen and nectar gathering *B. terrestris* workers by 14 recording days by 4 crops by 5 time intervals.

bee class 1 = *B. terrestris* marked nectar gathering workers
bee class 2 = *B. terrestris* feral nectar gathering workers
bee class 3 = *B. terrestris* marked pollen gathering workers
bee class 4 = *B. terrestris* feral pollen gathering workers

		CROP			TIME			TIME BY CROP		
Day	Bee class	%SS	F_S	F.prob	%SS	F_S	F.prob	%SS	F_S	F.prob
9	1	60.9	174.372	0.001	6.0	3.877	0.008	10.9	2.337	0.019
	2	38.0	11.312	0.007	7.2	3.142	0.023	13.7	1.987	0.047
	3	2.6	1.000	0.455	10.3	2.000	0.110	10.3	0.667	0.774
	4	15.2	4.921	0.047	16.2	5.217	0.001	20.1	2.155	0.030
10	1	58.3	19.387	0.002	5.4	7.742	0.000	16.1	7.742	0.000
	2	61.3	20.128	0.002	3.1	2.694	0.042	9.4	2.694	0.007
	3	3.8	1.000	0.455	5.1	1.000	0.417	15.2	1.000	0.463
	4	20.0	6.818	0.023	10.7	5.000	0.002	32.0	5.000	0.000
11	1	55.9	53.336	0.000	11.0	11.687	0.000	14.4	5.128	0.000
	2	52.3	32.777	0.000	8.6	5.320	0.001	15.3	3.144	0.002
	3	21.3	8.836	0.013	22.3	2.256	0.077	39.4	2.256	0.023
	4	53.4	38.975	0.000	9.3	7.005	0.000	16.8	4.221	0.000
12	1	67.4	46.344	0.000	1.2	1.159	0.341	5.1	1.639	0.112
	2	70.7	52.061	0.000	3.0	3.099	0.024	8.7	2.998	0.003
	3	0.9	1.931	0.226	6.0	1.218	0.315	21.8	1.463	0.172
	4	50.3	108.571	0.000	2.4	1.351	0.265	22.7	4.197	0.000
13	1	58.7	31.114	0.000	0.6	0.497	0.738	17.3	4.602	0.000
	2	58.1	77.668	0.000	5.4	5.725	0.001	18.7	6.648	0.000
	3	14.2	3.616	0.084	4.2	0.989	0.423	13.5	1.050	0.422
	4	42.9	19.461	0.002	5.6	2.666	0.043	20.3	3.231	0.002
14	1	64.9	166.190	0.000	1.1	0.832	0.511	9.3	2.443	0.014
	2	62.7	54.768	0.000	3.6	2.228	0.080	9.2	1.876	0.062
	3	8.3	8.097	0.016	1.9	0.380	0.822	10.4	0.682	0.760
	4	11.6	3.421	0.093	1.6	1.383	0.820	22.8	1.879	0.061
15	1	30.5	19.691	0.002	16.6	8.632	0.000	15.8	2.740	0.007
	2	35.9	17.132	0.002	11.3	7.682	0.000	24.0	5.432	0.000
	3	4.5	2.040	0.210	20.4	4.778	0.003	11.2	0.876	0.576
	4	3.4	1.045	0.438	16.3	3.766	0.009	10.1	1.785	0.663
16	1	32.4	9.716	0.010	4.4	2.909	0.031	31.6	6.955	0.000
	2	36.8	19.728	0.002	2.5	1.031	0.401	26.4	3.645	0.000
	3	4.0	3.000	0.117	1.3	0.281	0.889	23.3	1.726	0.090
	4	12.2	1.651	0.275	1.4	0.463	0.762	32.7	3.646	0.000
17	1	27.9	8.060	0.016	6.4	2.335	0.069	18.1	2.214	0.026
	2	23.9	4.168	0.065	2.4	0.831	0.512	26.2	2.977	0.004
	3	3.4	0.552	0.666	4.4	1.256	0.300	25.7	2.451	0.014
	4	11.7	3.390	0.095	9.3	3.649	0.011	36.3	4.721	0.000
18	1	10.8	4.543	0.055	13.4	3.680	0.011	19.8	1.818	0.072

	2	21.7	4.372	0.059	2.4	0.672	0.615	7.5	0.666	0.774
	3	4.3	1.000	0.455	2.7	0.602	0.663	15.1	1.133	0.358
	4	15.5	3.263	0.101	3.6	1.092	0.371	23.0	2.360	0.018
19	1	6.5	2.016	0.213	28.2	10.772	0.000	22.8	2.899	0.004
	2	7.5	1.059	0.433	14.7	5.850	0.000	25.4	3.370	0.001
	3	7.4	1.000	0.455	5.5	1.731	0.159	7.2	0.756	0.690
	4	8.0	1.889	0.232	5.3	1.063	0.385	14.7	0.979	0.482
20	1	44.4	9.189	0.012	4.9	2.647	0.045	12.0	2.178	0.029
	2	45.5	10.958	0.008	5.8	4.789	0.002	17.5	4.789	0.000
	3	-	-	-	-	-	-	-	-	-
	4	3.8	1.000	0.455	5.1	1.000	0.417	15.2	1.000	0.463
21	1	17.9	2.918	0.122	5.6	1.716	0.162	10.0	1.015	0.451
	2	30.1	9.487	0.011	0.5	0.145	0.965	7.6	0.800	0.648
	3	5.6	2.000	0.216	4.6	0.808	0.526	11.2	0.654	0.785
	4	16.8	4.008	0.070	1.3	0.275	0.892	4.5	0.308	0.985
22	1	4.0	1.000	0.455	2.7	0.596	0.667	15.5	1.135	0.356
	2	19.8	5.595	0.036	4.4	1.175	0.334	9.1	0.811	0.638
	3	15.8	2.000	0.216	4.6	1.915	0.186	13.8	1.615	0.119
	4	23.6	9.000	0.012	2.5	0.536	0.710	7.5	0.536	0.880

Table A5.3. ANOVA of all bee classes.

VARIATE: NUMBER OF BEES (NORMALISED)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR	F PR
ROW STRATUM	3	8.5228	0.17	2.8409		
COL STRATUM	3	2.0879	0.04	0.6960		
ROW.COL STRATUM						
CROP	3	304.2126	5.91	101.4042	36.632	<.001
RESIDUAL	6	16.6092	0.32	2.7682		
TOTAL	9	320.8218	6.24	35.6469		
ROW.COL. UNITS STRATUM						
DAY	21	597.4961	11.61	28.4522	174.549	<.001
LIN	1	24.1927	0.47	24.1927	148.417	<.001
QUAD	1	232.0074	4.51	232.0074	1423.321	<.001
CUB	1	96.4387	1.87	96.4387	591.633	<.001
QUART	1	2.8087	0.05	2.8087	17.231	<.001
DEVIATIONS	17	242.0486	4.70	14.2382	87.348	<.001
BEE CLASS	4	817.7810	15.89	204.4453	1254.232	<.001
TIME	4	108.1685	2.10	27.0421	165.898	<.001
LIN	1	4.1960	0.08	4.1960	25.742	<.001
QUAD	1	99.9925	1.94	99.9925	613.435	<.001
DEVIATIONS	2	3.9800	0.08	1.9900	12.208	<.001
DAY.BEE CLASS	84	512.3043	9.96	6.0989	37.415	<.001
DAY.CROP	63	348.2682	6.77	5.5281	33.914	<.001
BEE CLASS.CROP	12	154.5223	3.00	12.8769	78.997	<.001
DAY.TIME	84	130.1826	2.53	1.5498	9.508	<.001
BEE CLASS.TIME	16	143.3685	2.79	8.9605	54.971	<.001
CROP.TIME	12	21.6833	0.42	1.8069	11.085	<.001
DAY.BEE CLASS.CROP	252	317.1005	6.16	1.2583	7.720	<.001
DAY.BEE CLASS.TIME	336	253.0745	4.92	0.7532	4.621	<.001
DAY.CROP.TIME	252	134.6764	2.62	0.5344	3.279	<.001
BEE CLASS.CROP.TIME	48	36.8694	0.72	0.7681	4.712	<.001
RESIDUAL	7596	1238.1804	24.07	0.1630		
TOTAL	8784	4813.6768	93.56	0.5480		
GRAND TOTAL	8799	5145.1094	100.00			
GRAND MEAN	0.0772					
TOTAL NUMBER OF OBSERVATIONS	8800					

Table A5.4. ANOVA of all bumble bees.

VARIATE: NUMBER OF BEES (NORMALISED)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR	F PR
ROW STRATUM	3	6.3483	0.17	2.1161		
COL STRATUM	3	1.4664	0.04	0.4888		
ROW.COL STRATUM						
CROP	3	241.1748	6.39	80.3916	27.119	<.001
RESIDUAL	6	17.7864	0.47	2.9644		
TOTAL	9	258.9612	6.86	28.7735		
ROW.COL. UNITS STRATUM						
DAY	21	320.9243	8.50	15.2821	67.695	<.001
LIN	1	20.4177	0.54	20.4177	90.444	<.001
QUAD	1	156.9053	4.16	156.9053	695.044	<.001
CUB	1	51.9425	1.38	51.9425	230.090	<.001
QUART	1	2.0123	0.05	2.0123	8.914	0.003
DEVIATIONS	17	89.6465	2.38	5.2733	23.359	<.001
BEE CLASS	3	285.6700	7.57	95.2233	421.811	<.001
TIME	4	32.9667	0.87	8.2417	36.508	<.001
LIN	1	8.9177	0.24	8.9177	39.503	<.001
QUAD	1	23.5043	0.62	23.5043	104.117	<.001
DEVIATIONS	2	0.5448	0.01	0.2724	1.207	0.299
DAY.BEE CLASS	63	219.2231	5.81	3.4797	15.414	<.001
BEE CLASS.CROP	9	152.9921	4.05	16.9991	75.301	<.001
DAY.TIME	84	76.5441	2.03	0.9112	4.037	<.001
BEE CLASS.TIME	12	21.6947	0.57	1.8079	8.008	<.001
CROP.TIME	12	34.5269	0.91	2.8772	12.745	<.001
DAY.BEE CLASS.CROP	189	254.4184	6.74	1.3461	5.963	<.001
DAY.BEE CLASS.TIME	252	103.3289	2.74	0.4100	1.816	<.001
DAY.CROP.TIME	252	186.2257	4.94	0.7390	3.274	<.001
BEE CLASS.CROP.TIME	36	38.7806	1.03	1.0772	4.772	<.001
RESIDUAL	6024	1359.9099	36.04	0.2257		
TOTAL	7024	3506.7725	92.93	0.4993		
GRAND TOTAL	7039	3773.5483	100.00			
GRAND MEAN	0.0776					
TOTAL NUMBER OF OBSERVATIONS	7040					

Table A5.5. ANOVA of marked and feral worker bumble bees.

VARIATE: NUMBER OF BEES (NORMALISED)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR	F PR
ROW STRATUM	3	8.4170	0.35	2.8057		
COL STRATUM	3	3.0331	0.12	1.0110		
ROW.COL STRATUM						
CROP	3	186.3443	7.67	62.1148	21.638	0.001
RESIDUAL	6	17.2237	0.71	2.8706		
TOTAL	9	203.5681	8.38	22.6187		
ROW.COL. UNITS STRATUM						
DAY	13	220.4784	9.08	16.9599	76.323	<.001
LIN	1	8.9699	0.37	8.9699	40.367	<.001
QUAD	1	176.6284	7.27	176.6284	794.868	<.001
CUB	1	5.6678	0.23	5.6678	25.507	<.001
QUART	1	9.1487	0.38	9.1487	41.171	<.001
DEVIATIONS	9	20.0635	0.83	2.2293	10.032	<.001
BEE CLASS	3	193.7708	7.98	64.5903	290.671	<.001
TIME	4	13.4268	0.55	3.3567	15.106	<.001
LIN	1	0.1331	0.01	0.1331	0.599	0.439
QUAD	1	11.4582	0.47	11.4582	51.564	<.001
DEVIATIONS	2	1.8355	0.08	0.9178	4.130	0.016
DAY.BEE CLASS	39	77.4415	3.19	1.9857	8.936	<.001
DAY.CROP	39	309.8135	12.76	7.9439	35.750	<.001
BEE CLASS.CROP	9	93.0870	3.83	10.3430	46.546	<.001
DAY.TIME	52	54.0214	2.22	1.0389	4.675	<.001
BEE CLASS.TIME	12	4.4722	0.18	0.3727	1.677	0.065
CROP.TIME	12	49.4477	2.04	4.1206	18.544	<.001
DAY.BEE CLASS.CROP	117	133.9429	5.52	1.1448	5.152	<.001
DAY.BEE CLASS.TIME	156	52.2344	2.15	0.3348	1.507	<.001
DAY.CROP.TIME	156	144.5349	5.95	0.9265	4.169	<.001
BEE CLASS.CROP.TIME	36	18.6627	0.77	0.5184	2.333	<.001
RESIDUAL	3816	847.9570	34.92	0.2222		
TOTAL	4464	2213.2910	91.15	0.4958		
GRAND TOTAL	4479	2428.3091	100.00			
GRAND MEAN	0.0775					
TOTAL NUMBER OF OBSERVATIONS	4480					

Table A5.6. ANOVA of nectar gatherers with pollen and nectar energy.

VARIATE: NECTAR GATHERERS (NORMALISED) (ADJUSTED FOR COVARIATES)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR	COV EF	F PR
UNITS STRATUM							
DAY	21	74.2277	21.44	3.5347	23.552	0.864	<.001
LIN	1	14.5803	4.21	14.5803	97.151	0.575	<.001
QUAD	1	27.2580	7.87	27.2580	181.625	0.940	<.001
CUB	1	22.3302	6.45	22.3302	148.790	0.834	<.001
QUART	1	0.7820	0.23	0.7820	5.211	0.583	0.023
DEVIATIONS	17	18.7227	5.41	1.1013	7.338	0.914	<.001
CROP	3	47.9840	13.86	15.9947	106.575	0.290	<.001
TIME	4	4.4454	1.28	1.1114	7.405	0.957	<.001
LIN	1	0.3068	0.09	0.3068	2.044	0.864	0.154
QUAD	1	3.9315	1.14	3.9315	26.196	0.984	<.001
DEVIATIONS	2	0.0987	0.03	0.0494	0.329	0.997	0.720
DAY.CROP	63	86.7927	25.07	1.3777	9.180	0.943	<.001
DAY.TIME	84	17.7418	5.12	0.2112	1.407	0.987	0.023
CROP.TIME	12	9.3654	2.70	0.7804	5.200	0.987	<.001
COVARIATES	2	0.1404	0.04	0.0702	0.468		0.627
RESIDUAL	250	37.5196	10.84	0.1501		0.996	
TOTAL	439	278.2170	80.36	0.6338			
GRAND TOTAL	439	278.2170	80.36				
GRAND MEAN	0.048						

TOTAL NUMBER OF OBSERVATIONS 440 (COV EF = covariance efficiency)

Table A5.7. ANOVA of queens with pollen and nectar energy.

VARIATE: QUEENS (NORMALISED) (ADJUSTED FOR COVARIATES)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR	COV EF	F PR
UNITS STRATUM							
DAY	21	50.7174	18.94	2.4151	10.204	0.864	<.001
LIN	1	11.8087	4.41	11.8087	49.891	0.575	<.001
QUAD	1	10.3547	3.87	10.3547	43.748	0.940	<.001
CUB	1	0.0181	0.01	0.0181	0.076	0.834	0.782
QUART	1	0.0417	0.02	0.0417	0.176	0.583	0.675
DEVIATIONS	17	20.3606	7.60	1.1977	5.060	0.914	<.001
CROP	3	23.5916	8.81	7.8639	33.224	0.290	<.001
TIME	4	5.1850	1.94	1.2963	5.477	0.957	<.001
LIN	1	0.0217	0.01	0.0217	0.092	0.864	0.762
QUAD	1	4.6961	1.75	4.6961	19.840	0.984	<.001
DEVIATIONS	2	0.4354	0.16	0.2177	0.920	0.997	0.400
DAY.CROP	63	66.0277	24.66	1.0481	4.428	0.943	<.001
DAY.TIME	84	34.6841	12.95	0.4129	1.744	0.987	<.001
CROP.TIME	12	7.0560	2.63	0.5880	2.484	0.987	0.004
COVARIATES	2	0.3333	0.12	0.1666	0.704		0.496
RESIDUAL	250	59.1729	22.10	0.2367		0.998	
TOTAL	439	246.7680	92.15	0.5621			
GRAND TOTAL	439	246.7680	92.15				
GRAND MEAN	0.074						

TOTAL NUMBER OF OBSERVATIONS 440

Table A5.8. ANOVA of males with pollen and nectar energy.

VARIATE: MALES (NORMALISED) (ADJUSTED FOR COVARIATES)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR	COV EF	F PR
UNITS STRATUM							
DAY	21	61.7991	21.33	2.9428	14.480	0.864	<.001
LIN	1	6.5636	2.26	6.5636	32.296	0.575	<.001
QUAD	1	27.9178	9.63	27.9178	137.370	0.940	<.001
CUB	1	5.4734	1.89	5.4734	26.932	0.834	<.001
QUART	1	1.1847	0.41	1.1847	5.829	0.583	0.016
DEVIATIONS	17	17.7532	6.13	1.0443	5.139	0.914	<.001
CROP	3	24.1731	8.34	8.0577	39.648	0.290	<.001
TIME	4	23.6195	8.15	5.9049	29.055	0.957	<.001
LIN	1	15.8289	5.46	15.8289	77.886	0.864	<.001
QUAD	1	6.0994	2.10	6.0994	30.012	0.984	<.001
DEVIATIONS	2	0.8958	0.31	0.4479	2.204	0.997	0.112
DAY.CROP	63	70.1164	24.20	1.1130	5.476	0.943	<.001
DAY.TIME	84	33.6212	11.60	0.4003	1.969	0.987	<.001
CROP.TIME	12	6.7101	2.32	0.5592	2.751	0.987	0.002
COVARIATES	2	0.1265	0.04	0.0632	0.311		0.733
RESIDUAL	250	50.8075	17.53	0.2032		0.995	
TOTAL	439	270.9735	93.51	0.6173			
GRAND TOTAL	439	270.9735	93.51				
GRAND MEAN	0.070	TOTAL NUMBER OF OBSERVATIONS 440					

Table A5.9. ANOVA of pollen gatherers with pollen and nectar energy.

VARIATE: POLLEN GATHERERS (NORMALISED) (ADJUSTED FOR COVARIATES)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR	COV EF	F PR
UNITS STRATUM							
DAY	21	57.8554	18.98	2.7550	9.226	0.864	<.001
LIN	1	0.0032	0.00	0.0032	0.011	0.575	0.918
QUAD	1	20.6838	6.78	20.6838	69.266	0.940	<.001
CUB	1	2.6257	0.86	2.6257	8.793	0.834	0.003
QUART	1	1.9816	0.65	1.9816	6.636	0.583	0.011
DEVIATIONS	17	29.1674	9.57	1.7157	5.746	0.914	<.001
CROP	3	30.7496	10.09	10.2499	34.325	0.290	<.001
TIME	4	3.4939	1.15	0.8735	2.925	0.957	0.022
LIN	1	0.0821	0.03	0.0821	0.275	0.864	0.600
QUAD	1	2.1015	0.69	2.1015	7.038	0.984	0.008
DEVIATIONS	2	1.2633	0.41	0.6316	2.115	0.997	0.123
DAY.CROP	63	80.1091	26.27	1.2716	4.258	0.943	<.001
DAY.TIME	84	28.2899	9.28	0.3368	1.128	0.987	0.239
CROP.TIME	12	10.2234	3.35	0.8520	2.853	0.987	0.001
COVARIATES	2	2.2509	0.74	1.1254	3.769		0.024
RESIDUAL	250	74.6535	24.48	0.2986		1.022	
TOTAL	439	287.6259	94.33	0.6552			
GRAND TOTAL	439	287.6259	94.33				
GRAND MEAN	0.065	TOTAL NUMBER OF OBSERVATIONS 440					

Table A5.10. ANOVA of honey bees with pollen and nectar energy.

VARIATE: HONEY BEES (NORMALISED) (ADJUSTED FOR COVARIATES)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR	COV EF	F PR
UNITS STRATUM							
DAY	21	103.70992	29.82	4.93857	49.988	0.864	<.001
LIN	1	0.55963	0.16	0.55963	5.665	0.575	0.018
QUAD	1	30.54158	8.78	30.54158	309.144	0.940	<.001
CUB	1	10.39591	2.99	10.39591	105.228	0.834	<.001
QUART	1	1.06358	0.31	1.06358	10.766	0.583	0.001
DEVIATIONS	17	57.92157	16.65	3.40715	34.487	0.914	<.001
CROP	3	34.99548	10.06	11.66516	118.075	0.290	<.001
TIME	4	37.07764	10.66	9.26941	93.825	0.957	<.001
LIN	1	0.01679	0.00	0.01679	0.170	0.864	0.680
QUAD	1	35.51843	10.21	35.51843	359.520	0.984	<.001
DEVIATIONS	2	1.42840	0.41	0.71420	7.229	0.997	<.001
DAY.CROP	63	49.50652	14.23	0.78582	7.954	0.943	<.001
DAY.TIME	84	40.28085	11.58	0.47953	4.854	0.987	<.001
CROP.TIME	12	2.50414	0.72	0.20868	2.112	0.987	0.017
COVARIATES	2	2.16236	0.62	1.08118	10.944		<.001
RESIDUAL	250	24.69854	7.10	0.09879		1.079	
TOTAL	439	294.93549	84.80	0.67183			
GRAND TOTAL	439	294.93549	84.80				
GRAND MEAN	0.047						

TOTAL NUMBER OF OBSERVATIONS 440

Table A5.11. Relation between 5 bee classes (transformed $\log_e (x + 1)$) and weather variables (multiple regression and ANOVA).

Bee class	ANOVA F ratio	df	Signif-icance	Regression coefficients 1st coef. t value Signifi.	2nd coef. t value Signifi.	% variance accounted for (R^2) R^2 for 1st cof.	R^2 for 2nd cof.	R^2 for total
Nectar gatherers	17.54	3,106	***	Temp. 5.24 ***	R.H. -3.29 **	24.3	13.6	31.3
Pollen gatherers	3.74	3,106	*	R.H. -2.74 **	Light -2.50 *	2.1 (3rd coef)	- (4th coef)	7.0
Honey bees	29.20	4,105	***	Temp. 4.29 ***	R.H. -3.65 **	Wind -3.10 **	Light 2.85 **	50.9
Queens	3.17	3,106	n.s.	R.H. -2.44 *	Wind -1.39 n.s.	0.1 (3rd coef)	0.1	5.6
Males	12.37	3,106	***	Temp. 5.29 ***	R.H. -2.59 *	Light -2.10 *	-	23.8

$t_{0.05(2)[106]}=1.983$ $t_{0.01(2)[105]}=2.623$ $F_{0.05(2)[3,106]}=3.82$
$t_{0.01(2)[106]}=2.622$ $t_{0.001(2)[105]}=3.386$ $F_{0.01(2)[3,106]}=5.57$
$t_{0.001(2)[106]}=3.384$ $F_{0.001(2)[105]}=6.41$ $F_{0.001(2)[3,106]}=8.18$

Table A5.12. Relation between 5 bee classes (transformed $\log_e (x + 1)$) with weather variables and food from exposed flowers (multiple regression and ANOVA).

Bee class	ANOVA F ratio	df	Signif-icance	Regression coefficients 1st coef. t value Signifi.	2nd coef. t value Signifi.	3rd coef. t value Signifi.	% variance accounted for R^2 for 1st cof.	Total R^2
Nectar gatherers	16.68	3,105	***	Temp. 5.16 ***	R.H. -3.21 **	Light - n.s.	23.6	30.3
Pollen gatherers	3.73	3,105	*	R.H. -2.75 **	Light -2.50 *	Temp. 1.89 n.s.	2.1 (4th coef)	7.0
Honey bees	28.62	4,105	***	Temp. 4.28 ***	R.H. -3.62 ***	Wind -3.09 **	Light 2.83 **	50.6
Queens	5.98	3,105	**	R.H. -3.64 ***	Exnec. 3.14 **	Wind -1.78 n.s.	3.9	12.1
Males	11.74	3,105	***	Temp. 5.50 ***	Expol. -2.10 *	R.H. - n.s.	19.7	23.0

$t_{0.05(2)[105]}=1.983$
$t_{0.01(2)[105]}=2.623$
$t_{0.001(2)[105]}=3.386$

$F_{0.05(2)[3,105]}=3.25$
$F_{0.01(2)[3,105]}=4.53$
$F_{0.001(2)[3,105]}=6.41$
$F_{0.001(2)[4,105]}=5.46$

Exnec. = exposed nectar energy
Expol. = exposed pollen

Table A5.13. Relation between 5 bee classes (transformed $\log_e(x + 1)$) with weather variables, food from exposed flowers and pollen and nectar production from bagged flowers (multiple regression and ANOVA).

Bee class	ANOVA F ratio	df	Signif-icance	Regression coefficients 1st coef. t value Signifi.	2nd coef. t value Signifi.	3rd coef. t value Signifi.	% variance accounted for R^2 for 1st cof.	Total R^2
Nectar gather-ers	15.77	4,61	***	Temp. 4.10 ***	Necpro. 3.54 ***	R.H. -2.49 *	30.3	47.6
Pollen gather-ers	3.94	4,61	*	Exnec. 2.83 **	R.H. -2.77 **	Wind -2.04 *	3.8	15.3
Honey bees	18.54	4,61	***	Light 5.17 ***	Temp. 3.79 ***	Wind -2.22 *	35.4	51.9
Queens	6.98	4,61	***	Light 4.23 ***	Exnec. 4.14 **	Wind -2.02 *	5.2	26.9
Males	10.04	4,61	***	Temp. 5.52 ***	Rain -3.05 **	Expol. -2.51 *	23.4	35.7

$t_{0.05(2)[61]}=2.000$ $F_{0.05(2)[4,61]}=3.01$ Necpro.= nectar energy production
$t_{0.01(2)[61]}=2.659$ $F_{0.01(2)[4,61]}=4.14$ Exnec. = exposed nectar energy
$t_{0.001(2)[61]}=3.457$ $F_{0.001(2)[4,61]}=5.82$ Expol. = exposed pollen

Table A5.14. Factors influencing the number of *B.terrestris* nectar and pollen gatherers on borage and nectar gatherers on fodder radish. Including weather variables, pollen and nectar from exposed (borage and fodder radish) flowers, pollen, and nectar production from bagged (borage and fodder radish) flowers and honey bees (on borage).

Foragers	ANOVA F ratio	df	Signif-icance	Regression coefficients 1st coef. t value Signifi.	2nd coef. t value Signifi.	3rd coef. t value Signifi.	4th coef. t value Signifi.	Total R^2 (% var.)
Nectar gatherers on borage	10.73	4,61	***	Polgath. on borage 3.98 ***	Expol. on borage 2.70 **	Necgath. on f.rad. 2.16 *	Necpro. on borage 2.15 *	37.5
Pollen gatherers on borage	8.40	4,61	***	Necgath. on borage 3.72 ***	Wind -2.36 *	Exnec. on f.rad. 1.83 n.s.	Necpro. on f.rad. - n.s.	31.3
Nectar gatherers on fodder radish	31.60	4,61	***	Polgath. on f.rad. 4.68 ***	Honbee on borage 3.24 **	Temp. 3.24 **	Necgath. on borage - n.s.	65.3

$t_{0.05(2)[61]}=2.000$ $F_{0.05(2)[4,61]}=3.01$ Necpro.= nectar energy production
$t_{0.01(2)[61]}=2.659$ $F_{0.01(2)[4,61]}=4.14$ Exnec. = exposed nectar energy
$t_{0.001(2)[61]}=3.457$ $F_{0.001(2)[4,61]}=5.82$ Expol. = exposed pollen
Polgath.=pollen gatherers Necgath.=nectar gatherers Honbee =honey bees

Table A5.15. Factors influencing the number of *B.terrestris* nectar and pollen gatherers on borage and nectar gatherers on fodder radish. Excluding pollen, and nectar production from bagged flowers but including weather variables, pollen and nectar from exposed (borage and fodder radish) flowers and honey bees (on borage).

Foragers	ANOVA F ratio	df	Signif-icance	Regression coefficients 1st coef. t value Signifi.	2nd coef. t value Signifi.	3rd coef. t value Signifi.	4th coef. t value Signifi.	Total R^2 (% var.)
Nectar gatherers on borage	17.40	4,104	***	Polgath. on borage 6.44 ***	Expol. on borage 3.39 ***	Necgath. on f.rad. 2.75 **	Wind - n.s.	37.8
Pollen gatherers on borage	15.60	4,104	***	Necgath. on borage 6.73 ***	Wind -2.86 **	Temp. -2.21 *	Exnec. on f.rad. - n.s.	35.1
Nectar gatherers on fodder radish	54.39	4,104	***	Polgath. on f.rad. 5.43 ***	Honbee on borage 5.23 ***	Temp. 4.46 ***	Necgath. on borage 3.44 ***	66.4

$t_{0.05(2)[104]}=1.983$ $F_{0.05(2)[4,104]}=2.92$ Necpro.= nectar energy production
$t_{0.01(2)[104]}=2.623$ $F_{0.01(2)[4,104]}=3.95$ Exnec. = exposed nectar energy
$t_{0.001(2)[104]}=3.386$ $F_{0.001(2)[4,104]}=5.46$ Expol. = exposed pollen

Table A5.16(a) and A5.16(b). Foraging data for *B. terrestris* workers confined on $8m^2$ of (a) borage or (b) broccoli (Oct.-Nov.1987). Each trial represents one bee released into cage.

Table A5.16(a)

Crop	Borage						
Trial number	1	2	3	4	5	6	7
BEES	(n = 1)						
Foraging time(min)	15.3	12.8	23.4	24.8	14.5	8.2	7.5
Grooming time(min)	10.6	9.5	11.0	2.5	12.4	10.3	9.6
No.flowers visited	35	56	41	54	28	11	17
Mean handling time /flower (s)	26.2	13.7	34.3	27.8	31.0	44.5	26.5
Change in bee weight (mg)	18	66	26	111	35	34	34
Volume nectar collected (µl)	14	52	21	88	28	27	27
Conc. of nectar (% sugar)	55+	55+	55+	55+	51	55+	55+
Weight of pollen(mg)	0	0	25	0	0	0	0
FLOWERS							
Mean nectar/ flower (µl) n=20	0.45	1.18	1.18	0.93	2.35	2.35	2.35
Mean nectar conc. /flower (% sugar)	54	53	55+	51	46	46	46
Mean proportion flowers releasing pollen	0.95	0.80	0.40	0.95	0.95	0.95	0.95
Predicted no. flowers visited *	31	44	18	95	12	11	11
WEATHER							
Mean light intensity ($\mu Em^{-2}s^{-1}$)	675	1625	1420	895	1800#	1800#	1800#
Mean temperat. (C)	11.8	15.8	16.8	21.5	18.5	18.5	18.5
Mean wind speed (ms^{-1})	1.9	1.8	2.0	1.8	1.3	1.3	1.3

* = (nectar collected)/(nectar per flower)

\# recorded outside cage (14.4% of outside incident radiation lost passing through cage).

Table A5.16(b).

Crop	Broccoli						
Trial number	1	2	3	4	5	6	7
BEES	(n = 1)						
Foraging time(min)	13.6	17.0	15.5	12.7	20.4	25.8	20.6
Grooming time(min)	10.0	13.5	12.3	11.8	7.7	7.2	8.0
No.flowers visited	47	80	45	51	41	68	85
Mean handling time /flower (s)	17.4	12.5*	20.7	14.9	29.9	22.8	14.6
Change in bee weight (mg)	20	22	24	20	67	65	78
Volume nectar collected (µl)	16	17	19	16	53	52	62
Conc. of nectar (% sugar)	54	55+	55+	55+	55+	55+	55+
Weight of pollen(mg)	0	0	0	6	0	0	0
FLOWERS							
Mean nectar/ flower (µl) n=20	0.35	0.35	0.58	0.53	0.53	0.50	0.50
Mean nectar conc. /flower (% sugar)	51	51	42	55+	55+	55+	55+
Mean proportion flowers releasing pollen	1.00	1.00	0.95	1.00	1.00	1.00	1.00
Predicted no. flowers visited *	46	49	33	30	100	104	124
WEATHER							
Mean light intensity ($\mu Em^{-2}s^{-1}$)	1390	1105	1270	1383	1383	1850#	1890#
Mean temperat. (C)	18.0	18.5	19.0	20.3	20.3	19.5	19.5
Mean wind speed (ms^{-1})	1.8	1.3	0.9	0.8	0.8	0.4	0.4

recorded outside cage

12.5* robbing flowers

Table A6.1. ANOVAs of pollen dry weight returning on forager corbiculae of 2 pollen types (6-31 Oct.) and 3 pollen types (3 Nov.-8 Dec.) to 10 field foraging colonies (1987).

Day	Oct.6	10	13	17	20	24	27	31
df	1,18	1,18	1,18	1,18	1,18	1,18	1,18	1,18
F ratio	10.80	2.13	2.63	1.23	0.52	0.30	1.50	2.71
Probab.	0.004	0.161	0.122	0.282	0.481	0.591	0.237	0.117
Signif.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Day	Nov.3	8	10	14	17	21	24	Dec.1	8
df	2,27	2,27	2,27	2,27	2,27	2,27	2,15	2,15	2,12
F ratio	19.65	8.20	0.33	0.51	2.33	6.19	24.32	6.30	6.62
Probab.	0.000	0.002	0.721	0.605	0.117	0.006	0.000	0.010	0.012
Signif.	***	**	n.s.	n.s.	n.s.	**	***	*	*

$F_{0.05(2)[1,18]}=5.98$ $F_{0.05(2)[2,27]}=4.24$ $F_{0.05(2)[2,15]}=4.77$
$F_{0.01(2)[1,18]}=10.2$ $F_{0.01(2)[2,27]}=6.49$ $F_{0.001(2)[2,15]}=13.2$
$F_{0.001(2)[2,27]}=10.2$ $F_{0.05(2)[2,12]}=5.10$

Table A6.2. Pollen feeding trial with borage and crucifer pollen. Ratio of borage to crucifer pollen consumed from pollen pots.

				Trial 1					
Time (mins)	0	3	6	9	12	15	18	21	24
Borage:crucifer pollen consumed	0:0	0:1	1:2	1:3	1:4	3:4	4:5	5:6	6:6

				Trial 2 (colony conditioned to borage)			
Time (mins)	0	60	78	86	150	205	265
Borage:crucifer pollen consumed	0:0	0:1	0:3	1:4	3:4	4:4	6:6

Table A6.3. Relation of nectar energy uptake and energy harvest rate of workers returning to observation hives (transformed $\log_e (x + 1)$) with weather variables, exposed nectar and pollen, pollen availability and nectar production from bagged flowers, pollen and nectar gatherers and honey bees. (Oct.-Nov.1987), (multiple regression and ANOVA).

Bee class	ANOVA F ratio	df	Signif-icance	Regression coefficients 1st coef. t value Signifi.	2nd coef. t value Signifi.	3rd coef. t value Signifi.	Total R^2 (% var.)
Analysis without bagged pollen, and nectar production:							
Nectar energy uptake	5.55	4,36	**	Expol. -2.76 **	Rain -2.74 **	Light 1.37 n.s.	31.3
Energy harvest rate	2.35	4,36	n.s.	Honbee 1.93 n.s.	R.H. 1.66 n.s.	Polgath. 1.56 n.s.	11.9
Analysis with bagged pollen, and nectar production:							
Nectar energy uptake	3.14	4,16	n.s.	Bagpol. 1.99 n.s.	Expol. -1.87 n.s.	Light 1.78 n.s.	30.0
Energy harvest rate	2.34	4,16	n.s.	Honbee 2.12 *	Necpro. -1.67 n.s.	Expnec. -1.23 n.s.	21.2

$t_{0.05(2)[36]}=2.028$ $F_{0.05(2)[4,36]}=3.17$ Honbee =honey bees
$t_{0.01(2)[36]}=2.719$ $F_{0.01(2)[4,36]}=4.46$ Polgath.=pollen gatherers
$t_{0.001(2)[36]}=3.582$ $F_{0.001(2)[4,36]}=6.47$ Expol.=exposed pollen
$t_{0.05(2)[16]}=2.120$ $F_{0.05(2)[4,16]}=3.73$ Exnec.=exposed nectar energy
$t_{0.01(2)[16]}=2.921$ Necpro.=nectar energy production Bagpol=bagged pollen

Table A6.4. Correlation coefficient (r value, significance) matrix of 2 hourly nectar energy/bee and energy harvest rate of workers returning to one hive in relation to food from exposed and bagged flowers, weather and competition.

DF = 19	Nectar energy/ bee (joules)		Energy harvest rate (joules/min.)		
Energy harvest rate	0.448	*	-		
Temperature	-0.003	n.s.	0.111	n.s.	$r_{0.05(2)[19]}=0.433$
Relative humidity	-0.369	n.s.	-0.039	n.s.	$r_{0.01(2)[19]}=0.549$
Wind	0.315	n.s.	0.000	n.s.	$r_{0.001(2)[19]}=0.665$
Light intensity	0.462	*	0.134	n.s.	
Rainfall	-0.490	*	-0.099	n.s.	
Exposed pollen	-0.416	n.s.	-0.291	n.s.	
Exposed nectar energy	0.032	n.s.	-0.341	n.s.	
Bagged pollen	0.241	n.s.	-0.070	n.s.	
Nectar production	-0.075	n.s.	-0.220	n.s.	
Pollen gatherers	0.152	n.s.	0.181	n.s.	
Nectar gatherers	0.047	n.s.	0.195	n.s.	
Honey bees	0.281	n.s.	0.405	n.s.	

Table A6.5. Pearson correlation coefficient (r value, significance) matrix of mean 2 hourly pollen dry weight returning to 10 colonies from pollen gatherers.

DF = 63	Colony 1	Colony 2	Colony 3	Colony 4	Colony 5	Colony 6
Colony 1	1.000					
Colony 2	0.276 *	1.000				
Colony 3	0.328 **	-0.056 n.s.	1.000			
Colony 4	0.295 *	0.073 n.s.	0.674 ***	1.000		
Colony 5	0.035 n.s.	0.227 n.s.	0.337 **	0.428 ***	1.000	
Colony 6	0.283 *	0.057 n.s.	0.244 n.s.	0.425 ***	0.458 ***	1.000
Colony 7	-0.023 n.s.	0.294 *	-0.048 n.s.	0.198 n.s.	0.452 ***	0.312 **
Colony 8	-0.058 n.s.	0.234 n.s.	0.001 n.s.	0.104 n.s.	0.457 ***	0.112 n.s.
Colony 9	-0.012 n.s.	-0.140 n.s.	0.371 **	0.422 ***	0.341 ***	0.253 *
Colony 10	0.188 n.s.	-0.053 n.s.	0.633 ***	0.504 ***	0.166 n.s.	0.036 n.s.

	Colony 7	Colony 8	Colony 9	Colony 10	
Colony 7	1.000				
Colony 8	0.535 ***	1.000			$r_{0.05(2)[63]}=0.244$
Colony 9	0.056 n.s.	0.029 n.s.	1.000		$r_{0.01(2)[63]}=0.318$
Colony 10	-0.152 n.s.	-0.066 n.s.	0.308 *	1.000	$r_{0.001(2)[63]}=0.399$

Table A6.6. Pollen intake (transformed $\log_e (x + 1)$) into 10 colonies in relation to weather, food from exposed flowers and foraging competition (multiple regression and ANOVA).

Colony number	ANOVA F ratio	df	Signif-icance	Regression coefficients 1st coef. t value Signifi.	2nd coef. t value Signifi.	3rd coef. t value Signifi.	4th coef. t value Signifi.	Total R^2 (% var.)
1	11.93	4,60	***	Honbee 3.04 **	Necgath. 2.13 *	Polgath. -1.66 n.s.	Expol. - n.s.	40.6
2	6.72	4,60	***	Light 3.27 ***	Exnec. -2.81 **	Honbee -1.74 n.s.	Necgath. - n.s.	26.3
3	27.35	4,60	***	Necgath. 5.28 ***	Honbee 2.44 *	Rain -1.76 n.s.	Polgath. - n.s.	62.2
4	23.40	4,60	***	Necgath. 6.48 ***	Temp. 2.50 *	Exnec. -2.04 *	Rain - n.s.	58.3
5	6.73	4,60	***	Temp. 2.87 **	R.H. -2.79 **	Exnec. -1.23 n.s.	Honbee - n.s.	26.4
6	6.69	4,60	***	Honbee 3.32 **	Expol. 2.49 *	Wind 2.41 *	Exnec. -2.15 *	26.2
7	10.53	4,60	***	Temp 4.69 ***	Wind 3.10 **	Light 1.54 n.s.	Rain _ n.s.	37.3
8	4.61	4,60	***	Exnec. -2.90 **	Wind 2.53 *	Temp. 1.43 n.s.	R.H. - n.s.	18.4
9	3.82	4,60	*	Polgath. 2.50 *	R.H. -2.01 *	Temp. 1.20 n.s.	Honbee - n.s.	15.0
10	14.91	4,60	***	Necgath. 5.67 ***	R.H. -2.65 *	Wind 0.85 n.s.	Honbee - n.s.	46.5

$t_{0.05(2)[60]}=2.000$ $F_{0.05(2)[4,60]}=3.01$ Necgath.=nectar gatherers
$t_{0.01(2)[60]}=2.660$ $F_{0.01(2)[4,60]}=4.14$ Polgath.=pollen gatherers
$t_{0.001(2)[60]}=3.460$ $F_{0.001(2)[4,60]}=5.82$ Honbee =honey bee

Table A6.7. Pollen intake (transformed $\log_e (x + 1)$) into 10 colonies in relation to weather, food availability from bagged and exposed flowers and foraging competition (multiple regression and ANOVA).

Colony number	ANOVA F ratio	df	Signif-icance	Regression coefficients 1st coef. t value Signifi.	2nd coef. t value Signifi.	3rd coef. t value Signifi.	4th coef. t value Signifi.	Total R^2 (% var.)
1	7.81	4,34	***	Honbee 3.01 **	Necpro. -2.21 *	Necgath. 2.08 *	Light - n.s.	41.7
2	3.32	4,34	*	Bagpol 3.05 **	Light 1.10 n.s.	Temp. -1.10 n.s.	Honbee - n.s.	19.7
3	14.28	4,34	***	Honbee 3.93 **	Polgath. 2.91 **	Necpro. 2.29 *	Light -2.20 *	20.8
4	17.23	4,34	***	Polgath. 4.19 ***	Honbee 3.65 ***	Exnec. -2.96 **	Wind 2.42 *	63.1
5	3.76	4,34	*	Temp. 2.65 *	Rain -2.07 *	Expol. -1.44 n.s.	Honbee - n.s.	22.5
6	5.32	4,34	**	Necpro. 3.05 **	Wind 2.37 *	Exnec. -1.99 n.s.	Expol. - n.s.	31.2
7	8.52	4,34	***	Temp 5.16 ***	Rain -3.58 **	Necgath. -2.49 *	R.H. _ n.s.	44.2
8	2.65	4,34	n.s.	Wind 2.38 *	Exnec. -2.34 *	Polgath. 1.35 n.s.	Temp. - n.s.	14.8
9	5.43	4,34	**	Polgath. 2.96 **	Temp. 1.71 n.s.	Rain -1.56 n.s.	Expol. - n.s.	31.8
10	7.21	4,34	***	Polgath. 3.96 ***	R.H. -1.54 n.s.	Wind 0.85 n.s.	Exnec. - n.s.	39.5

$t_{0.05(2)[34]}=2.032$ $F_{0.05(2)[4,34]}=3.19$ Necpro.=nectar energy production
$t_{0.01(2)[34]}=2.738$ $F_{0.01(2)[4,34]}=4.51$ Bagpol =bagged pollen
$t_{0.001(2)[34]}=3.601$ $F_{0.001(2)[4,34]}=6.57$

Table A6.8. Pearson correlation coefficient matrix of 6 brood bionomic parameters for 10 field colonies (Oct - Dec 1987).

Colony		1	2	3	4	5	6	7	8	9	10
No. of cases	(n)	14	17	14	15	16	17	17	17	17	14
LA vs	rvalue	.530	.712	.173	.511	.666	.448	.547	.489	.424	.831
Numbees	Prob.	.026	.001	.277	.026	.002	.036	.012	.023	.031	.000
LA vs	rvalue	.195	.336	.720	.853	.720	.332	.495	.556	.490	.644
Maxfor	Prob.	.252	.094	.002	.000	.001	.096	.022	.010	.023	.006
LA vs	rvalue	.428	.541	.615	.626	.166	.552	.236	.343	.059	.763
Maxpol	Prob.	.063	.012	.010	.006	.270	.011	.181	.089	.411	.001
LA vs	rvalue	-.178	-.152	-.168	.506	.213	.228	-.006	.116	-.006	.518
Polpots	Prob.	.272	.280	.283	.027	.214	.189	.490	.329	.491	.029
LA vs	rvalue	-.123	-.047	.183	.241	.601	.140	-.046	-.129	.652	-.418
Necpots	Prob.	.338	.428	.266	.194	.007	.296	.431	.310	.002	.069
Numbees vs	rvalue	.327	.656	.355	.556	.784	.665	.847	.836	.713	.758
Maxfor	Prob.	.127	.002	.106	.016	.000	.002	.000	.000	.001	.001
Numbees vs	rvalue	.542	.791	.773	.490	.600	.663	.551	.638	.023	.826
Maxpol	Prob.	.023	.000	.001	.032	.007	.002	.011	.003	.464	.000
Numbees vs	rvalue	.290	-.164	.536	.461	.230	.602	.331	.262	-.317	.336
Polpots	Prob.	.157	.265	.024	.042	.196	.005	.097	.155	.108	.120
Numbees vs	rvalue	.016	.160	.470	.493	.524	.391	.300	.394	.175	-.670
Necpots	Prob.	.479	.270	.045	.031	.019	.060	.121	.059	.251	.004
Maxfor vs	rvalue	.440	.715	.537	.749	.436	.656	.555	.697	.118	.564
Maxpol	Prob.	.058	.001	.024	.001	.046	.002	.010	.001	.327	.018
Maxfor vs	rvalue	.293	-.320	-.097	.685	.220	.298	.193	.075	-.087	.109
Polpots	Prob.	.155	.106	.371	.002	.206	.123	.229	.388	.370	.355
Maxfor vs	rvalue	.534	-.094	.195	.330	.405	.488	.085	-.108	.329	-.680
Necpots	Prob.	.025	.360	.252	.115	.060	.024	.373	.340	.099	.004
Maxpol vs	rvalue	.058	-.135	.434	.453	.160	.590	.165	.420	.053	.505
Polpots	Prob.	.422	.302	.061	.043	.278	.006	.264	.046	.420	.033
Maxpol vs	rvalue	.032	.196	.643	.366	.481	.578	.167	-.018	.386	-.321
Necpots	Prob.	.457	.226	.007	.090	.030	.007	.261	.473	.063	.131
Polpots vs	rvalue	.478	.170	.594	.532	.184	.042	.053	.498	.254	.084
Necpots	Prob.	.042	.257	.013	.021	.248	.436	.419	.021	.162	.387

LA = larval area (cm^2)
Numbees = number of bees/colony
Maxfor = maximum foragers/2 hour/day
Maxpol = maximum pollen gatherers/2 hour/day
Polpots = number of half full pollen pots
Necpots = number of half full nectar pots

$r_{0.05(2)[12]}=0.532$ $r_{0.05(2)[15]}=0.482$
$r_{0.01(2)[12]}=0.661$ $r_{0.01(2)[15]}=0.606$
$r_{0.001(2)[12]}=0.780$ $r_{0.001(2)[15]}=0.725$

Table A6.9. Percentage of 10 colonies showing significant Pearson correlation coefficients for 6 brood bionomic variables for free foraging colonies 1987.

	Food demand		Foraging force		Food stores	
	Larval area (cm^2)	Number of bees	Max. number of foragers	Max. number of pollen gatherers	Pollen pots	Nectar pots
Larval area (cm^2)	-					
Number of bees	90%	-				
Maximum foragers	70%	80%	-			
Maximum pollen gatherers	50%	90%	80%	-		
Pollen pots	20%	30%	10%	40%	-	
Nectar pots	20%	40%	30%	30%	40%	-

Table A6.10. Correlation coefficient between total daily nectar volume and nectar energy returning in forager honey stomach, for 1 free foraging *B. terrestris* colony (1987), and 6 brood bionomic parameters.

		Food demand		Foraging force		Stores	
		Larval area cm^2	Number of bees	Max. number of foragers	Max. number of nectar gatherers	Pollen pots	Nectar pots
Total daily nectar volume (ul)	No.cases	16	16	16	16	16	16
	r value	-0.220	-0.325	-0.027	-0.022	0.628	0.734
	Probab.	0.206	0.110	0.460	0.468	0.005	0.001
	Signif.	n.s.	n.s.	n.s.	n.s.	**	**
Total daily nectar energy (joules)	r value	-0.206	-0.190	0.097	0.050	0.683	0.654
	Probab.	0.222	0.241	0.360	0.427	0.002	0.003
	Signif.	n.s.	n.s.	n.s.	n.s.	**	**

$r_{0.05(2)[14]}=0.497$
$r_{0.01(2)[14]}=0.623$

Table A6.11. Brood bionomic and developmental parameters at time of switch to male production by foundress queen for free foraging colonies reared in observation hives (1987). Ranked from highest to lowest P.I.

Colony number	8*	9*	4	5	3	2*	6	10	1	7*
P.I.	326	239	178	174	171	164	164	128	119	119
Date of switch to males	3-15	4-6	7-9	16-18	7-9	16-18	12-14	27-29	16-18	16-18
Month	Oct.	Oct.	Oct.	Oct.	Oct.	Oct.	Oct.	Sep.	Oct.	Oct.
Days from colony inception to male production	50-52	48-50	36-38	59-61	46-48	57-59	48-50	36-38	57-59	58-60
Live workers	18-20	13-14	13-14	18-20	18-19	11-12	13-16	13-16	20-22	18
Larval area (cm^2)	5.2-7.5	4.5-6.5	10.5-11.7	4.5	10.5-10.7	0.5	5.0-5.5	5.0-7.0	9.0-9.5	5.0-6.1
Worker:larval area ratio	2.7-3.5:1	2.2-2.9:1	1.2:1	4.0-4.4:1	1.7-1.8:1	22.0-24:1	2.6-2.9:1	2.3-2.6:1	2.2-2.3:1	3.0-3.6:1

* = requeened colony

Table A6.12. Equation calculated to predict pollen intake for free foraging colonies from indoor pollen consumption using larval area. The equation was not suitable for prediction because of the large difference between free foraging and indoor pollen consumption.

formula: $y = (e^{(1.085 \times \ln(x + 1) - 0.53)}) - 1$

where: y= pollen dry weight intake (g/week)
x= mean weekly larval area (cm^2)

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