COMPARATIVE SEASONALITY AND DIETS OF GERMAN (*Vespula germanica*) AND COMMON (*V. vulgaris*) WASP COLONIES IN MANAWATU, NEW ZEALAND

A thesis presented in partial
fulfilment of the requirements
for the degree of Master of
Science in Zoology at Massey
University

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1995

FRONTISPIECE: An overwintering German wasp nest found near Bulls on March 2 1994. Extracted on March 24 1994, the nest contained an estimated 570,500 worker/male cells and 32,500 queen cells (R. J. Harris, pers. comm.).

ABSTRACT

German wasp (*Vespula germanica*) and common wasp (*V. vulgaris*) colonies were studied in urban and rural habitats in Manawatu, from January to August 1993. Relative abundance of colonies, nest site preferences, colony dynamics, phenology and diet are described. Data quantifying vespulid wasp nest abundance in Manawatu between 1991-1994 were sourced from pest control companies and the Manawatu-Wanganui Regional Council. These data were compared with rainfall records for the same period.

Over 75% of nests examined in urban and rural Manawatu were built by common wasps. This trend persisted through the season with German wasps accounting for no more than 28% of nests reported in any one month. Most reports of wasps were made in January, with February and March also being high. Heavy rainfall in spring appeared to promote colony formation in the following year. Continued high rainfall between January-June, especially over 600 mm appeared, however, to suppress colonies during this time. Nest drowning is a possible reason for this. Different nest site preferences between the two species were evident in urban and rural habitats. Over half of all urban common wasp nests and a third of urban German wasp nests reported were in sites associated with buildings. Nests in such sites grow faster and larger than those in other sites. In contrast, all rural German wasp nests and 85% of rural common wasp nests were built in the ground. The invasion of Manawatu by common wasps does not appear to have modified the nest site preferences of German wasps.

Seasonal traffic rates for both species were similar, with colonies peaking in late March. Common wasp traffic rates were significantly higher in January-February, probably because of earlier nest initiations. Prior to queen production common wasp colonies were most active in the early afternoon. Around the time of queen production early evening activity increased, possibly as a result of the seasonal decrease in day length. Nests with high numbers of worker/male cells built before male production began produced significantly more queens than those with fewer cells. Although similar in size to German wasp nests, common wasp nests contained more queen cells.

Cell weights differed between the castes and species. German wasp nests therefore required more than twice as much effort to build as a common wasp nest of a similar size. The possible competitive effects of such differences are discussed.

Manawatu German wasp colonies appear to produce males earlier (early February) than common wasp colonies (early March). The reverse applies to queen production which may have started earlier (March 12) in common wasp colonies than in German wasp colonies (March 20). However, variation within and between the species does occur. The egg laying ability of the founder queen appears to limit oviposition in worker/male cells but the availability of empty queen cells appears to limit oviposition in queen cells. The size of the worker force limits the number of larvae that can be cared for. Reproductives were seen leaving nests from early May and continued until the colonies died. In an overwintering German wasp nest production of all three castes were at levels equivalent to an annual nest at peak.

German wasp foragers returned with a higher percentage of protein items (16%) than common wasp foragers (11%). Similar percentages of woodpulp were returned to colonies by both species. Diptera, Lepidoptera, Araneae, and Hemiptera were the main animal prey returned to urban and rural colonies. German wasp foragers returned with prey items that were significantly heavier than those carried by common wasps but woodpulp weight did not differ. However, common wasp colonies killed more invertebrates to meet their needs, suggesting that they represent a substantial threat to invertebrate communities. Both prey provision and woodpulp foraging increased dramatically with the onset of queen rearing, indicating the increased needs of colonies at this time. The ecological significance of woodpulp foraging on both species is discussed.

Key areas for future wasp research that are applicable within Manawatu and more widely in New Zealand, are outlined. Main areas needing investigation concern aspects of colony dynamics and phenology.

ACKNOWLEDGMENTS

To be thanked first and foremost are my supervisors, Dr Robin Fordham and Dr Murray Potter (Department of Ecology, Massey University); it was their constant enthusiasm for my topic, their helpful advice, and many hours of patiently wading through my draft manuscripts that have finally produced this thesis as it stands now. However, any errors of fact or significant misinterpretation are mine and mine alone.

There were many people in Palmerston North and elsewhere that provided me with wasp nest locations, but special thanks goes to Mr George Robinson of the Manawatu-Wanganui Regional Council, as well as the numerous pest control services around Manawatu; without their input this project would never have gotten off the ground. Dr Dave Leathwick of AgResearch (Flock House) also provided me with many nests and I appreciate the mind flow that came from the frequent wasp-related discussions we had.

My diet study would also never have eventuated without the generosity of Mrs Brady, Ms Janssen, and Mr and Mrs Ward, who allowed the wasp nests on their properties to continue while I sampled them through the season. Special mention must be made of Mr and Mrs Ward who, in the name of science, went as far as allowing me to attach the diet trap fixture to their house!

Dr Richard Harris of Manaaki Whenua Landcare (Lincoln) provided me with the necessary diet trap equipment and relevant literature when it came time to write up. Dr Kay Clapperton (Havelock North) and Dr Henrik Moller (Department of Zoology, Otago University) provided thoughtful comments during the formative stages of my research. Ms Helen Dick of AgResearch (Grasslands) and Dr Murray Potter also freely gave their time when I required statistical advice. Thanks also goes to Mr Paul Barrett (Department of Ecology, Massey University) who helped me to dig up 12 wasp nests in Apiti in one day, some of which were still alive!

Finally, I wish to express my deepest thanks to my wife, Rosalind, and my son, Jamie, who gave me the time and encouragement to continue until this project was completed.

The path was not always easy and it is to their understanding that I am indebted. I would therefore like to dedicate this thesis to them.

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Chapter 1 INTRODUCTION

1.1 Wasps worldwide

1.1.1 Early records

The wasp has featured in human affairs since at least the beginning of recorded human history. One of the earliest references to wasps is found in the Bible, where some 4000 years ago Hebrew writers recorded their aggressive nature (Holy Bible: *Exodus 23 v 28*). The death of Menes, the first Pharoah of Egypt, has been attributed to a sting from a wasp, and the Greek scientist Aristotle recorded very detailed observations of the biology of wasps during 300 BC (Spradbery 1973). Many other naturalists have contributed throughout the Anno Domini era, however, only in the last 30 years have significant advances in understanding the ecology of wasps been made.

Edwards (1980) counted more than 340 scientific publications dealing with wasps between 1973-1977, and calculated that this was around 12% of that written over the previous 300 years. In New Zealand, this situation is even more pronounced. During the 32 years between 1952 and 1983, only 12 scientific papers were published on wasps, but from 1984 to 1994 wasp literature from New Zealand research has grown by a further 53 papers, a rise of almost 1300%! This extraordinary increase reflects ecologists' concerns about the impact of social wasps on New Zealand's native biota.

1.1.2 Classification and distribution

Wasps are placed in the superfamily Vespoidea within the large Order Hymenoptera, which also contains the superfamilies of bees, ants and termites. The Vespoidea contains both social and solitary wasps, which are spread across three families, the Eumenidae, Vespidae and Masaridae (Fig. 1). True social wasps are found only in the Vespidae, within three subfamilies, the Polistinae, Vespinae and Stenogastrinae (Fig. 1). Although thousands of species of vespoid wasps have been described, only around 800 are considered social or sub-social (Spradbery 1973).

'Social' or eusocial wasps (Wilson 1971) meet three criteria (1) Care of the young is undertaken cooperatively by the adult insects. (2) Reproductive division of labour occurs, with the reproductive individual(s) being helped by the sterile members. (3) Colony labour is contributed by two or more coexistent adult generations.

The Vespinae, which contain the wasps central to this study, is split between four genera, the *Dolichovespula*, *Provespa*, *Vespula* and *Vespa* (Fig. 1). Vespine wasps differ in size, colouration, nest sites, colony size and diet, and these can differ at both the genus and species level. One illustration of this is the size (length) difference between two wasp species found in Japan. *Vespa mandarinia* queens, for example, measure between 40-45 mm but *Vespula vulgaris* queens are only half as long at 17-18 mm (Matsuura 1990).

In the early 1970s between 50-60 vespid species were described worldwide (Spradbery 1973). By 1990 this had risen to 74, of which 18 new species and subspecies were described in the 8 years between 1983-1990 (Matsuura 1990). The most diverse wasp group is the *Vespa*, but the wasp groups with the widest distribution are the *Dolichovespula* and *Vespula* (Table 1). The genus *Vespula* contains the two species considered in this thesis; the German wasp *Vespula germanica* and the common wasp *V. vulgaris*.

1.2 The genus *Vespula* in New Zealand

German and common wasps are the representative species of vespulid wasps in New Zealand. Two other species of social wasp are established in New Zealand, the Australian paper wasp (*Polistes humilis*) and the Asian paper wasp (*P. chinensis*) (Clapperton et al. 1989), but these belong to the subfamily Polistinae (Fig. 1) and are not considered hereafter.

1.2.1 Common wasps

The first report of vespulid wasps in New Zealand occurred in March 1921 when one common wasp queen was caught in the Wairarapa, but it appears this particular introduction failed to establish since individuals of this species were not seen again until April 1945 in Auckland (Thomas 1960; Donovan 1984). It is thought the 1945 invasion of common wasps was also not sustained because specimens were not observed again until 1982 in Dunedin (Donovan 1983). By 1983 they were also found in Christchurch, Nelson, Auckland, and Wellington, possibly being established in Wellington as early as 1978 (Donovan 1984). By 1987, it was well established in the North Island, around Auckland and areas of the lower North Island, and in the South Island it was found in the Nelson-Marlborough, Canterbury and Otago regions, with the southern most observation being in Invercargill (Clapperton et al. 1989). A resurvey between 1987 and 1991 revealed that the common wasp had increased its distribution throughout the lower and central North Island, and throughout the north-western and southern coasts of the South Island (Clapperton et al. 1994).

1.2.2 German wasps

Also in April 1945, seven German wasp nests were discovered in Hamilton, and it is considered

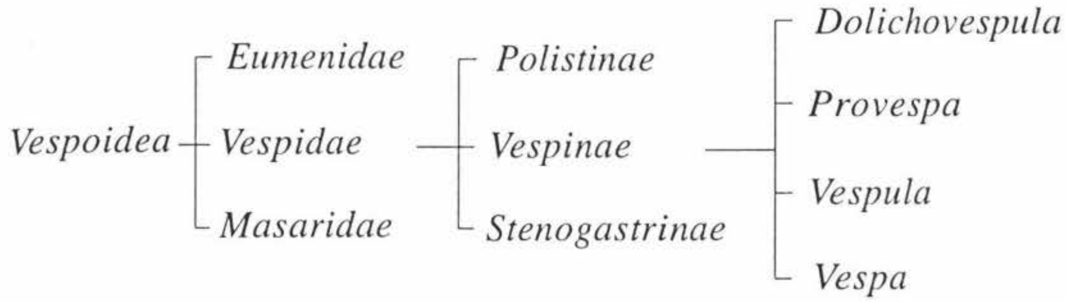

Figure 1 Classification of wasps (Hymenoptera) worldwide: only the connections between the family Vespidae and subfamily Vespinae are detailed because they specifically concern the wasps of this study.

Table 1 Classification of vespine wasps, species components of their respective genera, and worldwide distribution by 1990. Data sourced from Matsuura (1990).

Genera	subgenera	species	subspecies	Distribution
Dolichovespula	3	21	19	Inhabits most of Northern Hemisphere, including North America and most of Asia. Not naturally found in Southern Hemisphere.
Provespa	-	3	-	Confined to Southeast Asia.
Vespula	4	27	11	Same as *Dolichovespula*; introduced to Southern Hemisphere (South Africa, Australia, New Zealand, Chile, Hawaii, Ascension Islands).
Vespa	2	23	81	Inhabits Eastern Asia, New Guinea, and the Philippines. Two species extend across Eurasia.

that from this introduction this species became established (Thomas 1960). By 1951 they had colonised as far north as Whangarei and as far south as Palmerston North (Thomas 1960), and within 10 years they had reached the South Island and some offshore islands (Fordham 1961, 1962). By 1987 their distribution included most areas of both the North and South Islands, as well as Stewart Island (Clapperton et al. 1989), but they had not extended their range any further by 1991 (Clapperton et al. 1994).

1.3 Factors contributing to the successful invasion of New Zealand by vespulid wasps

All social insects, but particularly wasps, exhibit features which make them successful invaders. Aspects of their life cycle and certain behaviours allow them to readily colonise and establish in new territories. Such characteristics have led to the successful invasion and establishment of social wasps in New Zealand. A list of the most salient traits sourced from Townsend (1991) and Moller (in press) are summarised below.

(1) Wasps have very effective dispersal behaviours; unwitting human assistance given to queens hibernating in cargo or in vehicles introduces wasps into new regions and countries (Thomas 1960; Crosland 1991; Horwood et al. 1993). The strong flying ability of queens also allows rapid movement into new areas (Moller et al. 1990).

(2) Wasp queens have high reproductive rates; it is argued that invasion success is positively correlated with intrinsic growth rate of the invading species (Pimm 1989). One fertilised queen can produce hundreds of new queens, all potentially able to produce founding nests themselves. The nature of reproduction in social wasps also enhances their invasive abilities; queens inseminated in one region do not require males to be transported with them in order to reproduce in another.

(3) Wasp colonies maintain the nest environment at a level which enhances survival and growth rates; regardless of the time of day or ambient temperature, wasps regulate their nest temperature at around 30°C (Spradbery 1973; P. L. Godfrey, unpub. data).

(4) Wasp foragers are very efficient at gathering food; the broad diet of larval and adult wasps allow them to exploit most habitats and meet the demands of the colony.

(5) Wasps display effective predator defence behaviour; constructing nests in building cavities or in underground sites provides good protection from predators. If the colony is disturbed, venomous stings act as a potent deterrent to further agitation.

New Zealand habitats appear to ease the establishment of German and common wasps. Hibernating queens transported from overseas were introduced without any of the nest parasites, predators, or pathogens found in their donor country (Moller in press), and no New Zealand habitat contained similar malentities so colonisation has proceeded largely unhindered. Even with the introduction of a parasitoid of vespulid wasps (*Sphecophaga vesparum vesparum* (Curtis)) there has been little impact on wasp densities in New Zealand (Beggs et al. in prep.). Climate is considered to be the most frequent cause of failure of attempts by invading species to establish in a new area (Crawley 1986). The climate in New Zealand not only allows social wasps to survive, but has enhanced German wasp establishment by inducing a small proportion of German wasp colonies to overwinter (Thomas 1960; Plunkett et al. 1989). Much of New Zealand is suitable habitat for social wasps; worker wasps have been observed foraging in sub-alpine habitats (Beggs 1991; Fordham 1991). An abundance of food and an unfilled niche in the honeydew beech forest of the South Island have catered to the primary needs of both German and common wasps. The establishment of wasp colonies over a wide area in New Zealand indicates a lack of 'biotic resistance' to wasp invasion in most habitats (Simberloff 1986). Interestingly, however, the displacement of German wasps from honeydew beech forests in the South Island has been brought about by a 'biotic resistance' established when the common wasp invaded this habitat. Direct exploitation competition between German and common wasps for the limited honeydew resource has favoured the more efficient gathering ability of common wasps (Harris et al. 1994).

While the features mentioned above are all relevant to the wasps' successful invasion of New Zealand, chance and timing also play an important part in the success of any invasion (Crawley 1989). Upon the arrival of the queens, conditions have to be suitable for establishment, with the phenology of the invader synchronising with the habitat and its resources (Crawley 1989). Only then can the queen found her nest and begin to establish the Minimum Viable Beachhead Population (Moller in press). Records of failed introductions of German and common wasps suggest that time and chance may have played a role in deferring their establishment. The size of the initial inoculation may also have counted against their first efforts to invade. Often, the larger the inoculation the greater the chance of establishment, with repeated immigrations further increasing that probability of success (Simberloff 1989). It was probably a combination of the above factors that tipped the balance in favour of the German wasp invasion during the 1940s and the common wasp invasion during the 1970s.

1.4 Previous wasp research in New Zealand

The first documented research on vespulid wasps in New Zealand occurred between 1949 and 1952, when DSIR scientists undertook a general study of the ecology of the German wasp in the Waikato region (Thomas 1960). While describing the life history and phenology particular to this area, they also provided details of nest characteristics, the phenomenon of overwintering colonies, and results from various methods of control. The report of this three year study is invaluable since, at the time, it was the only work of its kind in the Southern Hemisphere, and it documented the ability of German wasps to invade new habitats.

Thomas (1960) assessed various methods of wasp control. Physical destruction of both hibernating and spring queens proved fruitless, as did attractant traps, but chemical control of wasps showed some success. Direct application of insecticides to nests and poison baits laid out for foragers were tested, the former being the most effective (Thomas 1960). Unfortunately, this method requires finding the nest, which is labour intensive and impossible in some terrain. Poisoned baits can be useful in such circumstances since foragers carry the poisoned material back to the nest, and this often results in the colony's death. Chemical control, however, has its limitations: for poison baits to be effective an uneconomic number of bait stations are required (Thomas 1960); pesticides once used in the past have either been banned (DDT, Mirex) (Perrott 1975) or are now moving out of public favour (eg. compound 1080) (Spurr 1991); and baits which are most acceptable to wasps lose their attractiveness within 2-3 days (Spurr 1991). As a result these options remain secondary weapons in the control of wasps.

The suggestion of biocontrol was raised soon after the arrival of the German wasp, and six potential agents were mentioned by Thomas (1960). A solitary-living ichneumonid wasp *Sphecophaga v. burra* (Cresson), was put forward as the most likely candidate, because it was known only to parasitise vespid wasps. A program of research beginning in 1985 saw the first release of a sibling subspecies *S. vesparum vesparum* (Curtis) (Donovan & Read 1987), and by 1990 a small population of the parasitoid was considered to have established at Pelorus Bridge near Nelson, and in Christchurch (Moller et al. 1991; Beggs et al. in prep.). Unfortunately to date, it continues to have little effect on the surrounding wasp population (D. M. Leathwick, pers. comm.).

While this research on wasp biocontrol was in progress, ecologists were also studying the impact of the two species on the honeydew beech forest ecosystem of the north-western South Island. Common wasps arrived there between 1984 and 1985 (Harris 1991), increasing the absolute number of wasps 2- to 6- fold in this habitat (Sandlant & Moller 1989). Within four years, however, they had displaced German wasps from this habitat but the high densities continued and concerns about their impact on endemic insects, and nectivorous and insectivorous birds remained (Beggs & Wilson 1991; Moller et al. 1988; Harris 1991).

A diet study of wasp colonies in the honeydew habitat quantified how much invertebrate protein and honeydew was being consumed, and confirmed the threat they posed to the local native fauna (Harris 1991). This study also revealed differences in the type of prey items returned to colonies of either species, suggesting that the insect orders specifically preyed upon by common wasps may be more vulnerable to depletion. Only one other comprehensive diet study has been made in a scrubland-pasture habitat near Hamilton (Harris & Oliver 1993).

The range of nest sites selected by German and common wasps has been studied in New Zealand habitats (Thomas 1960; Fordham et al. 1991; Moller et al. 1991b; Donovan et al. 1992), and the similarity between the two species suggests that there could be competition between spring queens for nest sites. Demographic differences between urban and rural German wasp nests have been described (Fordham et al. 1991) and some nest sites in particular have been recorded as producing larger nests than other sites (Moller et al. 1991b).

Studies of the phenology of vespulid wasps in Hamilton, Manawatu, and Nelson have been made (Thomas 1960; Fordham et al. 1991; Moller et al. 1991a), revealing that subtle differences between localities do occur. However, only the Nelson study was recent enough to examine the comparative phenology of both species in a single region. It has been shown, both within and among the two species, that variations in their phenological events do occur. It has been suggested that habitat may influence the phenology of wasp colonies (Fordham et al. 1991), but there are still too few data for solid conclusions to be made.

1.5 Aims of this study

The overall aim of this study was to investigate the comparative seasonality, abundance, and diets of vespulid wasp colonies in urban and rural Manawatu. It was hoped to determine whether or not the recent arrival of the common wasp in Manawatu was having an ecological effect on the resident German wasp. Determining any competitive differences in the ecology of the two wasp species could suggest areas for further investigation into why displacement of the German wasp in honeydew beech forests has occurred . This study had four main objectives:

1. The first objective was to determine the relative abundance and nest site preferences of German and common wasps in Manawatu. Where possible, comparisons between urban and rural habitats were to be made. The influence of nest sites on colony development were also to be determined.
2. The second objective was to examine aspects of colony dynamics in German and common wasp colonies in Manawatu. Where possible comparisons between urban and rural habitats were to be

made. Particular areas to be investigated were their traffic rates, nest sizes, and nest building efficiencies, in order to determine how they affect queen production.

3. The third objective was to describe the comparative phenology of German and common wasp colonies in Manawatu. Special attention was to be given to describing the appearance of the reproductive castes and composition of the life stages through the season. Where possible comparisons between urban and rural habitats were to be made.

4. The fourth objective was to determine the diet and foraging ecology of German and common wasp colonies in Manawatu. Where possible comparisons between urban and rural habitats were to be made.

Chapter 2 THE STUDY AREA

2.1 The Manawatu Region

The Manawatu region borders 19 km of the southern west coast of the North Island, and involves an area of about 105 200 ha (Esler 1978). The region is bordered on the west by the Tasman Sea and to the east by the northern extension of the Tararua Range. The lower reaches of the Rangitikei and Manawatu Rivers geographically define the northern and southern boundaries near the coast (Esler 1978). Major settlements in this area include Bulls, Feilding, Ashhurst and Palmerston North (Burgess 1988). It is within this sprawling urban area that the majority of wasp nests were encountered.

Sand country predominates on the west coast of this region, comprising dunes, sand plains and swamps (Manawatu-Wanganui Regional Council 1993). The soils are free-draining but prone to erosion. Much of the dune system has been stabilised with the introduced marram grass (*Ammophila arenaria*) and tree lupin (*Lupinus arboreus*), and protection forestry using pines (*Pinus radiata*) (Manawatu-Wanganui Regional Council 1993).

Inland almost a half of Manawatu lowlands consist of river terraces built by the three main rivers of this region, the Rangitikei, Manawatu, and Oroua (Esler 1978). These extensive terraces reflect the dynamics of the actively rising landscape and downcutting action of these rivers (Heerdegan 1987). The highly fertile alluvial plains support intensive sheep and cattle farming, as well as cereal cropping, horticulture, and vegetable cash crops (Saunders 1987).

2.2 Soils

The soils of the Manawatu are grouped broadly under four classifications: (1) yellow-brown sands and organic gley soils on the coast, (2) recent and organic soils on the river flats, (3) yellow-grey earths on the terraces, and (4) yellow-brown soils on the greywacke hills (Esler 1978). The soils of the river terraces were principally formed from wind blown or volcanic loess; they are fairly acid and poorly drained. Where a high water table exists through this landform, a heavy gley soil occurs which has particularly bad drainage (Manawatu-Wanganui Regional Council 1993).

2.3 Climate

The Manawatu region is characterised by a windy climate, boasting moderate temperatures, rainfall and sunshine. The predominant wind flow is between west-northwest and southwest, the winds often becoming strongest in spring and early summer (Burgess 1988). Winds in these directions occur on nearly half of the 320 wind days at Palmerston North each year. Gusts exceeding 64 km per hour are often recorded on 4-8 days per month throughout the course of the year (Burgess 1988).

Rainfall is well distributed throughout the year, with an average of 173 rain days per year at Palmerston North. Rainfall is highest in the hills and declines towards the coast, averaging around 2000 mm on the Tararua Range, 1000 mm at Palmerston North, and 750 mm on the coast (Burgess 1988, NZ Yearbook 1994).

The Manawatu region is fairly cloudy, with an annual average of only 1814 sunshine hours at Palmerston North. The Tararua Range receives about 1400 sunshine hours and the coast over 2000 sunshine hours annually (Burgess 1988, NZ Yearbook 1994).

Air temperatures in Manawatu are warmest in January and February, with a mean of around 16.6°C, though temperatures over 25°C are frequent during these months (Burgess 1988). The annual range in mean temperatures from summer to winter is about 9-10°C, with the mean temperature in June being 8.1°C (Burgess 1988). Ground frosts are common during this period, but can occur between March and November. Sixty to seventy percent of these are slight (-1.0°C to -2.9°C) (Burgess 1988).

Chapter 3 THE DIET STUDY

3.1 The Diet Trap

To analyse the diet of German and common wasps (Chapter 7), a diet trap fixture was placed over the entrance of each colony chosen for sampling. This was attached during the day, and 4-5 days were allowed for the colony to become accustomed to the new entrance, before sampling commenced. The fixture consisted of a PVC pipe (50 cm length × 10 cm diameter), which was located over the entrance so that all wasps would exit and enter the nest through this pipe (Plate 3.1). Depending on the nest situation, the pipe was supported by various materials (earth, bricks, wood, shelving brackets) and any new entrances formed by the wasps were covered over. The second component of the diet trap was the trap cartridge which was supplied by Richard Harris, Maanaki Whenua Landcare (Lincoln) (Plate 3.1). It consisted of a 1.5 litre softdrink bottle with its base removed and had a funnel with an inner aperture of 15 mm inserted into the bottle. The funnel was joined to a threaded attachment that allowed it to be unscrewed from the bottle, so that the contents of the bottle could be recovered. Around the outer circumference of the cartridge was a 1 cm layer of foam seal (available from Pararubber NZ Ltd), which held the bottle tight in the pipe for the specified sampling time. At the end of the sample the cartridge was removed, the wasps inside gassed, and their foods collected (Plate 3.2)

3.2 Diet trap localities

3.2.1 36 Limbrick Street, Palmerston North.

This urban common wasp nest was first sampled on February 19 1993, and was situated in the front garden of a house in Palmerston North (Plate 3.3). A subterranean nest, it was built under a hedge bordering the property and behind a flower garden. The entrance faced north-west.

3.2.2 44 Morris Street, Palmerston North.

This common wasp nest was also found in urban Palmerston North, but was located between the inner and outer walls of a house (Plate 3.4). It was first sampled on February 26 1993. The nest entrance consisted of a 0.5 cm wide × 15 cm long gap in

PLATE 3.1 THE DIET TRAP AND FIXTURE

An empty diet trap cartridge stands next to the trap fixture attached to the urban German wasp nest. To sample the colony the bottle neck end of the cartridge was into the pipe first and jammed in for the specified time. Note the foam strip around bottom of the bottle's exterior designed to prevent wasps by-passing the container. The PVC pipe was supported by the beer crate underneath and soil and rubble elsewhere.

PLATE 3.2 DIET SAMPLING IN PROGRESS

At the conclusion of the sampling time the cartridge was removed and the wasps in were gassed with CO_2. The wasps and the foraged items were tipped onto a tray fo counting and sorting. Fresh prey items were put into sealed vials and taken back t lab for weighing and identification.

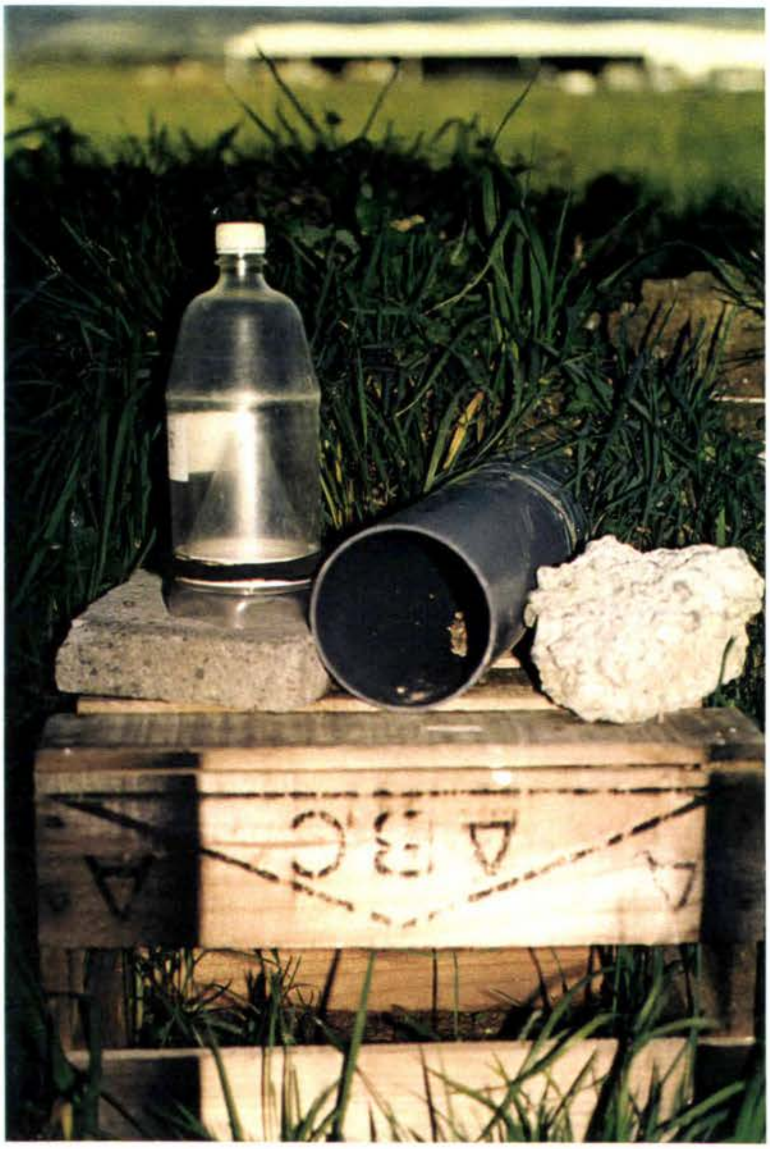

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PLATE 3.3 36 LIMBRICK STREET, PALMERSTON NORTH

This subterranean common wasp nest was found under a hedge in an ornamental garden in suburban Palmerston North. This photo was taken prior to the attachmen the diet trap on 14 February 1993. Note the two distinct pathways of wasps enterin and exiting the nest, and the chewed leaf lying across the entrance that formerly blocked the passageway.

PLATE 3.4 44 MORRIS STREET, PALMERSTON NORTH

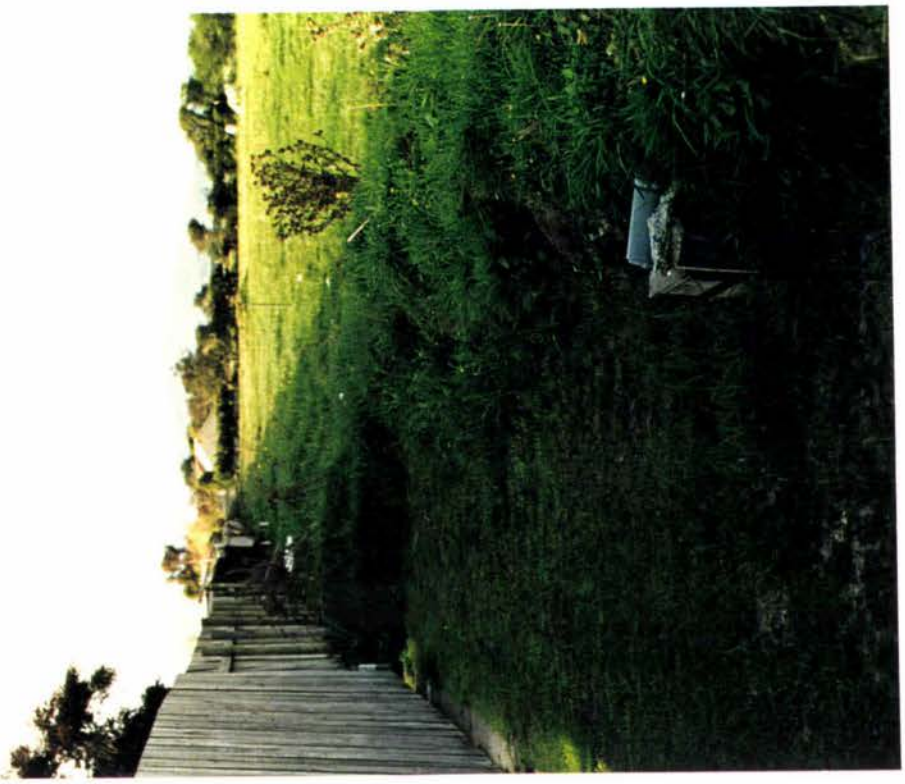
This common wasp nest was built in the cavity between the inner and outer walls o house in Morris St, Palmerston North. The backyard of this house was never mow with long grass covering the whole rear section. Note the polyfiller used to plug th gaps in between the planks where the wasps originally exited.

PLATE 3.5 38 ACACIA STREET, PALMERSTON NORTH

This urban German wasp nest was built in an embankment adjoining a wasteland are used for grazing cattle. The fences to the left of the picture demarcate the beginning the extensive Kelvin Grove residential area.

PLATE 3.6 RING ROAD, MASSEY UNIVERSITY

This rural common wasp nest was situated in an area containing both native and exo plant cover, but was built in the exposed root system of a fallen willow tree (*Salix* spp.). Part of the nest envelope is visible to the lower right of the trap fixture (4 o'clock) where the earth fell away after a rain storm. This opening was blocked after this photograph was taken.



the weatherboards, on the north-facing rear wall of the house. However, all but 5 cm of this entrance was plugged with Selleys 'No More Gaps' and the diet trap was fixed over the remaining gap. The backyard of this house was unkempt, with knee-length grass being the predominant ground cover.

3.2.3 38 Acacia Street, Palmerston North.

This German wasp nest was located in an artificial embankment bordering an urban property and a wasteland used for grazing cattle (Plate 3.5). It was first sampled on March 31 1993 and had a west facing entrance.

3.2.4 Ring Road, Massy University, Palmerston North.

The only rural nest in this diet study was a common wasp nest located 20m north-west of the Massey University boiler house, in a wooded area above the Ring Road (Plate 3.6). Built in the earth surrounding the root mass of a fallen willow tree (*Salix* spp.), it had a double entrance, the largest one facing south and a smaller one facing north. Sampling commenced on March 30 1993, after the north entrance was blocked.

Chapter 4 SPECIES ABUNDANCE AND NEST SITE PREFERENCE

4.1 INTRODUCTION

The German wasp *Vespula germanica* (Fab.) was accidentally introduced to New Zealand in 1944 and within 7 years had become established in Manawatu (Thomas 1960). Common wasps *V. vulgaris* (Lin.) are a more recent introduction, invading both the North and South Islands soon after their arrival in the late 1970s (Donovan 1984; Clapperton et al. 1989b; Donovan et al. 1992), and establishing in Manawatu by the mid-1980s (Fordham et al. 1991).

Fordham et al. (1991) studied Manawatu German wasps in the absence of common wasps over a 20 year period, providing data from a situation that may not be repeated again in New Zealand. Using this research as a foundation, my study was initiated to investigate ecological effects on German wasps that may be attributable to the recently arrived common wasps. Research elsewhere (Sandlant & Moller 1989; Harris et al. 1991; Clapperton et al. 1994; Harris et al. 1994) has shown that in the face of competition from common wasps, German wasps have become displaced in honeydew beech forests of the north-western South Island. This chapter examines the hypothesis of species replacement in Manawatu wasp populations, and describes the relative abundance of both vespulid species in rural and urban habitats.

Previous studies (Fordham et al. 1991; Moller et al. 1991b; Donovan et al. 1992) have described the sites in which vespulid wasps build their nests. Here nest site selection by the two species in Manawatu are compared to provide information on an area of potential resource demand overlap. The effects of monthly rainfall and nest site selection on colony development are discussed.

4.2 METHODS

Vespula wasp nests were located in Manawatu between January and August 1993. This was achieved through contact with pest control services, the Manawatu-Wanganui Regional Council and members of the public. The pest control companies involved were Kiwi Pest Control Ltd, Boracure Pest Control Ltd, Premier Pest Control Ltd, JAE Pest Control Services, and A Real Pest Control Ltd. Records from the same pest control companies and the Manawatu-Wanganui Regional Council were later surveyed, to determine the number of wasp nests eradicated in urban Manawatu between 1991-1994. To determine the possible relationship between seasonal rainfall and wasp nest abundance, rainfall data for 1990-1994 was obtained from the Department of Geography, Massey University (R. G. Heerdegen), and correlation analyses were undertaken.

For each nest the 'traffic rate' (average number of wasps leaving and returning to the nest in 10 1-min intervals) was recorded. Since the traffic rate is an accurate index of the number of workers in a colony (Malham et al. 1991), it gives an indication of the colony's size and activity. Between February and April, traffic rates for colonies occupying different nest sites were compared to measure the effect nest site location has on colony development. The species of each colony was determined by hand-netting exiting foragers and identifying them following Clapperton et al. (1989a). Nest sites were ascribed to a list modified from Moller et al. (1991b): above ground (eg. in trees or in rotten tree stumps); subterranean; under building; within wall of building; under roof or eaves of building.

To investigate the effect habitat may have on nest site preference, nest sites were classified under two categories: (i) Urban and (ii) Rural. Nest habitat was classed as urban if over 75% of the area of a circle with radius 300m from the nest contained land devoted to urban habitation. Nests were considered rural if 75% of a similar area contained land given to rural use (eg. farms). The radius of 300m was chosen because it covers the average distance *V. germanica* queens may fly when searching for a suitable nest site (Thomas 1960; Edwards 1980).

Chi-square analyses were used to compare the overall abundance of each species, their seasonal abundance, and their nest site selection. Student's *t*-test was used to compare the two species mean traffic rates.

4.3 RESULTS

4.3.1 Species abundance

Between January and August 1993 87 *Vespula* wasp nests were identified and examined (Table 4.1). Sixty five were found within the Palmerston North City boundary: The remaining 22 were found in rural Manawatu. Twelve of these were found in one day during a Regional Council wasp eradication program in Apiti. The other 10 sites were in Ashhurst, Pohangina, and Bulls. Fifty five nests were from urban areas, while 32 nests were designated rural. The majority (75.8%) of the nests in rural and urban habitats were common wasps (Table 4.1).

The survey of Manawatu pest control companies and the Manawatu-Wanganui Regional Council provided data on total wasp nest abundance during the years of 1991-1994 (Table 4.2). Between 1991 and 1993, the total number of recorded wasp nests destroyed in urban Manawatu rose from 445 nests to 684 nests, an increase of 54%, with the biggest increase occurring in 1993.

Table 4.1 Common and German wasp nests in urban and rural habitats in Manawatu and outlying areas in 1993.

Species	*n*	% Total nests	*n*	% rural	*n*	% urban
V. vulgaris	66	75.8	23	71.9	43	78.2
V. germanica	21	24.2	9	28.1	12	21.8

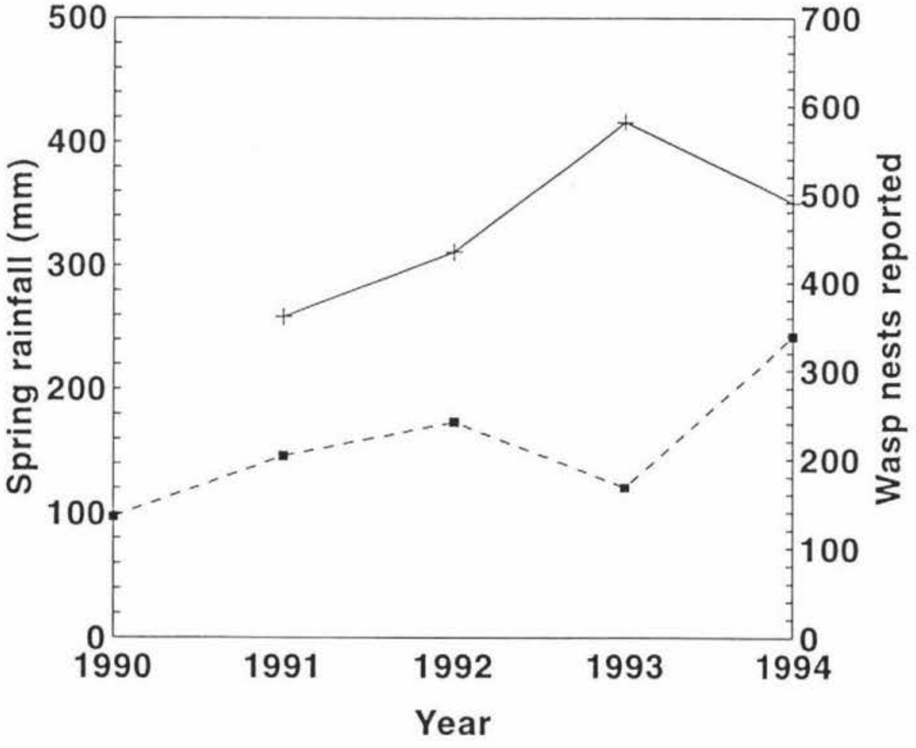


Figure 4.1 Total spring rainfall (September-October) during 1990-1993 and the number of *Vespula* spp. wasp nests destroyed in Manawatu during January-June 1991-1994. + = wasp nests; ■ = rainfall.

Table 4.2 Number of *Vespula* spp. wasp nests destroyed in Manawatu, over 10 day intervals between 1991-1994. Nests were destroyed by pest control companies and the Manawatu-Wanganui Regional Council. * denotes data not available.

		1991	1992	1993	1994	Total mean (±1SE)
January	1-10	26	38	31	28	30.8±2.6
	11-21	35	42	48	47	43.0±3.0
	22-31	46	60	54	50	52.5±3.0
February	1-10	48	28	54	50	45.0±5.8
	11-21	32	53	48	35	42.0±5.0
	22-31	33	22	31	42	32.0±4.1
March	1-10	36	41	58	44	44.8±4.7
	11-21	36	33	55	38	40.5±4.9
	22-31	19	29	48	51	36.8±7.7
April	1-10	22	16	30	30	24.5±3.4
	11-21	19	18	39	26	25.5±4.8
	22-31	3	18	21	18	15.0±4.1
May	1-10	5	12	18	14	12.3±2.7
	11-21	6	5	13	12	9.0±2.0
	22-31	6	6	6	18	9.0±3.0
June	1-10	4	6	10	11	7.8±1.7
	11-21	2	3	6	10	5.3±1.8
	22-31	4	5	11	6	6.5±1.6
July	1-10	2	1	4	1	2.0±0.7
	11-21	-	-	-	2	0.5±0.5
	22-31	-	1	-	-	0.3±0.3
August	1-10	-	-	4	-	1.0±1.0
	11-21	1	-	-	-	0.3±0.3
	22-31	-	-	4	-	1.0±1.0
September	1-10	-	-	1	-	0.3±0.3
	11-21	1	-	5	1	1.8±1.1
	22-31	1	-	2	2	1.3±0.5
October	1-10	-	-	7	*	2.3±2.3
	11-21	2	2	6	*	3.3±1.3
	22-31	-	2	7	*	3.0±2.1
November	1-10	2	3	9	*	4.7±2.2
	11-21	2	5	11	*	6.0±2.6
	22-31	4	4	6	*	4.7±0.7
December	1-10	10	16	10	*	12.0±2.0
	11-21	12	12	14	*	12.7±0.7
	22-31	14	17	13	*	14.7±1.2
Total		445	485	684	534	

For the first nine months of 1994, 534 wasp nests were destroyed: Calculating the mean wasp nests destroyed per ten-day interval for October-December 1991-1993 (Table 4.2: 7±1 wasp nests per 10 day interval) revealed that an extra 54-72 colonies could have been exterminated during this same period in 1994. A total figure for 1994 of between 588-606 nests is a decrease of between 11-14% from 1993. Statistical analysis of monthly data from January-June 1991-1994 revealed significant differences between seasons (Table 4.2: $\chi^2 = 31.59$, df = 15, $P < 0.01$). Analysis of ten-day interval data between January 1-10 and July 1-10 1991-1994 also revealed significant differences between years (Table 4.2: $\chi^2 = 87.19$, df = 54, $P < 0.01$). Total spring rainfall during September-October in 1990-1993 was positively correlated with wasp nest abundance in the following years (January-June 1991-1994) (Fig. 4.1: $r = 0.938$). Between 1991-1994 a tight negative correlation existed between the total monthly rainfall that fell between January-June and the wasp nest abundance of this period (Fig. 4.2: $r = 0.913$).

4.3.2 Seasonal abundance

Wasp nest sightings rose through November and December, increased rapidly into January and maintained a sustained peak until March (Fig. 4.3). Although the highest mean number of wasp nests seen and destroyed occurred in late January (Fig. 4.3: 52.5±3.0), similar high mean levels of more than 40 nests each ten-day interval continued until the end of March. From April onwards the number of nests reported declined continuously although a few nests were discovered through winter (Fig. 4.3).

The subsample of nests seen and identified between January-August 1993 revealed that similar proportions of each species were found in January/February and March/April (Table 4.3). German wasps never comprised more than 28% (11/40) of nests in any one of these months. The German wasp nest found in July was over-wintering (Table 4.3).

4.3.3 Nest sites

All German wasp nests and the majority (87%) of common wasp nests found in rural habitats were in the ground. The remaining nests were associated with buildings (Table 4.4). Ground nest sites dominated for German and common wasps in urban areas, but grouping the three categories associated with buildings (under building; in wall; in roof/eave) together accounts for 56% of the common wasps nests, and 33% of the German wasps nests in urban sites. However no significant difference was found between the relative abundance of either species in urban ground or building associated nests (Table 4.4). No German wasps were found above the ground, or in walls of buildings.

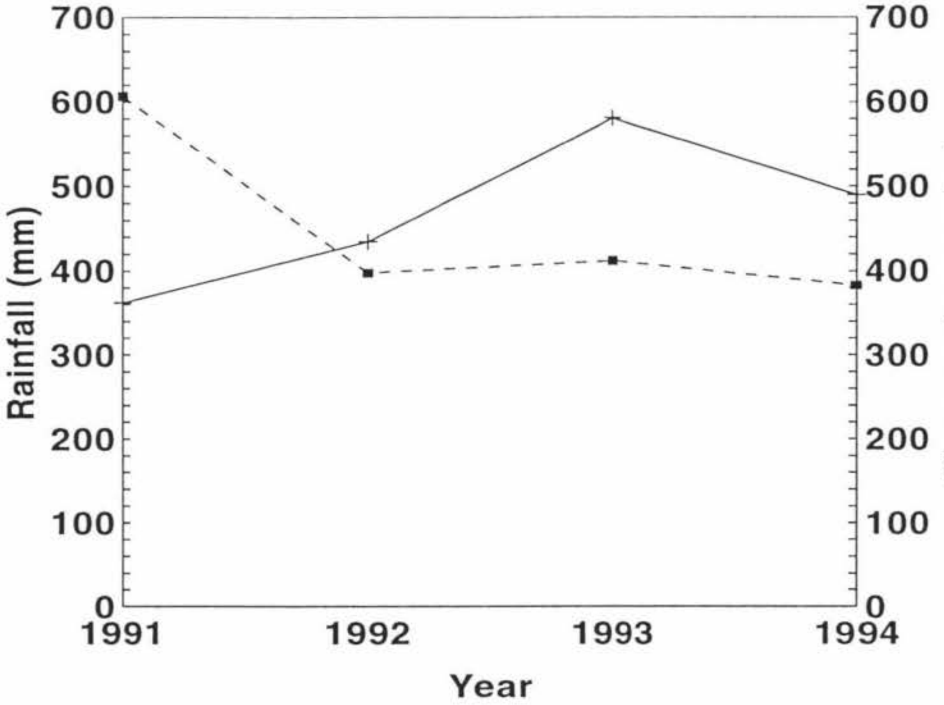


Figure 4.2 Total monthly rainfall and number of *Vespula* spp. wasp nests destroyed in Manawatu during January-June 1991-1994. + = wasp nests; ■ = rainfall.

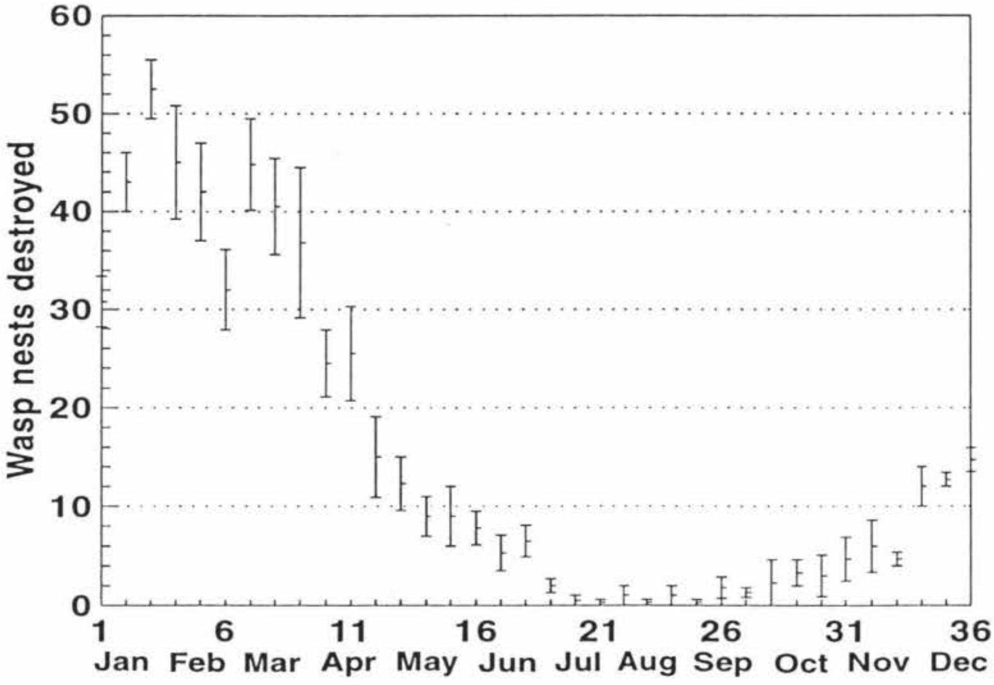


Figure 4.3 Mean number of *Vespula* spp. wasp nests destroyed in Manawatu, over 10 day intervals between 1991-1994. Nests were destroyed by pest control companies and the Manawatu-Wanganui Regional Council. Bars show mean±1SE.

Table 4.3 Number of German and common wasp nests seen each month January-August 1993.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
V.vulgaris	3	19	12	29	2	-	-	1
V.germanica	1	4	2	11	2	-	1	-
Total	4	23	14	40	4	-	1	1

Table 4.4 Nest sites of German (V.g) and common (V.v) wasps in urban, rural and combined habitats in Manawatu 1993.

Habitat	Species	no. of nests	% above ground	% in ground	% under building	% wall of building	% under roof/eave
Urban	V.v	43	2	42	17	9	30
	V.g	12	-	67	8	-	25
Rural	V.v	23	-	87	-	9	4
	V.g	9	-	100	-	-	-
Combined	V.v	66	1	58	11	9	21
	V.g	21	-	81	5	-	14

Table 4.5 Traffic rates (mean±1SE) for German and common wasp nests in different sites during February and March-April 1993. The figure under the traffic rate is the number of nests sampled. No data was available for nests above the ground.

Nest site	February 1-18		March 11-April 11	
	V. vulgaris	*V.germanica*	*V. vulgaris*	*V. germanica*
Ground	26.5±1.6 6	-	40.4±2.7 6	28.9±1.9 3
Roof/eave	45.7±3.3 2	19.5±2.8 3	56.8±3.2 3	-
Under building	26.1±2.8 5	10.2±1.1 1	-	-
Wall of building	55.5±2.2 2	-	32.2±3.5 2	-

4.3.4 Traffic rates

Between 1 February-18 February 1993 common wasp nests recorded the highest mean traffic rates over all nest sites (Table 4.5). No German wasp nests for 'in ground' or 'in wall' nest site comparisons were available in this period. The two highest traffic rates recorded were for common wasp nests associated with buildings (in walls; in roof/eave), although the traffic rates were nearly as high for nests in the ground and under buildings. However, their traffic rates were around half those in the other building sites. German wasp nests followed this trend with roof nests being almost twice as busy as those found under buildings (Table 4.5). When access to the nests under buildings was available (86% of cases), 33% were in the ground and 67% were attached to the walls or floor. A statistical comparison of the mean traffic rates over all sites during this period revealed that the traffic rate for common wasp nests were significantly higher than that for German wasp nests (Table 4.5: $t = 5.59$, df = 56, $P = 0.001$).

Between 11 March - 11 April 1993 common wasp nests continued to have the highest mean traffic rates over all sites (Table 4.5). Only data for German wasp ground nests could be compared for this period because no common wasp nest sites under buildings were available. Common wasp 'roof/eave' nests recorded the highest traffic rate, with ground nests second. German wasp ground nest traffic rates were 28% lower than common wasps in the same situation. During this period, the mean traffic rate for common wasps over all sites remained significantly higher than that of the German wasp (Table 4.5: $t = 5.88$, df = 89, $P = 0.001$).

4.4 DISCUSSION

4.4.1 Data biases

The 87 *Vespula* wasp nests surveyed in Manawatu and outlying region are by no means a complete record of their distribution. The same problems and biases discussed by Moller et al. (1991b) occurred in this study. In particular, members of the public destroyed nests without reporting them and not all nests reported to my various sources were passed on to me. Urban wasp nests in easily found locations, and those deemed a nuisance by the public, are probably over-represented in this sample. Lower public activity in rural areas could have meant that fewer rural nests were reported. Of those that were reported perhaps most were in obvious positions, resulting in a possible over-represention of these nests also.

4.4.2 Species abundance

The relatively recent invasion of common wasps into Manawatu could be having an effect on local German wasp abundance. In a 20 year study of German wasps in Manawatu, Fordham et al.

(1991) encountered their first common wasp nest in 1987. Donovan et al. (1992) encountered their first common wasp nest in Christchurch in January 1984, and suggest that nests may have become established there about four years earlier, however, no reasons for arriving at this conclusion are given. If this analogy is applied to the Manawatu invasion, it could be suggested that the common wasp established there around 1983. If so, the relative abundance of German wasp nests appears to have declined by 75% in around 10 years. Fechney (1989) reported 92% (56/61) of nests found in Wellington were common wasps, a proportion derived 11 years after the common wasp had become established there. With no reliable measure of German wasp nest density in Manawatu prior to 1993, my study may just have recorded an abundance of common wasp nests in Manawatu. The number of German wasp nests being produced now may still be similar to the numbers of nests produced prior to the common wasp invasion, but rising numbers of common wasps may have swamped my sample. If this is so, it would indicate that competition between the two species was negligible. As a result, the total number of vespulid wasp nests in Manawatu may have increased significantly since about 1983.

4.4.3 Effect of seasonal rainfall on nest abundance

Figures from the major pest control companies in Manawatu show that reportings of wasp nests significantly varied between 1991-1994, with a general increase over those four years. This suggests that the introduction of the common wasp has increased the social wasp nuisance in Manawatu, and may have raised wasp nest densities.

The establishment of German wasps in Australia involved a lag period of 1-5 years where few nests were reported, before a population explosion was experienced (Crosland 1991). Nest quantities appeared to stabilise in their hundreds, with outbreaks of increased abundance occurring during years of high rainfall (Horwood et al. 1993). Results from this study shows that rainfall does effect wasp nest abundance in Manawatu, but different effects occur with the passing of the season. High spring rainfall appears to have a positive effect on nests initiated during that season, as indicated by high nest abundance in the following year. By contrast Fox-Wilson (1946, cited in Spradbery 1973), recorded that high spring rainfall in England suppressed wasp numbers, possibly because underground colonies were drowned. Madden (1981) found that German wasp nests in Tasmania were positively correlated with spring rainfall, and concluded that an increase in rainfall would promote plant growth, and in turn, provide more nectar and invertebrates for the establishing colonies. These two very different results indicate that further study is required before the exact nature of how spring rainfall influences wasp nest abundance can be determined.

Further into the season the effect is reversed, with high rainfall during the January-June period appearing to limit wasp nest abundance. This was particularly apparent in 1991. Rainfall for the first six months of 1991 was 606.4 mm and the last time it rose over 600 mm was in 1976 (R. G. Heerdegan, unpub. data). Over the 20 years between 1975-1994 the average total rainfall for the first six months was 421.9±28.3 mm. This suggests that the higher than normal half-yearly rainfall in 1991 may have caused more wasp nests to drown and therefore reduced wasp nest abundance that year. Horwood et al. (1993) found that high rainfall in the year of establishment did not have a negative influence on German wasp colonies in Australia, and suggests that this was because a higher proportion are found in buildings when compared to ground nest sites, and are therefore less exposed to flooding. Of the 87 nests seen in Manawatu in 1993, two German wasp ground nests were found to be drowning at the time of extraction. Although this represents only 2.3% of all nests surveyed, flooding may still be a real threat to subterranean colonies in Manawatu, and may account for fewer nests being found in years of high rainfall. Data from 1991-1994 may not be enough to confirm whether this is a true phenomenon in Manawatu, but continued monitoring of wasp nest abundance and total monthly rainfall should establish how valid it is.

Data for 1993 are particularly interesting because the half-yearly rainfall increased marginally from 1992 (14.2 mm) but nest abundance rose significantly by almost 200 nests. In that year rainfall during the first six months did not appear to influence wasp nest abundance. Archer (1980) comments on various studies which have revealed that years of wasp abundance are often followed by years of scarcity, and notes that the scale of the variation can differ between localities. Such variation can have a cyclic element (Fox-Wilson 1946, cited in Spradbery 1973) and it is possible that the nest abundance observed in 1993 was the 'peak' in such a cycle. More observations over a greater time frame are essential before it can be determined whether or not a consistent cycle of wasp nest abundance and scarcity occurs in the Manawatu.

4.4.4 Species replacement

There are no comprehensive records of German wasp nest densities prior to the invasion of common wasps so changes to the total density of vespulid nests in Manawatu remain unclear. Because pest control companies destroy nests without identifying the species involved, the accuracy of my relative frequency estimates of the two vespulid wasps in Manawatu also remains unknown.

In some situations in New Zealand a complete reversal in species abundance has been reported. Common wasps have been replacing German wasps in some areas (Sandlant & Moller

1989), displacing it completely in honeydew beech forest within 3-4 years of invasion (Moller et al. 1990; Harris et al. 1994). The present study shows that common wasps dominate in both urban and rural habitats in Manawatu, but results from a nation wide postal survey in 1987 showed German wasps were more abundant than common wasps (64.7%) in rural areas (Harris et al. 1991). A nation wide resurvey between January 1987 and July 1991, however, revealed that this situation has altered, with common wasps now making up the greater proportion of samples collected from rural areas (Clapperton et al. 1994). My data are consistent with this wider trend.

Clapperton et al. (1989b) suggested that the spread of common wasps into rural areas may have been slow and this could have accounted for the higher German wasp numbers in rural locations in 1987. However, the potential of common wasps to colonise new territory appears to have been fully realised in the last seven years. Moller et al. (1990 unpubl. report) estimated the speed of the common wasp invasion front, in the West Coast region of the South Island, to be at least 30 km yr^{-1} westwards. The speed of colonisation appears to be partially influenced by human movements. Thomas (1960) detailed the connection between the spread of the original successful German wasp invasion in New Zealand and the arterial transport routes of the North Island. New nest sightings occurred principally at towns along the main railway trunkline and state highways. Although nest sightings may relate to distribution of people, the data could suggest a significant level of human-assisted dispersal. This same process has also been involved in the establishment of German wasps in Australia (Crosland 1991; Horwood et al. 1993).

Harris et al. (1991) believe the coexistence of the two species in urban areas may only be a transient phase, but the recent results of Clapperton et al. (1994) suggest that further displacement of German wasps in other habitats is unlikely. The present study alone cannot confirm whether this is so in Manawatu, but further monitoring will determine what effect, if any, the common wasp invasion is having on the resident German wasp.

4.4.5 Seasonal abundance and nest site effects

January consistently contained the greatest number of reports of German and common wasp nests, although similar high levels were also reported in February and March. Nests of both species attain their peak numbers between late March and mid-April (Fordham et al. 1991; Moller et al. 1991a), but it is apparent that as colonies and their traffic rates begin to increase, so too does the frequency of nest sightings. The similar proportions of each species found throughout the 1993 season suggests that the relative proportions of German and common wasp nests remains steady through time. If we assume equal likelihood of finding nests of either species, then the higher proportion of common wasp nests found throughout the season confirms that they are the most abundant species.

The largest nests during February were common wasp nests in the roof/eaves or walls of buildings. These had traffic rates twice that of ground nests. Moller et al. (1991b) reported similar results and suggested that reasons for this difference include earlier successful nest initiation, different growth rates, and different degrees of restriction on peak size by the nest cavity.

Well insulated nest sites (eg. roof/eaves or walls of buildings) requiring no cavity expansion, contained the largest common and German wasp nests in February 1993. The advantages such nest sites offer could have positive effects on nest growth. With little or no worker effort required to enlarge the nest cavity, more workers can undertake nest building or foraging activities. The superior insulation of such sites also means that they do not require large quantities of woodpulp for insulation (pers. obs.). This will allow more of the gathered woodpulp to be used in actual cell construction and nest enlargement. Nests in such sites would be superior to those in other sites, growing to a larger size with a greater number of workers, which in turn would increase the colony's reproductive potential. The difference in the common and German wasp traffic rates for the same situation (roof/eave) in February is probably because common wasps initiate nests earlier (Moller et al. 1991a).

Nest sites in the ground and under buildings do not possess the advantages of nest sites in buildings for German and common wasps. In February, the common wasp nests had similar traffic rates for these two sites, but the traffic rates were lower than for wall/roof nest sites. This possibly suggests that debris removal and the use of more woodpulp for insulation had the overall effect of lowering the nest building rate. This leads to fewer workers and ultimately the production of fewer reproductives (Chapter 5).

4.4.6 Nest site preference

In rural habitats common and German wasps differed in their preferred nest sites. All of the German wasp nests found were in the ground, even on farms where a variety of buildings were available. Common wasps showed more flexibility, with 15% of nests established in buildings. In rural Nelson 13% of common wasps nests found were established in buildings (Moller et al. 1991b).

For the common wasp over half of urban nests in Manawatu were in sites associated with domestic dwellings. These nests grew faster and larger than those in other sites. If common wasps preferentially utilise these sites, they may, according to Archer (1985), have a competitive advantage over German wasps by producing more queens.

German wasps appear to prefer building ground nests even if buildings and other nest sites are abundant. The overall nest site preference of German wasps in Manawatu confirms this with 81% of nests being found in the ground. Fordham et al. (1991) obtained a similar result of 82%. Although German wasps must now compete with common wasps, their nest site preference does not appear to have been modified from that recorded during 1969-1989, when interspecific competition was virtually absent. Spradbery (1973) suggests that common wasps select nest sites opportunistically whereas German wasps favour ground sites. Common wasps may out compete German wasps in this respect by utilising any suitable nest site.

The present co-existence of common and German wasps in Manawatu may be facilitated by a reduction in their inter-specific competition. The differences in nest site preference may be one potential factor. Matsuura (1990) notes that direct conflict between queens for nest sites may be prevented if they initiate nests at different times. Large common wasps nests have been found early in the season in Nelson (Moller et al. 1991a) and Manawatu (pers. obs.), suggesting an earlier initiation by common wasp queens. A consistent monitoring program over a number of years will show if the two species can continue to coexist in urban and rural Manawatu.

Chapter 5 COLONY DYNAMICS

5.1 INTRODUCTION

The German wasp *Vespula germanica* was accidentally introduced near Hamilton in 1944 (Thomas 1960), and by 1961 had spread to some offshore islands and to the south of the South Island (Fordham 1961; 1962). By 1987, its distribution included Stewart Island (Clapperton et al. 1989b). Specimens of the common wasp *V.vulgaris* were found as early as 1921, and although found again in 1945 it failed to establish (Thomas 1960). However, the species was considered to have successfully invaded by the late 1970s when nests in Dunedin and Wellington were found (Donovan 1984). Since then it has invaded nearly all areas of the country including some high altitude sub-alpine habitats (Beggs 1991; Fordham 1991).

The successful exploitation of new habitats by both species indicates that their colony dynamics are similar. Harris et al. (1991) however, question their complete coexistence in all habitats. Common wasps have displaced German wasps from some areas of the honeydew beech forests in the north-western South Island, suggesting that similar events could occur in other localities. However, results from a recent nationwide postal survey suggest otherwise, with both species coexisting in all other habitats (Clapperton et al. 1994).

Displacement of one species by the other has not been recorded overseas, suggesting that the unique features of the honeydew beech forest habitat influences these two wasp species in different ways. Reasons for the displacement are not clear, but principally appear to be related to the differential foraging efficiencies of both species for the honeydew resource (Harris et al. 1994).

Many areas of wasp colony dynamics have been studied overseas, including their seasonal and diurnal activity (Potter 1965), nest initiation and growth (Spradbery 1971, Archer 1980), and queen production (Archer 1972). Similar research in New Zealand has shown that, unlike in the northern hemisphere, colony dynamics of common and German wasps can differ.

Nest initiations can take place over a four month period (Donovan 1991), and some evidence suggests that common wasps begin earlier (Fechney 1989; Moller et al. 1991a). Some colonies of German wasps are able to overwinter in New Zealand, which results in nests of extraordinary size (Thomas 1960; Spradbery 1973; Plunkett et al. 1989; pers. obs.). Even annual German and common wasp nests can be much larger than those recorded in England (Donovan 1984; Fordham et al. 1991).

It is likely that the lack of major predators and effective competitors for vespulid wasps in New Zealand plays a large role in generating these differences. The relatively milder climate and abundance of food during the winter months probably also contribute to this. The question of how they influence both species remains unanswered.

This study was initiated to explore aspects of colony dynamics in Manawatu wasp colonies, with the aim of determining any differences between the two species. This chapter describes the seasonal activity of German and common wasps, their nest building efficiencies, and resulting production of virgin queens.

5.2 METHODS

5.2.1 General data

Vespula wasp nests were located in Manawatu between January and August 1993. This was achieved through contact with pest control services, the Manawatu-Wanganui Regional Council, and members of the public.

For each nest the date, time of day (NZST), and the 'traffic rate' (average number of wasps leaving and returning to the nest in 10 1-min intervals) was recorded. Since the traffic rate is an accurate index of the number of workers in the colony (Malham et al. 1991), it is a good indicator of the colony's size and activity. The species of each colony was determined by hand-netting an exiting forager and identifying it (following Clapperton et al. 1989a). Weather conditions (sunshine; precipitation; cloudcover; windstrength) were also estimated at each site and confirmed by meteorological data from AgResearch Grasslands, Palmerston North.

To begin investigating the possible effect habitat may have on colony dynamics, all nest sites were first grouped into two categories: (i) Urban and (ii) Rural. Nest habitat was classed as urban if over 75% of the area of a circle with radius 200m from the nest contained land devoted to urban habitation. Nests were considered rural if 75% of a similar area contained land given to rural use (eg. farms). The radius of 200m was chosen because most wasps travel less than 200m to forage (Edwards 1980), thus any habitat effect should result from the availability of resources within this area.

5.2.2 Traffic rates

The traffic rates for both species within the two habitat classes were plotted on a Julian day calendar, to compare seasonal activity levels, and to determine colony peak and decline. To supplement the one-off records, traffic rate observations from the diet trap colonies (Chapter 7) were also incorporated. Traffic rates for a single common wasp colony were also recorded over a period of 3 days in early March, and again in early April. For this nest three recordings per day were taken at 0900, 1300, and 1700 hours respectively to detect differences in the diurnal traffic rate during the peak of the season, and relate that to the dynamics of the colony. Unfortunately during this time, no suitable German wasp nest was available for comparison.

5.2.3 Nest size

All 41 nests extracted for the phenology investigation (Chapter 6) were utilised in the analysis of nest size. To determine the effect habitat may have on nest size, the total number of cells of both the worker, male, and queen castes were counted, and recorded chronologically according to species and habitat. Combined worker and male cell quantities were analysed only from nests where queen production was under way, since this normally signals the end of all construction of worker and male cells (Spradbery 1973).

To standardise queen cell construction, only nests found after the third week in April were used, because the majority of nests would then have passed their peak queen production (Chapter 7), and the construction of additional queen cells would be minimal. One overwintering German wasp nest found in July was not considered in the analyses of either the worker/male or queen cells, because such perennial nests have complex colony dynamics compared with annual nests.

The data were analysed by Student's *t*-test and Analysis of variance (ANOVA).

5.2.4 Nest initiation and peak of colony growth

The relationship between nest initiation and colony dynamics was assessed in nests where queen rearing had begun, by measuring the growth in the numbers of worker/male cells. The total worker/male cell number in each colony was divided into two categories: (i) worker/male 'peak' and (ii) 'peak' to queen. The colony's peak was considered to occur in the comb bearing the highest number of cells, and pre-dating subsequent combs with fewer cells. This was because the appearance of the male caste marked the end of the peak of worker production, and the diminished worker force was then able only to produce a lower number of cells in each subsequent comb. Once established, this pattern continued until queen rearing began, when all construction of worker and male cells stopped.

The worker/male 'peak' therefore measures the number of cells up to and including the comb where the 'peak' was noted, while the peak-to-queen category measures the quantity of worker/male cells built between the 'peak' and the onset of queen rearing.

Nests in the worker/male 'peak' category were ranked from the highest cell number to the lowest, and the 33% and 66% percentiles were calculated. This provided three worker/male 'peak' groups, into which nests of similar size could be allocated and compared. The percentile calculations gave the following ranges: group 1: 10534-5820 cells, group 2: 5819-3509 cells, and group 3: 3508-1823 cells (*Appendix 1*). Only nests extracted after the third week in April were analysed, for the reasons mentioned above.

Student *t*-tests within and between the two species were employed, to compare both the number of cells in the worker/male 'peak' group, their related 'peak' to queen cell quantities, and each nest's corresponding number of queen cells.

5.2.5 Nest building effort

To determine the foraging effort required to build cells of different castes in both species, the weight of woodpulp collected by foragers and the weight of constructed cells were measured in the following ways. Because the fresh weight of woodpulp returned by foragers of both species was not significantly different (Chapter 7), a combined sample of 125 pellets from both species were divided into five sub-samples of 25 pellets and dried at 90^0c for 24 hours. Dry weights were recorded and a combined mean with its standard error was calculated.

The amount of woodpulp required to build cells of each caste in both species was determined by carefully removing virgin cells (without meconia) of the worker/male and queen castes from four nests of both species. Only cells in the middle of the comb that contained first- or second-instar larvae were used, so that the levels of cell construction between species were standardised. One sample (30-60 cells) per nest was taken, the larvae removed, and the cells then dried at 90^0c for 24 hours. Dry weights were recorded and since the individual means within each caste and species did not differ significantly, overall means and their standard errors were calculated. Dividing the mean cell weight by the mean weight of the woodpulp pellets gave an estimate of the number of woodpulp loads required to build each type of cell. Significant differences were measured by Student's *t*-test.

To determine the total amount of woodpulp required for a complete nest, two common wasp and three German wasp ground nests, with intact nest envelopes, were extracted during the 1994 season and the number of cells of each caste were counted. The envelope material was broken up and dried at 90^0c for 24 hours, before the absolute weight was measured. The supporting struts between each comb layer were counted, removed, then dried at 90^0c for 24 hours and weighed. The struts attached above the first layer were not included in this analysis. To complement these results, strut measurements from two other common wasp nests were recorded. One-way ANOVA was used to ascertain whether any interspecific differences for the strut weights occurred. The total weight of woodpulp used in cells for each nest was calculated using the estimates of woodpulp pellets per caste cell.

To determine the relative efficiencies of queen rearing between both species, ratios of worker cells to queen cells were calculated from nests where queen production was under way. Student *t*-tests between the two species, over three periods, were calculated.

5.3 RESULTS

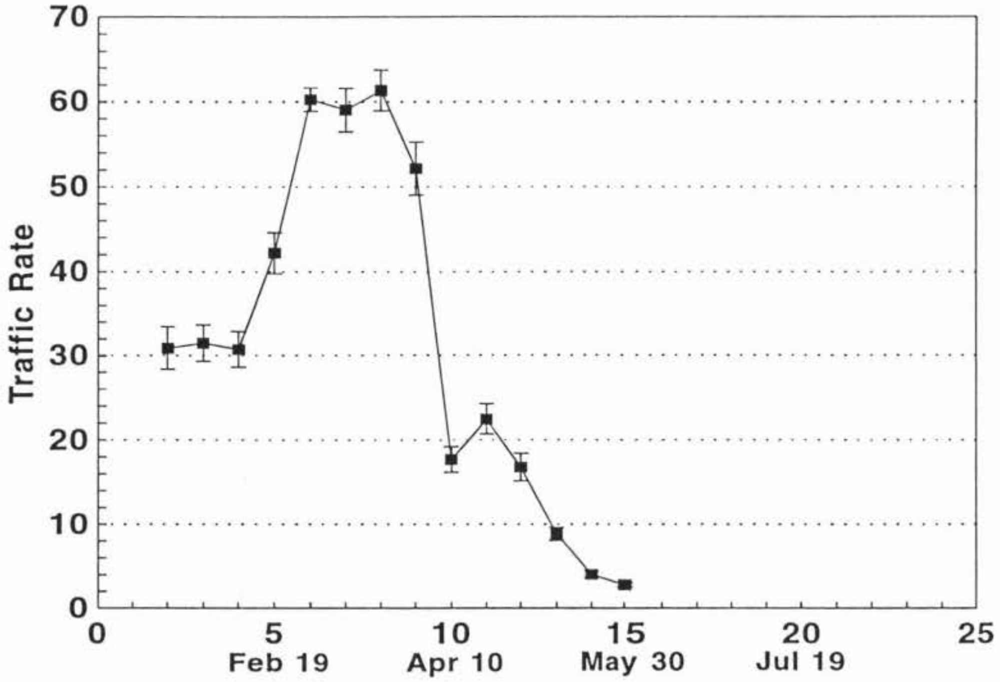
5.3.1 Seasonal traffic rate

Because of the fluctuating supply of nests through the season and uneven spread of nests between species and habitat, comparisons of the traffic rates in these divisions were not possible. However, pooling the habitat data gave a pattern to the seasonal rate of each species (Fig. 5.1). Both the German and common wasp colonies showed a similar 'boom and bust' cycle in their traffic rates. Observations in late January and early February revealed German wasp colonies were more variable than the common wasp for the same period, although both species had similar mean traffic rates of around 26-30 wasps minute^{-1} in the week beginning January 21 1993 (Fig. 5.1). Common wasp traffic rates dramatically increased through February, generally peaking in March, with the highest mean rate occurring around the week of March 22 1993. Although there were no data for German wasp activity from late February to early March, the period of their recorded peak matches that of the common wasp. However, the peak rate of the common wasp colonies were significantly higher than those of the solitary German wasp colony at this time (ANOVA $P < 0.001$). The highest common wasp mean for an individual colony peaked at 86.2 wasps minute^{-1}, compared to the German wasp's 39.7 wasps minute^{-1}. The highest recorded single common wasp traffic rate was 106 wasps minute^{-1}, while for the German wasp it was only 51 wasps minute^{-1}. Common wasp traffic rates tapered off after the peak, declining rapidly through April, but some colonies continued into early June with traffic rates under 5 wasps minute^{-1} (Fig. 5.1). While the majority of German wasp nests were well into decline by the end of May, one German wasp colony remained at strength, continuing at around 20 wasps minute^{-1} from mid May to mid July, before dying at the end of July.

5.3.2 Diurnal traffic rate

For a single common wasp nest the overall traffic rate pattern for three days in early March showed a steady increase in colony activity (Fig. 5.2a). The traffic rate on March 9 1993 remained steady throughout the day, averaging 56.9 wasps minute^{-1}, but by March 11 had significantly increased to 82.3 wasps minute^{-1} (ANOVA $P < 0.001$). On the final two days the traffic rates in the early

A



B

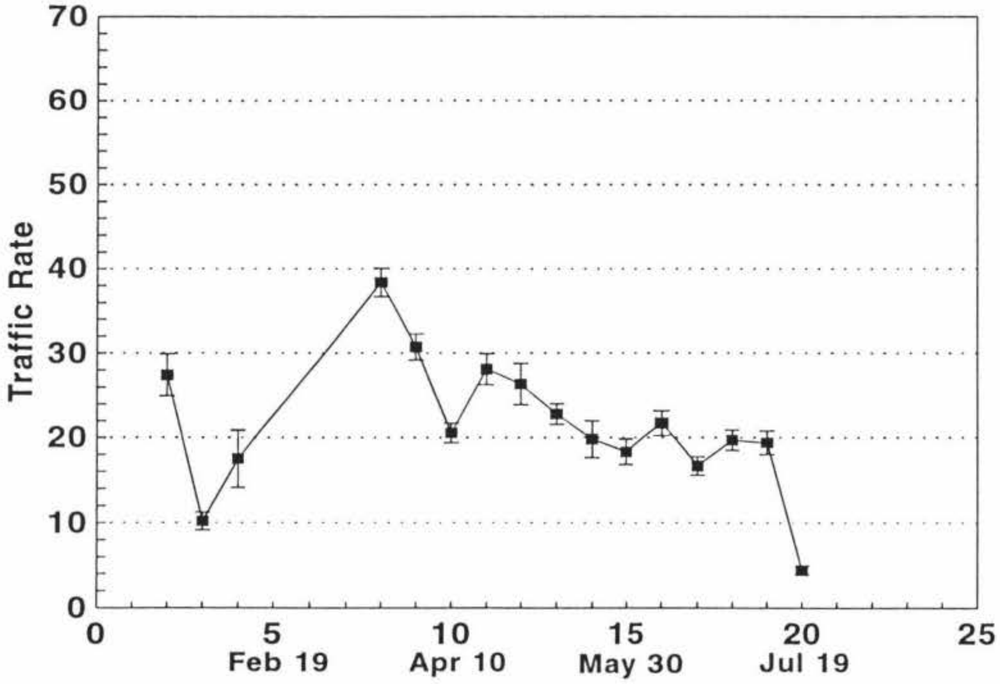
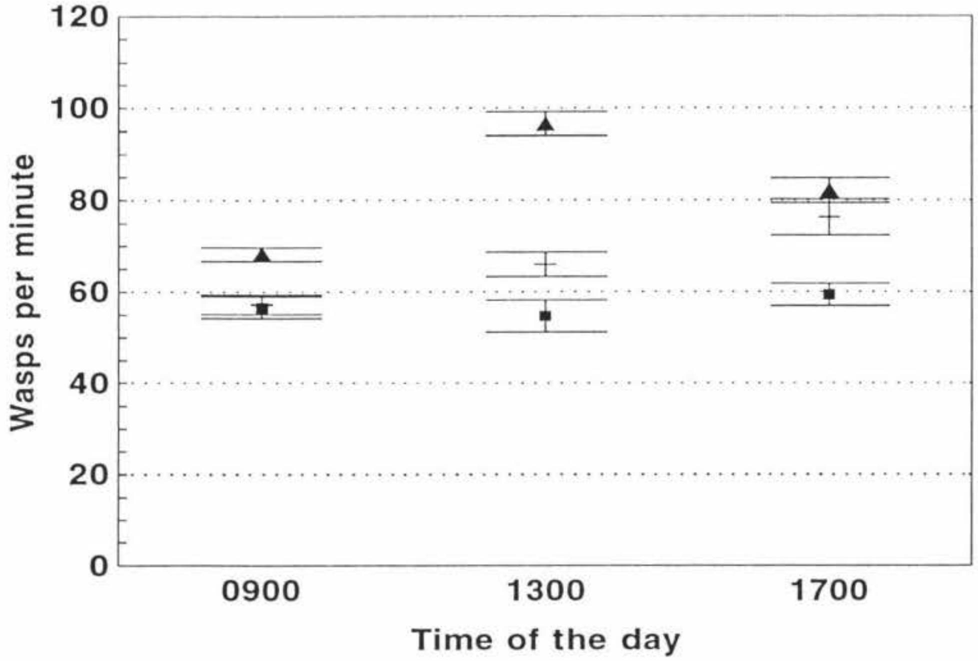


Figure 5.1 Mean traffic rates (wasps entering and leaving every 10 minutes) of (**A**) common and (**B**) German wasp nests in Palmerston North, recorded within 10-day intervals, between January 21 and July 22 1993. Bars show mean±1SE.

A



B

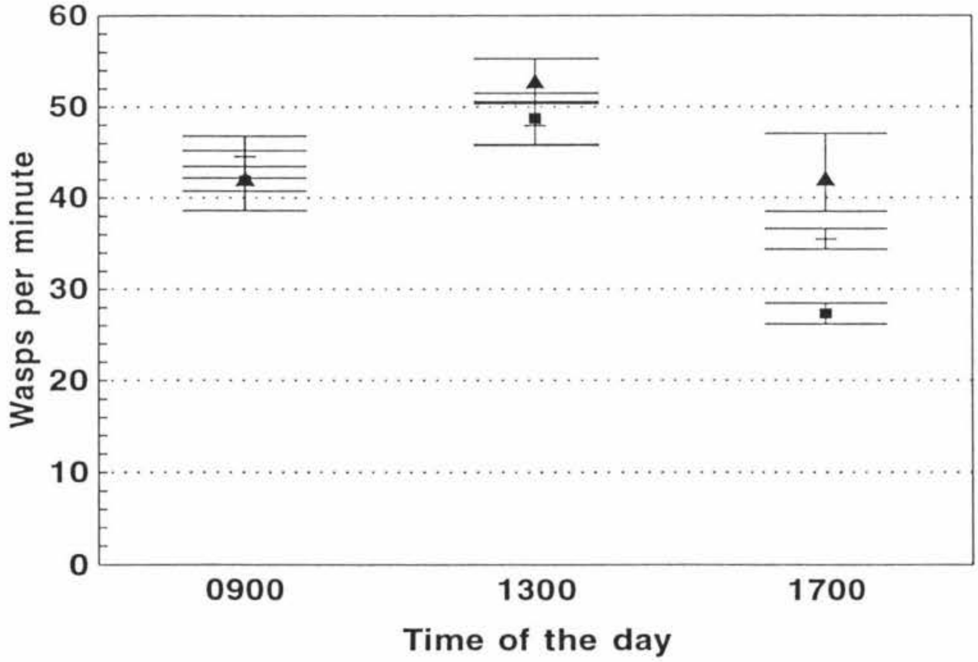


Figure 5.2 Diurnal traffic rates of a Palmerston North common wasp nest, recorded between (**A**) March 9 - 11 and (**B**) April 1 - 3 1993. Observations taken at 0900, 1300, and 1700 hours (NZST). (■) = March 9 & April 1; (+) = March 10 & April 2; (▲) = March 11 & April 3. Bars show mean±1SE.

afternoon and evening were significantly higher than those recorded in the morning (ANOVA $P < 0.001$).

When traffic rates were recorded between April 1 - April 3 1993, the overall activity levels had declined (Fig. 5.2b). Traffic rates remained significantly different for both the time and day of recording (ANOVA $P < 0.001$), with the highest activity consistently being observed in the early afternoon, where a three day mean of 49.8 wasps minute^{-1} was recorded. Evening traffic rates in April averaged the lowest for the period at 34.9 wasps minute^{-1}, in direct contrast to the March recordings of the same time. However, between April 1 - April 3, the individual 1700 hour traffic rates differed significantly, with evening activity steadily increasing from 27.1 to 42.1 wasps minute^{-1} (ANOVA $P < 0.001$).

5.3.3 Nest size between species and habitat

The number of worker/male cells in urban and rural common wasp nests did not differ significantly from those found in urban and rural German wasp nests (*Appendix 2*). However, queen cell numbers did differ significantly between the two species. In rural common wasp nests, there were greater numbers of queen cells compared to rural German wasp nests (*Appendix 2*: $t = 2.97$, df = 6, $P = 0.025$). Only one urban German wasp nest was available in the appropriate period so a *t*-test for the urban habitat could not be undertaken. Queen cells from a combined sample of urban and rural common wasp nests were also significantly higher in number than the comparable German wasp sample (Fig. 5.3: $t = 3.18$, df = 8, $P = 0.013$). Common wasp nests found between April 23 - August 20 had a mean number of 2112±264 queen cells, in comparison to the German wasps' 936±258 queen cells.

The 11 nests extracted at Apiti on day 106 (April 16) showed no significant difference between the quantity of worker/male cells in nests of either species, but were highly different in queen cell quantity (Fig. 5.4: $t = 9.36$, df = 7, $P = 0.0001$).

5.3.4 Nest initiation and queen rearing

Common wasp group 1 nests produced significantly more worker/male cells before their 'peak', than did common wasp group 2 nests (Table 5.1: $t = 2.85$, df = 4, $P = 0.046$), but the number of cells produced after the 'peak' did not differ significantly between these two groups. Queen cell counts were also significantly higher for common wasp nests in group 1 when compared to group 2 (Table 5.1: $t = 3.03$, df = 4, $P = 0.039$). Although the worker/male numbers before 'peak' and during the 'peak' to queen cell period were not significantly different between the common and

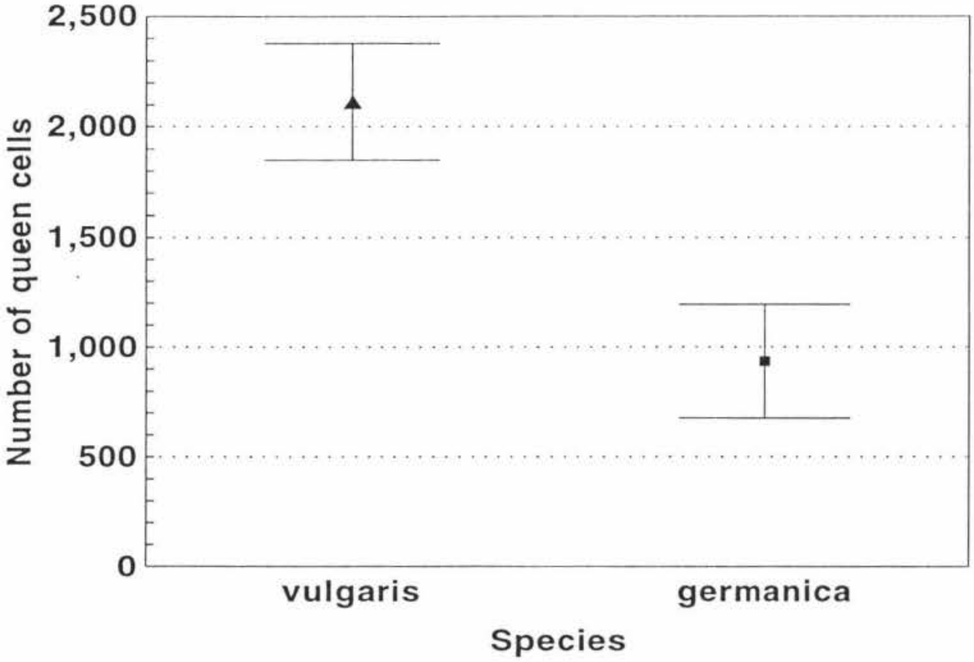


Figure 3 The number of queen cells built in German ($n = 4$) and common wasp ($n = 9$) nests, extracted in Palmerston North between April 23 and August 20 1993. Sample includes combined rural and urban nests. Bars show mean±1SE.

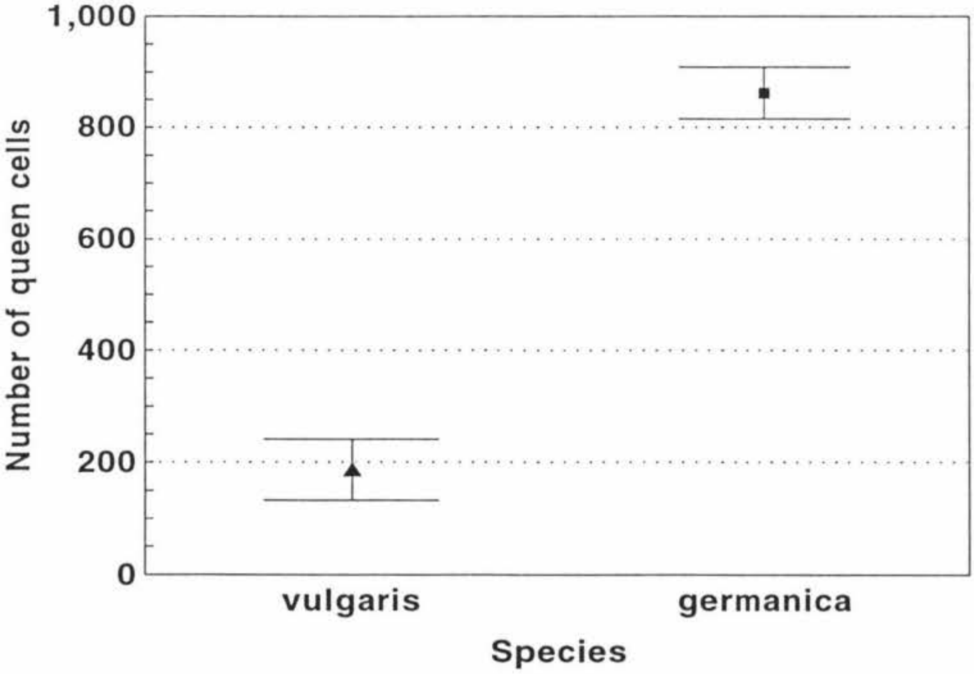


Figure 4 The number of queen cells built in German ($n = 3$) and common wasp ($n = 8$) nests, extracted in Apiti on April 16 1993. All nests were rural. Bars show mean±1SE.

Table 5.1 Division of total worker/male cell growth in Manawatu German and common wasp nests into two categories, and their corresponding queen productivity. Categories are worker/male 'peak' and 'peak' to queen (see text for criteria). All nests were extracted between April 23 - August 20 1993. w/m = worker/male.

	w/m cells to 'peak'			w/m 'peak' cells to queen			Total w/m cells	total queen cells		
V. vulgaris	group 1	group 2	group 3	group 1	group 2	group 3		group 1	group 2	group 3
FH1	7177	-	-	3369	-	-	10546	2287	-	-
POH4	7549	-	-	5152	-	-	12701	3645	-	-
FH2	6689	-	-	3618	-	-	10307	2353	-	-
Ring Rd	5873	-	-	5180	-	-	11053	2615	-	-
Limbrick	10534	-	-	1989	-	-	12523	2317	-	-
Gibbs	-	5210	-	-	1488	-	6698	-	1247	-
Pork	-	5446	-	-	4005	-	9451	-	1055	-
Feilding	-	5217	-	-	2531	-	7748	-	2037	-
mean±1SE	7564±794	5291±78	-	4330±486	2675±730	-	-	2643±257	1446±301	-
V. germanica										
Colyton	6948	-	-	3676	-	-	10624	1308	-	-
Acacia	9711	-	-	106	-	-	9819	1424	-	-
POH3	-	-	2813	-	-	0	2813	-	-	676
mean±1SE	8330±1382	-	2813	1891±1785	-	-	-	1366±58	-	676

German wasp group 1 nests, the resulting numbers of queen cells were different, with common wasps building significantly more queen cells (Table 5.1: $t = 4.85$, df = 4, $P = 0.0084$).

5.3.5 Woodpulp and nest building

Woodpulp pellets had a mean dry weight of 0.054±0.002mg pellet^{-1}. The weight of woodpulp required to build cells of corresponding castes between the two species was significantly different (Table 5.2: worker/male: $t = 8.14$, df = 5, $P = 0.0005$; queen: $t = 9.49$, df = 3, $P = 0.0025$). German wasp worker/male and queen cells took 74% and 63% more woodpulp respectively, than their common wasp counterparts. In real terms this equates to an estimated requirement of 9 woodpulp loads to build a common wasp worker/male cell, averaging a dried weight of 0.47mg. In comparison a German wasp worker/male cell with a mean dried weight of 0.82mg would need 15 foraging trips. Common and German wasp queen cells took 57.4% and 47.6% more woodpulp respectively, than that required to build their worker/male cells. A common wasp queen cell, with an average dried weight of 0.74mg, would need 14 woodpulp loads, whilst the German wasp equivalent, weighing around 1.21mg, would need 23 such trips.

For the five nests examined, a strongly positive correlation between envelope weight and total cell weight was discovered (Table 5.3: $r = 0.997$). Nests with higher amounts of woodpulp used in cell building had nearly equivalent amounts of woodpulp used in their nest envelopes, regardless of species. Strut weights were significantly different between the two species, with German wasp nests averaging 19.06±0.15 mg strut^{-1}, and common wasps 13.53±0.14 mg strut^{-1} (Table 5.3: ANOVA $P < 0.05$).

Direct comparisons of the woodpulp requirements, and total foraging effort for nest building in both species, is difficult because of the differences in cell numbers, but extrapolation can allow some comparison. For example a German wasp nest containing 10315 worker/male cells and 2592 queen cells (Table 5.3), can be compared with a common wasp nest containing 10465 worker/male cells. Assume that a similar number of 2592 queen cells is added to the common wasp nest. Calculation of the extra woodpulp needed to build 2592 common wasp queen cells, and the related increase in envelope size gives a result of around 38g. This brings the total number of woodpulp trips for such a common wasp nest to around 270,800. The German wasp nest had an estimated 445,800 woodpulp trips. This comparison suggests that around 65% more foraging effort is required to build a German wasp ground nest of similar dimensions.

5.3.6 Worker cell : queen cell ratio

Variability within and between each species in the worker cell : queen cell ratio is evident, even in

Table 5.2 Dry weight of woodpulp (mg±1SE) required to build virgin cells of different castes of German and common wasps. Cell samples taken from four different nests per species in Manawatu 1993.

	worker/male	queen	% difference queen to w/m
V. germanica	0.82±0.03	1.21±0.04	147.6
V. vulgaris	0.47±0.03	0.74±0.02	157.4

Table 5.3 Woodpulp required (g) to build *Vespula* spp. ground nests (cells, struts, and envelope), and the estimated number of woodpulp foraging trips required. Dry weights are used throughout. Strut weights do not include struts on comb layer 1. V.v = *V. vulgaris*. V.g = *V. germanica*. w/m = worker/male. qn = queen. wp = woodpulp.

Species	Date	No. w/m cells	No. qn cells	Σw/m cells weight (g)	Σqn cells weight (g)	Σall cells weight (g)	envelope weight (g)	No. of struts	wp strut^{-1} comb^{-1} ±1SE (mg)	Σstruts weight (g)	Σall wp weight (g)	Total trips
V.v	3/2	10465	-	49.19	-	49.19	55.74	215	17.5±2.5	3.31	108.24	200,444
	9/2	10142	-	-	-	-	-	246	15.5±2.4	4.16	-	-
	29/4	4612	430	21.68	3.18	24.86	25.65	127	14.1±1.3	1.90	52.41	97,055
	29/4	4757	-	-	-	-	-	79	11.7±1.3	0.79	-	-
V.g	2/2	5316	-	43.59	-	43.59	43.80	125	21.4±6.6	1.65	89.04	164,880
	31/3	10315	2592	84.58	31.36	115.94	114.35	380	26.4±2.2	10.48	240.77	445,870
	29/4	3401	295	27.89	3.57	31.46	34.70	163	14.1±1.3	1.34	67.50	125,000

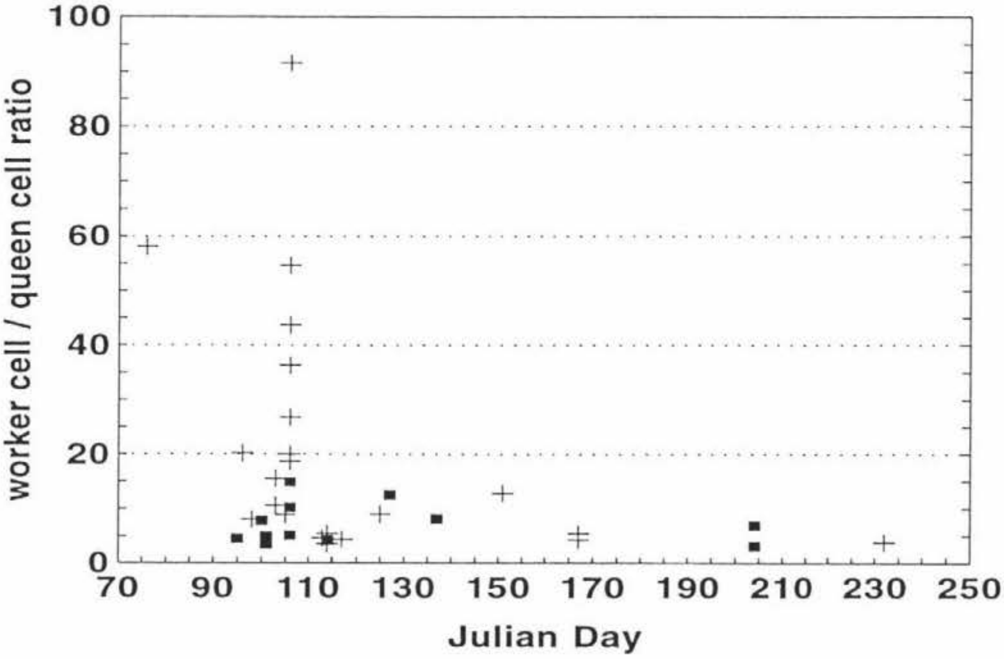


Figure 5.5 Individual worker cell : queen cell ratios of German (■) and common (+) wasp nests extracted in Palmerston North, between March 17 and August 20 1993. Day 76 = March 17; Day 106 = April 16; Day 150 = May 31.

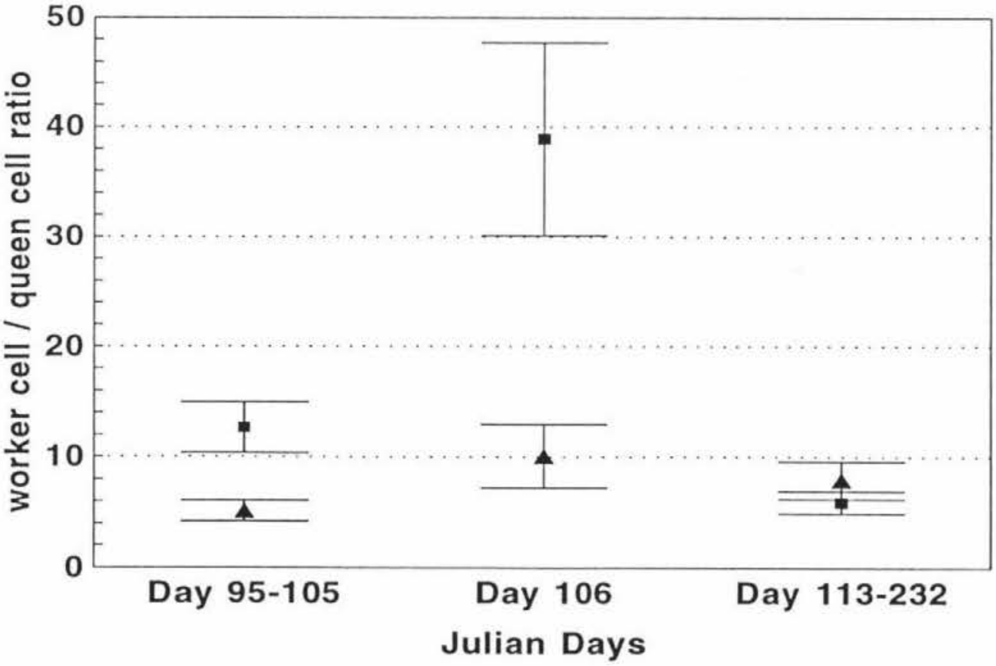


Figure 5.6 Mean worker cell : queen cell ratios of German (■) and common (▲) wasp nests extracted in Palmerston North, between April 5 and August 20 1993. Day 95 = April 5; Day 106 = April 16. Bars show mean±1SE.

nests extracted on the same day (Fig. 5.5). Common wasps showed a pattern of initially high ratios, but apart from five nests taken on day 106, the ratio declined as more queen cells were built. German wasp worker cell : queen cell ratios could not be compared at the beginning of early queen rearing, but over two comparable periods, day 95-105 and on day 106, were significantly lower than the common wasp ratios (Fig. 5.6: day 95-105: $t = 3.03$, $df = 5$, $P = 0.029$; day 106: $t = 3.13$, $df = 8$, $P = 0.014$). In both these periods German wasps had mean ratios of 10 or lower, whilst common wasps had averages of 12.6 and 38.9. During the period of day 113-232, common and German wasp ratios were similar, recording means of 5.9 and 7.9 respectively.

5.4 DISCUSSION

5.4.1 Seasonal traffic rate

In Christchurch City queens of both *Vespula* species generally begin building nests around September-November (Donovan 1991). Within about 40 days of the nest initiation in England, the first crop of adult workers hatch, and begin foraging (Spradbery 1991). This activity increases as the colony grows, and in Manawatu colonies, for both species, rates close to 30 wasps minute^{-1} were reached by late January. However, in the two following 10-day intervals, German wasp traffic rates were significantly lower than those of common wasps. This variation was caused by recording two small German wasp colonies, one of which had a traffic rate of only 3 wasps minute^{-1}, and contained 471 worker cells. In contrast a common wasp nest in the same period had a mean traffic rate of 24.8 wasp minute^{-1}, and 9715 worker cells.

The wide variation observed between the two species in this early period is probably due more to the date of nest initiation than to any nest site effect (Chapter 4), because the nest sites of these small German wasp colonies were in similar locations to the common wasp colonies recorded in the same period. Donovan (1991) suggests that German wasp nests initiated in late January are started by queens leaving overwintered colonies during late spring and early summer. This could explain the small sizes and very low traffic rates of these colonies.

The peak for Manawatu *Vespula* colonies in late March is very similar to that recorded in urban Nelson (Moller et al. 1991a). However, compared with the Nelson data the highest individual traffic rates of colonies in Manawatu were around 75% and 50% lower for the German and common wasp respectively. This is likely to be a result of chance sampling of smaller colonies, rather than some geographical advantage offered to Nelson colonies.

Chance sampling of these small colonies may also explain the significant difference in the two species peak traffic rates. Reports of German wasp colonies were few at this time, and all the nests seen were much less active than the common wasp colonies, but results from larger samples taken in Nelson suggest that these low German wasp traffic rates are outliers from the general pattern.

The similar seasonal point of decline in the two species suggests that there is little overall difference between the time that each species switches to the production of sexuals. However, a closer examination of a sub-sample of extracted nests indicate that differences in the initiation of reproductives do occur (section 5.4.4).

The maintenance of a high traffic rate into late-July appears to be common for German wasps. Moller et al. (1991a) record German wasp colonies declining at a slower rate than common wasps in 1988. My nest showed signs of overwintering (Chapter 6), but was in an area with a high water table and may have prematurely died by drowning.

The traffic rate of a wasp colony can be used to estimate the number of workers it contains (Malham et al. 1991). Related to this is the suggestion that the number of workers in a colony has a direct effect on the number of queens a colony can produce (Archer 1972). Since the German wasp colony's traffic rate at peak was around 50% lower than the common wasp rates for the same period, we can assume that the number of German worker wasps were around half those of the common wasp colonies. If this was so, we could assume the production of queens to be considerably lower in the German wasp colony. With the season's end, the Acacia St German wasp nest had only built around half as many queen cells as the Limbrick and Ring Rd common wasp nests (*Appendices 2*). Since these three nests were involved in the peak traffic rate analysis discussed above, their final quantities of queen cells appear to support the idea that the size of the worker population bears directly on the number of queens produced.

5.4.2 Diurnal traffic rate

The traffic rate recordings of the common wasp colony between March 9-March 11 1993 illustrate the large daily increases that occur during colony expansion, just prior to the colony peak. Foraging workers cater for all the demands of the colony (Spradbery 1973), and the rapid increase in activity suggested that queen rearing was about to start (Chapter 7). Short of immediate dissection of the nest, only an investigation of the types and proportions of food items carried by returning wasps could verify this externally (Chapter 7).

The April 1 - April 3 traffic rates reflect the start of the colony's decline. The traffic rate had slumped to around 39-45 wasps minute^{-1} for this 3 day period, indicating that a reduction in worker recruitment had resulted in the worker force falling to nearly half of that recorded three weeks earlier.

Spradbery (1973) from Potter (1965) states that diurnal peaks in the traffic rate occur within two hours of the colony awakening, and in the last hour before nightfall. Colonies become active in the twilight period just prior to dawn (pers. obs.), and as sunrise was about 0614 hours between March 9-11, my recordings at 0900 hours will have missed this morning peak. Sunset occurred around 1841 hours and although my 1700 hour observations were outside the range of the evening peak, on March 10 the colony appeared to have an early evening peak.

A later sunrise and earlier sunset in April meant my recordings were closer to the times noted as being periods containing increased colony activity. However, even with the 1700 hours observations being within the range of the evening peak, no such increase was seen on either of the 3 days. Instead, traffic rates remained consistently highest around the middle of the day (1300 hours).

The steady increase in early evening traffic rates observed over the three days may be caused by the seasonal decrease in day length. Spradbery (1973) mentions that foraging activity increases with a reduction in day length, and the 63 minute loss of foraging time between 9 March and 1 April may mean that, in order to satisfy the colony's demands before nightfall, an increase in activity was required.

5.4.3 Nest size between species and habitat

Colony dynamics of German wasps appear to be affected by nest site and habitat, where urban nests have been reported to be larger and more productive than rural nests (Fordham et al. 1991). In the same paper H. Moller (pers. comm.) mentioned that nests found in forest habitats were smaller than those found in rural habitats. In Manawatu such differences between urban and rural nests were not observed in the counts of worker/male and queen cells of either species, but the sample size was small. Two small rural nests did occur but their size appeared to be due to restrictions on their cavity expansion.

There was a significant difference between the two species in the number of queen cells in nests extracted on day 106 (April 16), and again in those collected between April 23 and August 20 1993. This appears to be due to a difference in the timing of the switch to queen production. By April 16, German wasp nests found at Apiti contained significantly more queen cells than the common wasp nests, even though the numbers of worker/male cells did not differ significantly. An earlier switch to queen rearing by German wasps seems to explain their higher numbers of queen cells.

The opposite appears to have occurred in the sample of nests taken between April 23 - August 20 1993, where the common wasp had a significantly greater number of queen cells per nest. Again, worker/male cell quantities were similar between species, but the common wasp was more productive by appearing to initiate queen production earlier than the German wasp. This contrasts with the findings of Spradbery (1971) and Moller et al. (1991a). However, these authors also mention for both species that considerable variation in the initiation of queen rearing can occur.

5.4.4 Nest initiation and queen rearing

Common wasp nests in group 1 (10534-5820 cells to 'peak') produced, on average, 1200 more queen cells than the group 2 nests (5819-3509 cells to 'peak'), possibly because of an earlier nest initiation or a later switch to male production. Donovan (1991) shows up to four months variation in nest initiations for both species. This means that a nest started earlier in the season can produce more worker cells, and thus have a larger worker force before the switch to male rearing occurs. Similarly, nests which do not initiate male production till late in the season have a longer period to continue building their worker force which, like an earlier nest initiation, will be reflected by the higher number of worker cells up to the 'peak'.

Archer (1972) reported in the common wasp that larger nests produced more new queens. This is most likely the result of a greater number of workers, which means that group 1 nests, with higher numbers of 'peak' worker cells should be better able to produce more queens. The results from Manawatu support this idea.

The two German wasp nests in group 1 produced significantly fewer queen cells than the similar sized common wasp nests, possibly because they switched to queen production later. Colonies which begin queen rearing too late in the season miss out on optimal conditions, and their reproductive potential becomes reduced (Spradbery 1971). Initiation of queen cell construction was found to be very variable in individual colonies in England (Spradbery 1971), and New Zealand colonies are no different (Moller et al. 1991a). Previous studies have not described significant differences in queen cell quantities between nests of either species (Spradbery 1971; Moller et al. 1991a), so it appears that these two nests may be chance recordings of a late move into queen rearing. I would expect a larger sample of German wasp nests to give similar queen cell results to that of the common wasp.

Phenological variance may not be the only factor contributing to queen production. Physical restrictions on colony size can also effect the number of queen cells produced, where the nest site substrate can either hinder or enhance cavity expansion. Comparison of the common wasp nest at Ring Rd and at Anzac Park illustrate this. Both had similar dimensions within the two categories, but queen comb growth in the Anzac Park nest was less than half that of the Ring Rd nest. A band of hard clay in the nest cavity of the Anzac Park nest appeared to restrict the growth of lower queen combs, to about 1600 queen cells fewer than the Ring Rd nest.

Nests built in a soft substrate such as compost are able to produce larger nests more quickly than those built in a hard substrate (Spradbery 1971). The Fielding nest is an example of this, being ground-based but built in garden mulch and sawdust. Found on August 20 1993, with only 7748 worker/male cells built, it nevertheless had also produced over 2000 queen cells. The low number of worker/male cells for the date of reporting indicate that it must have been initiated very late, yet it had still managed to produce a quantity of queen cells similar to that of an early initiated group 1 nest. The worker force for this nest would have been substantially lower than that found in a group 1 nest, but the easy extraction of loose material to enlarge the nest cavity would have speeded the production of a similar number of queen cells. In another comparison, a similar-sized group 2 ground nest (eg. Gibbs *Appendix* 2), with a typical hard substrate, produced almost 800 fewer queen cells than the Feilding nest.

Overall, it appears that endogenous and exogenous factors can both affect queen production, with no single factor being clearly dominant.

5.4.5 Woodpulp and nest building

Spradbery (1971) found that common wasp queen cells contained 40% more material than their worker/male cells, but unfortunately provided no separate component weight measurements, with which the Manawatu data could be compared. Although common wasp queen cells contained, on average, 57% more material, recalculating using the standard error gives a value of 44%. Because this value is similar to that given by Spradbery, I infer that the remaining caste weight measurements are also accurate.

The weight of woodpulp pellets returned by foragers of both species does not differ, so in comparison with common wasps, the larger cells of German wasps put the species at a foraging and cell building disadvantage. Cells of all German wasp castes require 63-74% more woodpulp than that required by cells of the equivalent common wasp caste. In addition, struts in German wasp nests require around 41% more woodpulp than those in common wasp nests. Therefore, in order to build nests of a similar size to common wasps, German wasps would have to at least double their woodpulp foraging effort.

Diet analysis (Chapter 7) showed no such difference in foraging for woodpulp by the two species. Rather, German wasps had a lower rate of woodpulp return throughout the season. The only noticeable rise in woodpulp return occurred around the time of queen rearing, and was observed in both species. The time of day that the diet was sampled, and a low traffic rate, may explain why the woodpulp return of this German wasp nest was lower than that of the common wasp nests.

If the true foraging pattern includes both species returning with similar woodpulp rates, then the lower woodpulp requirements of common wasp nests should enable them to produce nests about twice the size of German wasps. The proportion of foragers of both species returning with woodpulp appeared to be similar throughout the season (*Appendix 3)*, which supports the idea that common wasps should be able to build bigger nests for similar foraging effort. Results in this study and elsewhere (Spradbery 1971; Moller et al. 1991a) show that this is not so. The three ground-based nests under consideration were of a comparable size, which indicates that some other factor is influencing both species.

If common wasps used relatively more woodpulp in other parts of their nest (eg. nest envelope), it could explain where their 'surplus' woodpulp is going, and why their nest sizes are not significantly different to that of the German wasp. This study, however, has shown that this is not the case. The weight of nest struts are different in the two species, with German wasps requiring more woodpulp, but nest envelope weights between the two species do not differ. However, they do appear to be related to the number of cells found in the nest, with larger nests, containing greater numbers of larvae and pupae, requiring more insulation.

Archer (1977) found that, in the process of cavity expansion, the heaviest debris loads were carried by the largest wasps. German worker wasps are generally bigger than their common wasp counterparts, therefore they should be able to remove heavier debris loads from ground nests. If both species started to build ground nests in a similar substrate, at the same time, the German wasp should be able to excavate its nest cavity quicker than the common wasp. However, the extra woodpulp needed to build their bigger cells would slow down their nest growth. Similarly, the common wasp's ability to build bigger nests, as facilitated through a reduced woodpulp requirement, would be offset by slower expansion of the nest cavity. If the ability to excavate the ground nest cavity is unequal between the two species, then it may help explain why their dissimilar building requirements do not promote different sized nests.

Clary et al. (1993) found, in a common wasp ground nest that rainfall appeared to promote excavation of the nest cavity. Significantly more wasps carried out mud pellets after a period of high relative humidity, than prior to it. These results could be an observation of the common wasp taking advantage of conditions which allow a faster cavity expansion. If this strategy was not shared by both species, it could indicate that common wasps do have a reduced capacity to enlarge their ground nests.

More research on the diurnal return of woodpulp, and the corresponding removal of debris by both species should clarify these results, and help explain why nest sizes do not differ between the species.

5.4.6 Worker cell : queen cell ratio

Spradbery (1973) states that the worker cell : queen cell ratio measures the efficiency of queen production between wasp species. His research in England showed that throughout the season German wasps had lower ratios than common wasps, thereby suggesting that they may be more 'efficient' at queen rearing.

However this measurement may not just indicate the efficiency of queen rearing, but may also record the effects of an earlier nest initiation, the late production of males, or the effects of an earlier switch to queen production. Nests which start earlier, or produce males later, than other nests, should have greater numbers of worker/male cells than those initiated weeks or months later. If, at the beginning of queen rearing, such a nest was compared with one extracted at the same time but initiated later in the season, a higher worker cell : queen cell ratio should be found in the nest started earlier in the season.

The reverse is true for similar sized nests extracted at the same time, but where one has had an earlier switch to queen rearing. The higher number of queen cells found in this nest would produce a lower ratio.

Neither situation appears to be species specific, though it is suggested that some common wasps may initiate their nests earlier than German wasps (Fechney 1989; Moller et al. 1991a; Moller et al. 1991b). An earlier analysis in this chapter revealed differences in the 'peak' size of individual common wasp colonies, suggesting the timing of nest initiation can differ within the common wasp species. Overall, worker/male cell counts from nests taken throughout the 1993 season showed no significant difference between the two species. This indicates that, in this sample, common wasps did not initiate nests earlier than German wasps, although one nest extracted at its demise contained 18696 worker/male cells, which was 33% bigger than the next largest common or German wasp nest. Similar large early season common wasp nests were found in Manawatu in 1994 also (D. M. Leathwick, pers. comm.).

It is difficult to pinpoint exactly why the worker cell : queen cell ratios differed between the two species extracted between days 95-105. The mean worker/male and queen cell calculations between the two species were not significantly different, so it appears that differential nest initiation and queen rearing did not play a significant role in nests taken during this period.

However, the significantly lower ratios recorded for German wasp nests taken on day 106 may be explained by an earlier switch to queen production. No significant difference was found between the worker/male cell numbers of both species but there was for the number of queen cells. This indicates that although nest initiation appeared to be similar between the two species, the German wasp managed to build more queen cells sooner than the common wasp. Because all nest sites were built in a similar substrate and located in the same habitat, they all should have experienced similar conditions for expansion. The ratio measures relative growth, so that if queen production began at the same time, even in nests of different size, similar interspecific ratios should be found. The results show that the ratios are not similar, and it seems likely that the different timing of queen rearing between the two species may explain these differences. Why it occurred in this particular area is not clear.

The nests extracted over the 119 day period between days 113-232 had similar ratios, possibly because relative growth between both species is similar (Moller et al. 1991a). Common wasp nests examined around the same time in Dunedin in 1983, also showed similar low values (Donovan 1984). Ratios are lowered with every additional queen cell that is built, so as the season progresses, any disparity between the two species becomes reduced. German wasp nests had significantly fewer queen cells for the period, which is reflected in their slightly higher ratio at this time.

Chapter 6 PHENOLOGY

6.1 INTRODUCTION

The phenology of vespulid wasp colonies is complex, providing many areas of entomological research (see Spradbery 1971; Edwards 1980 for review). The introduction of German and common wasps to New Zealand, has allowed research showing that the general ecology of both species in New Zealand conditions is similar to that found elsewhere, but there are some differences in their phenology.

In New Zealand, nests are initiated in spring by a founder queen that has successfully hibernated over winter (Donovan 1991). However, Fechney (1989) and Moller et al. (1991a) believe that the timing of nest initiations may differ between the species. Common wasp nests are often found earlier in the season than German wasp nests, and comparatively small German wasp nests have been found late in the season (Donovan 1991; pers. obs.). Donovan (1991) suggests that queens departing late from perennial nests may be one source of this difference.

The queen builds the first 25-40 cells herself and over the next 40 days rears the first few workers to adulthood (Spradbery 1991). This initial period of low activity is soon replaced by one of rapid growth, where successive workers take over the foraging and nest building activities. This period is essential in establishing the future productivity of the colony. If common wasps consistently have an earlier start to their phenological cycle, then they should be better placed to produce more workers and therefore grow quicker during the favourable months of the season.

Exponential growth follows during the first couple of months in the new season, when thousands of worker wasps can be produced (Spradbery 1973). However, the season climaxes with the switch to the production of the reproductive castes, when new males and virgin queens are reared. Moller et al. (1991a) found that German wasp colonies in Nelson began producing sexuals earlier and over a longer period than common wasps, suggesting that this phenological difference may allow queen production in German wasps to be higher in these colonies. A comparison of Manawatu colonies was undertaken to determine if such important differences in phenology occurred elsewhere in New Zealand.

The successful mating and hibernation of these new queens prime the annual cycle to begin the following spring. However, for some unknown reason, a small proportion of German wasp nests are re-queened, and survive through the winter. This is a relatively common occurrence in

New Zealand and Tasmania, and has been reported on a small scale in California (Akre et al. 1993; Ratnieks and Miller 1993). It is suggested that the climate particular to these areas allow perennial nests to occur. With the arrival of spring, the head start produced by a well established worker force can mean nests of an extraordinary size are produced by the summer months (Thomas 1960; Spradbery 1973; Plunkett et al. 1989; pers. obs.). Associated with this are the large but as yet undetermined quantities of virgin queens that are produced throughout the extended season. It is unknown what, if any, effect the lack of hibernation may have, on the phenology shown by queens which successfully initiate nests in the new season.

Fordham et al. (1991) studied the phenology of annual German wasp colonies in Manawatu, spanning a period of 20 years. Since then common wasps have become well established in the area. Using the baseline results of Fordham et al. (1991), and those from similar work undertaken on the two species in Nelson (Moller et al. 1991a), this study was initiated to describe the comparative phenology of both species in Manawatu. The appearance of the two reproductive castes in both species are described, as are the relative cell contents of the various life stages throughout the season. Detailed phenological data from an overwintering German wasp nest, and observations of *V. germanica* wasps mating are also recorded.

6.2 METHODS

Vespula wasp nests were located in Manawatu between January and August 1993, by means of pest control services, the Manawatu-Wanganui Regional Council, and members of the public. Nests suitable for extraction were poisoned by carbaryl powder blown through the entrance, or removed live, and frozen for later investigation. Of the 41 nests collected, 14 were not used because they deteriorated, despite refrigeration. Adult hatched wasps were not counted because many were lost during collection.

After dissecting each nest, the total number of cells was counted, and the worker/male cells were distinguished from the larger queen-rearing cells. Absolute counts of the various cell production activities were then made under the following categories: Empty cells (small/large); egg cells (small/large); larvae cells (small/large); and pupae cells (worker/male/queen). These were then converted to percentages, and plotted over the course of the season. The percentage of the different castes making up the total pupae cells were also calculated, so that their seasonal patterns could be determined.

The study set out to investigate the phenology of German and common wasp colonies, but an overwintering German wasp nest found in late July was dissected and analysed by the above method. The results of this dissection are included here.

The departure of reproductives from the live nests with diet traps attached (Chapter 3), was recorded at every opportunity.

6.3 RESULTS

6.3.1 Empty cells

Between late January and early February, both species had 6-9% of worker and male cells empty (Fig. 6.1a). During the intervals prior to queen rearing, the percentage of empty worker and male cells rose, and then fell shortly afterwards. This decrease was followed quickly by a rapid increase, where percentages of greater than 90% occurred by interval 13 (early-May). The overwintering German wasp nest extracted in late-July had only 4.7% of worker and male cells empty. In contrast the annual nest extracted on the same day had 56.2% of worker/male cells empty (Fig. 6.1a).

The common wasp nest extracted in interval 8 (mid-March) had 47.2% of the queen cells empty, but by interval 10 (early-April), this value had dropped to zero. A gradual rise during intervals 11-12 was replaced by a rapid increase from interval 13 (early-May) onwards, where all nests had more than 85% of their queen cells empty (Fig. 6.1b). Throughout the season German wasp nests had fewer empty queen cells than common wasp nests, but their patterns were very similar. The initial percentage of 9.6±3.2% in interval 10 (early-April) declined to 1.2% by interval 12 (late-April), then increased rapidly to more than 85% after interval 13 (early-May) (Fig. 6.1b). The two German wasp nests extracted in interval 21 were very different, with the overwintering nest showing only 0.7% of empty queen cells.

6.3.2 Cells with eggs

Initially nests of both species had high percentages (c.24-30%) of worker/male cells with eggs (Fig. 6.2a). These dropped to c.9-13% by interval 10 (early-April), with the German wasps experiencing a brief rise in late April, before declining like the common wasp to around zero in May. The two German wasp nests taken on July 23 both had similar percentages of around 15-17% (Fig. 6.2a).

Common wasp nests showed a high percentage (53-91%) of queen cells with eggs during intervals 8 and 10 (mid-March and early-April), but this dropped to 19.6% by intervals 11 and 12 (mid-late April) (Fig. 6.2b). German wasp queen cells had a similar percentage around this time, peaking at 23.9±1.8% in interval 11 (mid-April). Egg laying in both species began to decline in late April, though the German wasp decreased at a slower rate than the common wasp (Fig. 6.2b). Two common wasp nests extracted in mid-June had a mean queen egg cell percentage of 10.1±0.8%, whilst the overwintering German wasp nest taken on July 23 had a percentage of 24.4% (Fig 6.2b).

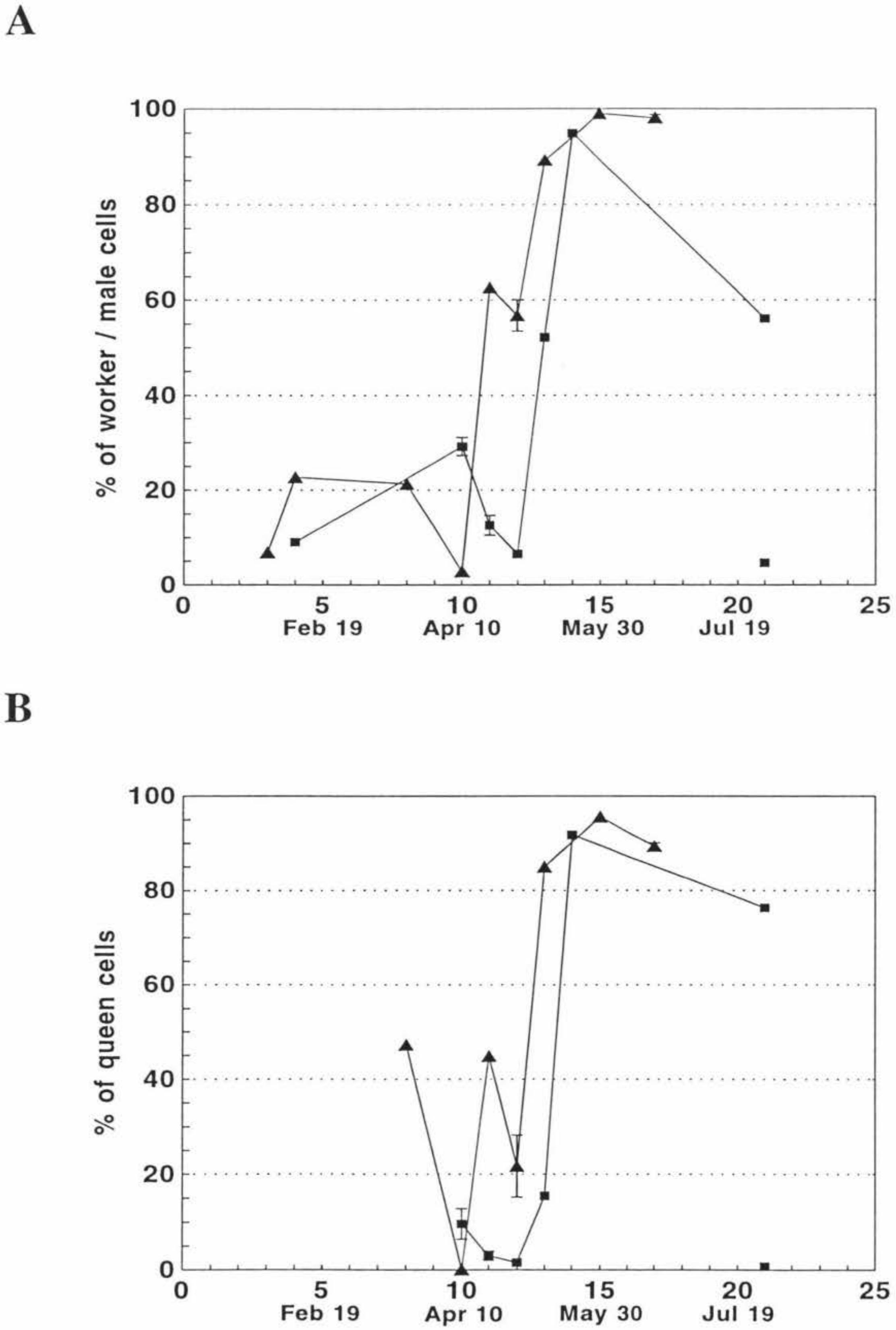
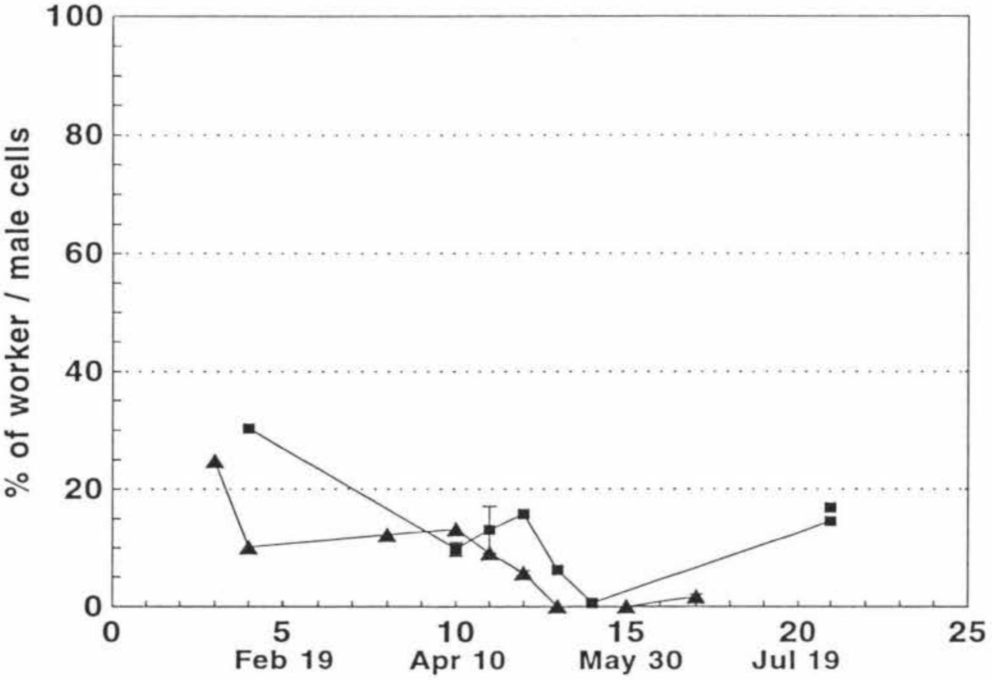


Figure 6.1 The percentage of empty cells in (■) German and (▲) common wasp nests, extracted in Palmerston North between January 23 and July 23 1993. (**A**) worker / male cells only (**B**) queen cells only. Bars show mean±1SE. Markers not joined by lines represent data for an overwintering nest.

A



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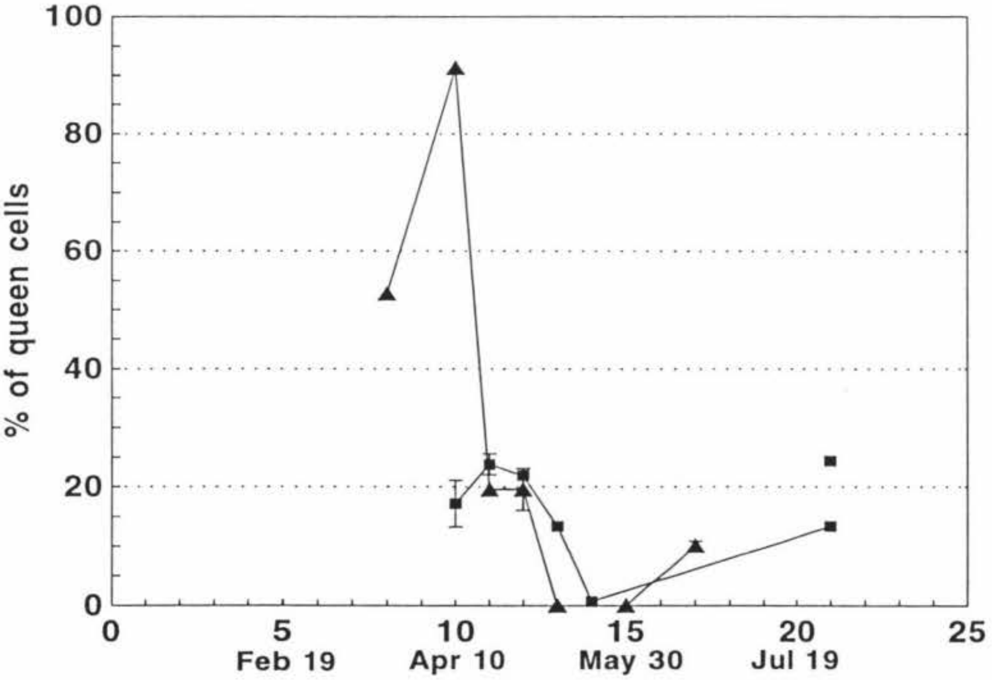


Figure 6.2 The percentage of cells containing eggs in (■) German and (▲) common wasp nests, extracted in Palmerston North between January 23 and July 23 1993. (**A**) worker / male cells only (**B**) queen cells only. Bars show mean±1SE. Markers not joined by lines represent data for an overwintering nest.

6.3.3 Cells with larvae

The percentage of worker/male and queen cells containing larvae was fairly constant for both species from February to mid-March (Fig. 6.3a), with common wasps around 32% and German wasps around 25%. However, in interval 10 (early-April) common wasp larvae rose to 38.1%, and by interval 12 (late April), the German wasp percentage had risen to 52.6%. From mid-April onwards, common wasp larvae declined in percentage, but German wasps lasted until late April before doing the same. The overwintering German wasp nest removed in interval 21 (late-July) had a percentage similar to the two German wasp nests extracted in interval 11 (mid-April) (Fig. 6.3a).

For both species the percentage of larvae grew faster in queen cells than in worker/male cells. Common wasps peaked at about 33% in intervals 11-12 (mid-late April), while the German wasp did so at around 43% in intervals 12-13 (late April-early May) (Fig. 6.3b). The queen larvae percentage of the suspected overwintering German wasp nest extracted on July 23 was comparable to that of the peak larvae percentage during interval 13 (early May).

6.3.4 Cells with pupae

German and common wasp nests had very similar percentages of worker pupae at c.35% in intervals 3-4 (late January-early February) (Fig. 6.4a). German wasp nests dropped to around 21% by interval 10 (early April), and continued down to zero by interval 14 (mid-May). Common wasp worker percentages remained above 30% during the same period, declining after interval 10 (early April), to zero in early May (Fig. 6.4b).

German wasp male pupae appeared in interval 4 (early February) at 0.6% and rose to a peak of 15±3.7% by interval 11 (mid-April) (Fig. 6.4a). Common wasp male pupae were not found in nests by interval 4, and used only 1.2% of cells by interval 8 (mid-March). They rose however, to a peak of 6.9±2.5% in interval 12 (late April), and declined to zero by early May (Fig. 6.4b).

The percentage of German wasp queen cells bearing pupae was greatest in interval 10 (early April) at 46±0.1% (Fig. 6.4a). After this it decreased steadily to zero in interval 14 (mid-May). The overwintering German wasp nest extracted in late-July had pupal percentages very similar to those found for each caste during their respective peaks (Fig. 6.4a). Common wasp queen pupae peaked at 28.9% in interval 11 (mid-April), and rapidly decreased to zero by interval 13 (early-May) (Fig. 6.4b).

6.3.5 Seasonal pupal composition

German wasp nests dropped from nearly 100% worker pupae in early February, to around 50% by early April. Over the same period, male pupae rose from 1.8% to over 30%, while queen pupae

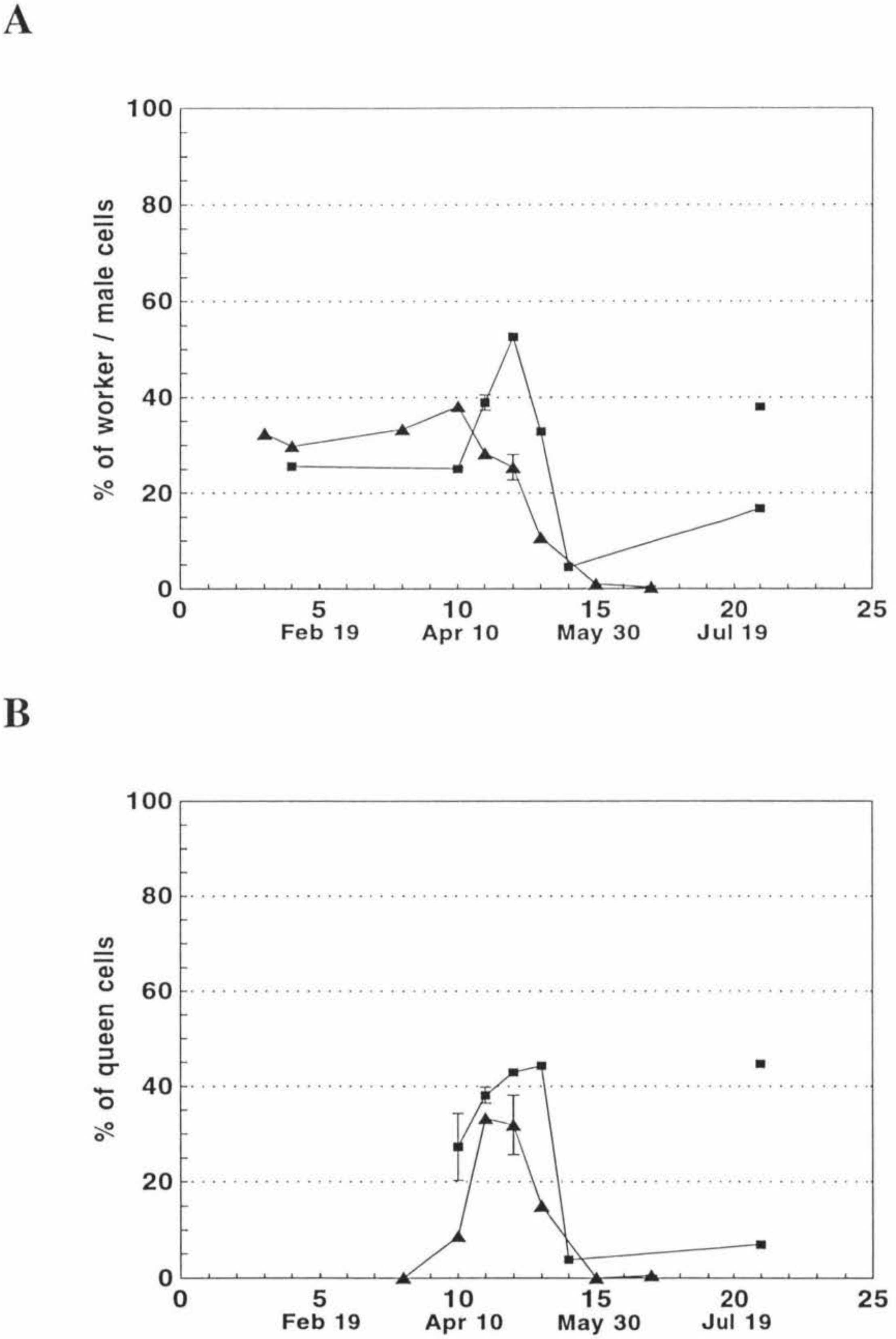


Figure 6.3 The percentage of cells containing larvae in (■) German and (▲) common wasp nests, extracted in Palmerston North between January 23 and July 23 1993. (**A**) worker / male cells only (**B**) queen cells only. Bars show mean±1SE. Markers not joined by lines represent data for an overwintering nest.

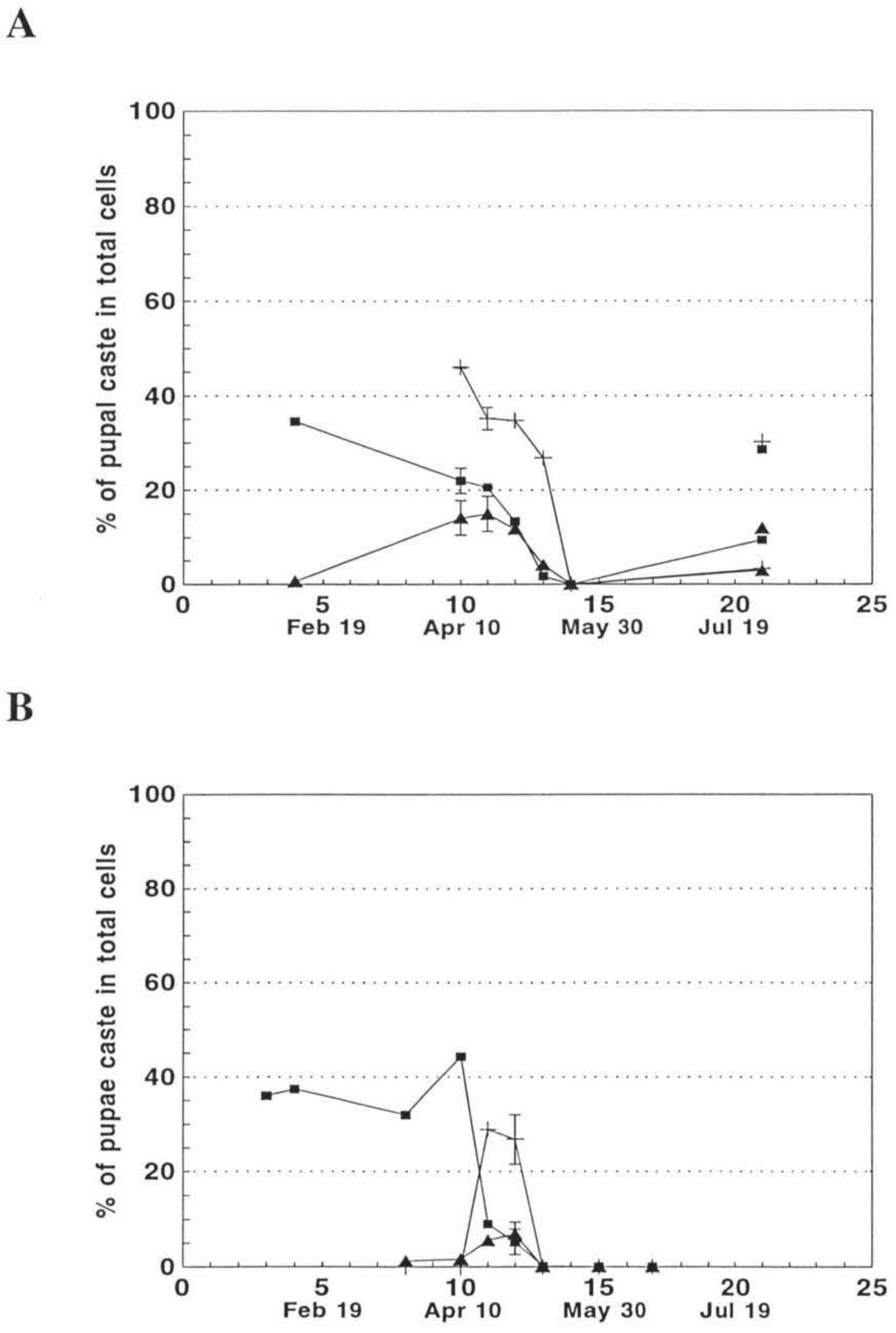


Figure 6.4 The percentage of pupae cells of each wasp caste found in *Vespula* wasp nests in Palmerston North, between January 23 and July 23 1993. The queen percentage is calculated from the queen cells only. (**A**) German wasp (**B**) common wasp. (■) = worker (▲) = male (+) = queen. Bars show mean±1SE. Markers not joined by lines represent data for an overwintering nest.

appeared initially at just under 20% (Fig. 6.5a). Worker pupae continued to decline through April, reaching zero by mid-May. Male and queen pupae rose to their respective peaks in early May, then also dropped to zero by mid-May. The composition of pupal castes in the overwintering German wasp nest appeared similar to that of German wasp nests around late March (Fig. 6.5a). Common wasp nests maintained a high percentage of worker pupae right through to early April, before declining very sharply to zero in early May (Fig. 6.5b). Male pupae recorded low percentages (under 4%) through March and early May, but rose to a peak of around 30% in early April. Queen pupae rose from zero percent in early April to a peak of 44.6±13.4% in late April, then declined sharply to zero by early May (Fig. 6.5b).

6.3.6 Peak pupae level

The percentage of larvae that were supported through to the pupal stage is shown in Figure 6.6. Between late January and mid-March, the percentage for both species stayed under 38%, but rose to around 45% by early April. The percentage of total pupae in common wasp colonies declined after this, while German wasp colonies lasted until late April before doing the same. The overwintering German wasp nest had a percentage equal to that found during the peak of the annual nests.

6.3.7 Departure and mating of the reproductives

Queens and males were regularly seen leaving German and common wasp nests from early May through to July (Table 6.1). No queens or males were seen leaving the Morris St common wasp nest during any of the sampling periods. The highest rate of queen departure was 24 queens per hour, recorded at two separate common wasp nests on May 5 1993. The German wasp nest observed on May 15 had queens leaving in the morning, but another sample in the afternoon revealed no departures. On only one occasion were queens observed leaving in the afternoon.

No pattern was evident in the departure, with males and queens leaving randomly. Both castes flew out and above the nest, some circling a few times before flying away.

In mid-June and early July mating was observed outside the German wasp nest. Both copulations took place on the ground, less than 5m from the nest entrance. From the time of discovery, copulation lasted between 20-30 minutes (pers. obs.). During one mating, another male tried to break the union, but the queen fended him off. After separation, in both cases, the queen preened her body, then flew away from the nest. Shortly after, the males involved did the same.

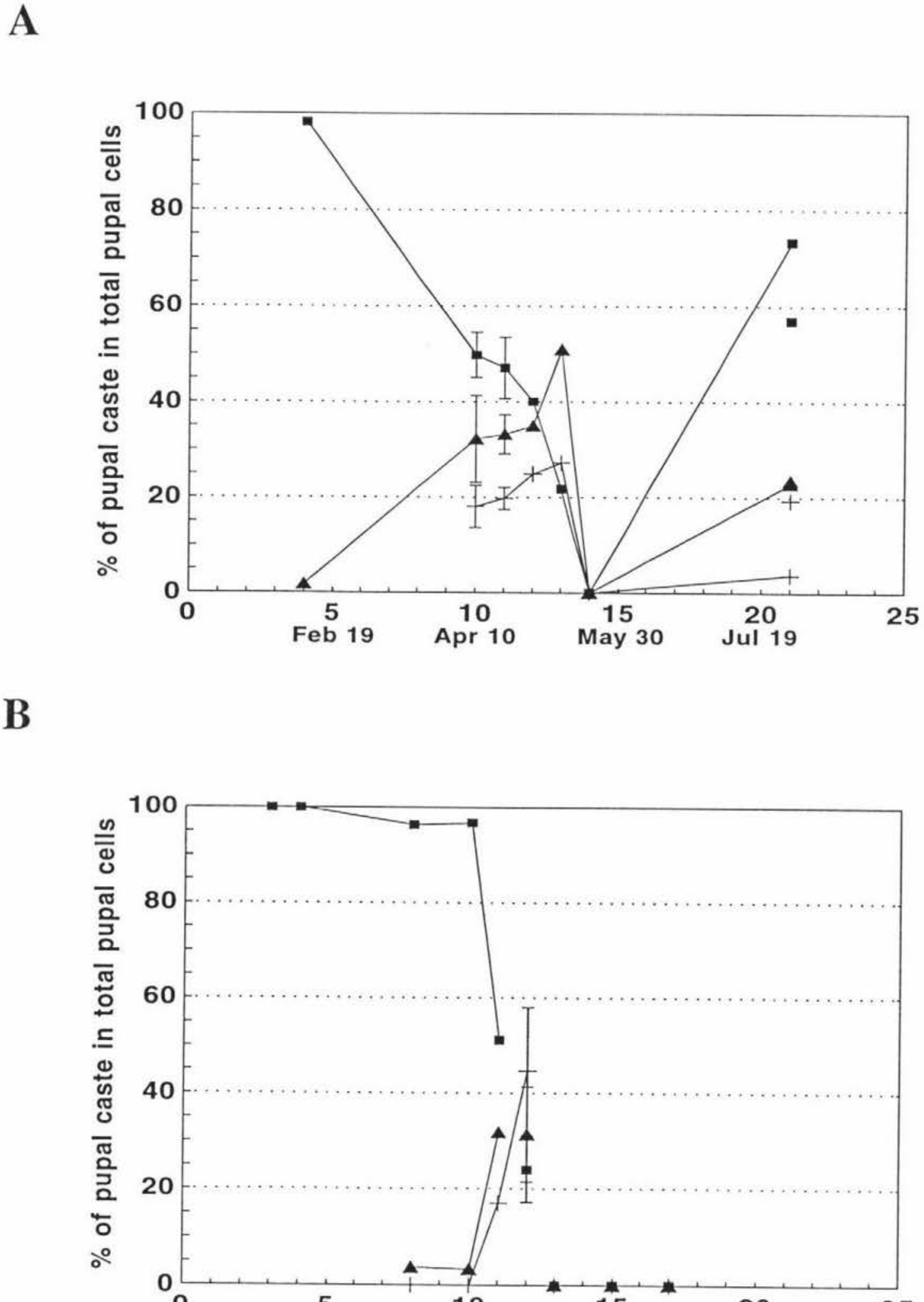


Figure 6.5 The percentage of pupae of each wasp caste, calculated from the total number of pupal cells found in *Vespula* spp. wasp nests in Palmerston North. Nests were extracted between January 23 and July 23 1993. (**A**) German wasp (**B**) common wasp. (■) = worker (▲) = male (+) = queen. Bars show mean±1SE. Markers not joined by lines represent data for an overwintering nest. Lines joining common wasp markers are broken to aid perception of trends.

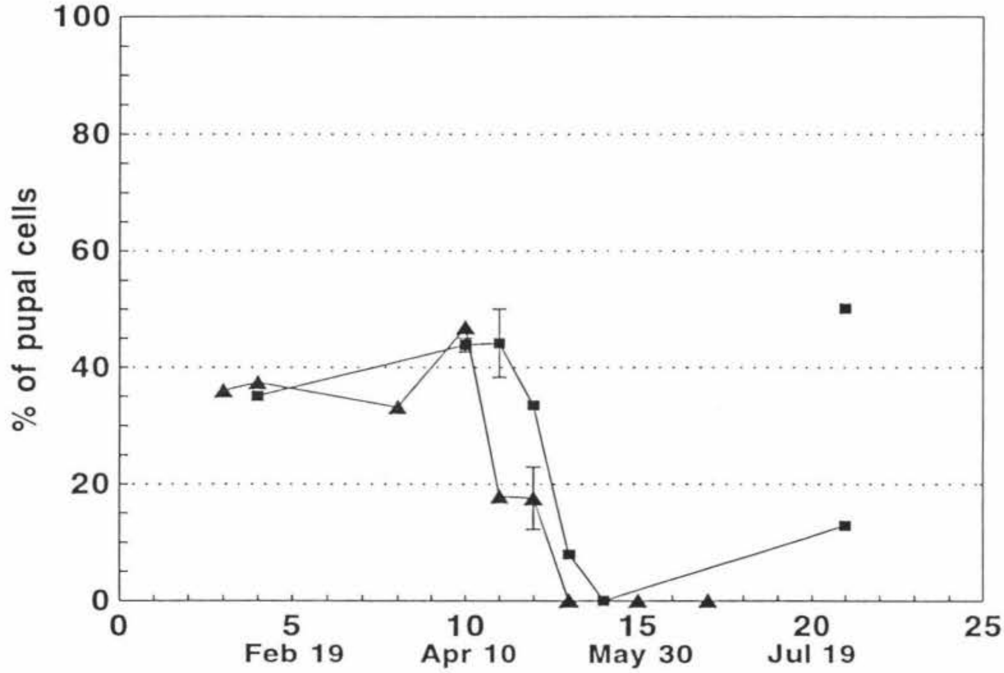


Figure 6.6 The percentage of cells that can support pupae in *Vespula* spp. wasp nests, extracted in Palmerston North between January 23 and July 23 1993. The percentage was calculated using the total number of pupae divided by the total number of worker / male cells. (■) = German wasp (▲) = common wasp. Bars show mean±1SE. The marker not joined by a line represents the percentage for an overwintering nest.

Table 6.1 Observations of queens and male wasps leaving *Vespula* spp. wasp nests in Palmerston North, between May and July 1993. * denotes day when mating was also observed. † = denotes the last observation before the colony's death. No reproductives were seen leaving the Morris St common wasp nest, so no record is displayed.

Date	Time NZST	Duration (minutes)	Ring Road V.v **rural**	Limbrick St V.v **urban**	Acacia St V.g **urban**
May 3	1105	10	3 queens	-	-
May 4	1300	10	2 queens	-	-
May 5	0930	10	-	4 queens / 18 males	-
May 5	1140	15	6 queens	-	-
May 6	1050	22	6 queens	-	-
May 7	1310	20	0	-	-
May 10	1030	10	-	-	2 queens
May 12	1020	30	-	-	0
May 13	1030	30	-	-	3 queens / 13 males
May 13	1125	10	0	-	-
May 13	1442	30	-	-	0
May 15	0908	42	-	-	2 queens / 46 males
May 15	1255	30	-	-	0
May 16	0950	40	-	-	2 queens / 12 males
May 17	0833	30	-	-	14 males
May 17	1337	30	-	-	0
May 18	0947	40	-	-	1 queen / 6 males
May 18	1105	10	-	1 queen / 9 males	-
May 28	1046	10	1 queen / 3 males	-	-
May 28	1142	10	-	0	-
May 28	1355	15	-	-	0
May 31	1150	10	-	-	0
June 3 †	0952	10	4 males	-	-
June 3 †	1325	10	-	1 male	-
June 3	1410	10	-	-	0
June 8	1500	10	-	-	0
June 10	1450	10	-	-	0
June 16 *	1015	10	-	-	1 queen
June 22	1400	10	-	-	0
June 25	1000	10	-	-	0
June 29	1110	10	-	-	2 queens / 1 male
July 2	0935	10	-	-	0
July 6 *	1015	10	-	-	1 queen / 2 males
July 9	0945	10	-	-	0
July 15	1315	10	-	-	0
July 22 †	1255	10	-	-	0

6.4 DISCUSSION

6.4.1 Appearance of the reproductives

6.4.1.1 Males

Production of male German wasps began in early February. Only 0.6% of all pupal cells contained males, but one had successfully emerged as an adult. No males were found in the common wasp nest taken in early February, and a lack of other nests in February and early March prevented pinpointing the switch to male production. However, common wasp nests extracted after mid-March contained male pupae and emerged males. The nest taken on March 17 and another taken on April 6 had very few male pupae, similar to the German wasp nests two months earlier. This indicates, for these two colonies at least, that the switch to male production was relatively late. These nests most likely reflect an annual fluctuation in phenology rather than a strategy peculiar to Manawatu common wasp colonies.

Fordham et al. (1991) found male production in Manawatu German wasp nests generally began sometime between January 30 - February 18, a period my results support. In Nelson, the appearance of males was similar for both species, but about two weeks later than those in Manawatu (Moller et al. 1991a). Fordham et al. (1991) suggested that different climate profiles and possibly a difference in the availability of habitat between different regions may have an effect.

When male production peaked in late April, proportionally there were twice as many male pupae in German wasp nests as in common wasp nests. In England, Spradbery (1973) found that German wasp nests produced males earlier than common wasps, leading to higher numbers of male German wasps. Earlier initiation by German wasps was also recorded in Nelson (Moller et al. 1991a). My data suggest that this occurred in Manawatu. If male production starts later in common wasp nests and relatively fewer are reared, then the resulting higher proportion of workers should have a positive effect on their colony dynamics. Knowing when the production of males occurs allows an assessment of how the differences may affect the following queen production. Such discussion is found in Chapter 5. Further comparison of the percentages of male pupae and number of emerged males, in both species, may shed light on the production of queens.

6.4.1.2 Queens

The presence of eggs in queen cells in the common wasp nest of March 17 indicated the start of queen production. This suggests that the switch had occurred sometime about March 12, because eggs take about five days to hatch (Spradbery 1973). Initiation of common wasp queen brood in Nelson is similar (Moller et al. 1991a). However, another Manawatu common wasp nest taken 3 weeks later had also just begun queen production, with the majority of cells containing eggs. Both Spradbery (1971) and Moller et al. (1991a) record a wide range in the initiation of queen rearing, and Manawatu nests appear to be no different.

Spradbery (1971) and Strambi (1990) suggest that a queen-produced pheromone causes workers to build queen cells, but what stimulates the queen in the first place to produce this remains unclear. Spradbery (1971) discounts seasonal factors such as photoperiod and temperature, and also suggests that intrinsic colony factors such as a decreasing ratio of larvae : workers may not be significant. He considers the physiological age of the queen to be the most likely requisite for initiating queen cell construction, but this has yet to be tested. Possibly the time when the queen started hibernation, its duration, or when it ceased affects the physiological age of queens, in such a way that differences in queen initiation result.

Because German wasp nests were scarce until early April, the start of queen rearing cannot be determined directly. However, by April 5, queen pupae were well established in one nest and, by April 10, emerged virgin queens were found in another. Fordham et al. (1991) calculated that German wasp queens emerged about 20 days after the first queen cells were built. Working backwards from the April 10 data suggests queen production began around March 21, matching the date given by Fordham et al. (1991), but about a week later than the range found for German wasp nests in Nelson (Moller et al. 1991a).

Spradbery (1971) and Moller et al. (1991a) record colonies of German wasps initiating queen production earlier than common wasps. My results do not appear to support this, but suggest that Manawatu German wasps may start queen production later than common wasps.

The decline in the frequency of queen pupae in German wasp nests after mid-April, and the increase in queen larvae during the same period illustrate the effect of a declining worker force. Worker pupae declined steadily after mid-April, indicating that the falling worker force was not being replaced. When larvae are tended less frequently by the remaining workers, natural starvation results. Harris (in press) found that the maximum period of queen larval starvation after which queen pupae could still hatch was five days. If the threshold weight required for successful pupation is not reached, the larvae die. Archer (1980) also suggested that a large number of larvae late in the season, along with few accompanying pupae, indicates neglect by workers. Although there are not enough workers to continue tending all the larvae, the queen still lays eggs which hatch into queen larvae. However, these larvae never pupate, and the pupal percentage eventually drops to zero (Archer op. cit.).

6.4.2 Cell use

6.4.2.1 Empty worker and male cells

The low frequency of empty worker/male cells in early season nests of both species is possibly related to the small size of the nest. This may also help explain the low percentages found in some nests during April as well. Similar sized early season German and common wasp nests had comparable empty worker/male cell percentages, but as the season progressed and nest sizes increased, more cells became disused. This may have several causes. Larger nests may reduce the queen's ability to move freely through the vertically higher, earlier produced comb, because the distance required to service it is too great. Laying eggs in cells found higher in the nest may become harder to achieve as the nest grows downwards, since this is where the queen spends most of her time (Spradbery 1971). Furthermore, Spradbery (1971) also suggests that decomposing faecal material in the higher cells may make them less attractive for oviposition. However, the egg laying ability of the queen may be the most significant factor. After the initiation of the colony, the number of cells may no longer limit oviposition (D. M. Leathwick, pers. comm.), but there does appear to be an upper limit to the rate at which the queen can lay eggs. The highest daily oviposition rate recorded in a German wasp nest is 330 eggs day^{-1} (Spradbery 1971). The highest values I recorded were 304 eggs day^{-1} in an annual common wasp nest, and 342 eggs day^{-1} in an annual German wasp nest. For comparison, the overwintering German wasp nest, probably with several fertile queens inside, recorded 950 eggs day^{-1} (unpub. data). Although larger nests have more cells available for oviposition, the queen cannot infinitely increase her egg laying to accommodate all empty cells. Since most of the oviposition will be carried out in the newest cells, many older cells remain empty.

Three small nests found during April further support this idea. A common wasp nest found in early April, containing 4166 worker/male cells, had only 2.8% of empty worker/male cells. Two German wasp nests found in mid and late April, containing 2813 and 4799 worker/male cells, had empty cell percentages of 6.5% and 10.5% respectively. In comparison, two other German wasp nests found in early April, containing 10178 and 7404 worker/male cells, had empty worker/male cell percentages of 31.1% and 27.3% respectively. It would seem that smaller nests may contain fewer empty worker/male cells, until at least the peak of the season, because these cells available for oviposition are at a premium, and the queen will utilise as many of them as she is able.

However, once queen rearing has begun, worker production decreases (Spradbery 1973), and the size of the nest no longer appears to influence the percentage of empty worker/male cells. A small German wasp nest found in early May had only 4188 worker/male cells, but because queen rearing was well under way, the attention given to laying eggs and rearing larvae in these cells had dropped markedly. As a result, over 50% of the worker/male cells were empty.

6.4.2.2 Empty queen cells

The high percentage of empty queen cells in the common wasp nest found on March 17 probably reflect a recent switch to queen rearing. Only 103 eggs had been laid in the total 195 queen cells, and none had hatched. It has already been suggested that the switch to queen rearing probably occurred around March 12. If workers can concentrate on building queen cells because they have no queen larvae to tend to, then their rate of cell building may outstrip the queen's rate of egg laying. A five day period of intensive queen cell building may explain why so many queen cells were empty at this time.

The converse of this may be seen in the common wasp nest taken in early April. Having built only 206 queen cells, this nest appears to have initiated queen rearing late in the season. Larvae were found in 18 of these cells, the remainder containing eggs. Matsuura (1990) comments that workers give the queen larvae priority, and the increased attention needed to satisfy the larvae's extra protein requirements (Chapter 7) may result in fewer workers available to build cells. It is possible that the extra-nidal activities associated with these larvae slow the rate of cell building to a level where the queen could manage to lay eggs in the remaining empty cells. This could account for the lack of empty queen cells at this time. Low percentages were also evident in the German wasp nests found during the peak of queen rearing (mid-late April), and may also result from a distracted worker force.

The sudden rapid increase in the percentage of empty queen cells matches the pattern shown in the worker/male cells. Continuing mortality of the worker caste without further recruitment results in a declining number of workers in the colony. Not only does their ability to provide for the queen larvae decrease, but eggs take longer to hatch as the colony gets older (Brian & Brian 1952, cited in Spradbery 1973), possibly because of lower nest temperatures. Uncared for larvae are removed from the nest (Spradbery 1973; pers. obs.), and eggs are cannibalised by the remaining workers (Matsuura 1990).

6.4.2.3 Worker and male brood

The percentage of worker/male cells containing eggs began to decrease in late March-early April, probably because of the switch to queen rearing. Spradbery (1973) considers that the demand for oviposition in the newly built queen cells overrides the previous attention given to the worker/male cells. However, although all worker/male cell construction stops, oviposition continues in these cells at a reduced rate. As the season progresses, the increasing mortality of worker and male eggs (Archer 1980), and a reduction in the fecundity of the aging queen (Spradbery 1973) brings the percentage of worker brood to zero.

Both vespulid species had fairly stable larval percentages of around 30-40% throughout the growth phase of the season, and were very similar to those recorded by Spradbery (1971). Fordham et al. (1991) calculated c.18% of the total comb area in German wasp nests was used by larvae, but that study employed a different, less precise census method. Fordham et al. (1991) suggest that the rather stable percentage of larvae throughout the season indicates a limit to the number of larvae that can be serviced by workers. The steady percentage of cells used to rear pupae supports this conclusion. Initially around 35% for both species, it rose to about 45% after queen production began. This rise during the production of queens is the result of an increasing number of queen pupae, without a relative increase in the number of worker/male cells. Pupation indicates completion of larval development, thus the decline in the total pupal percentage reflects the decreasing attention given to all larvae. It may also reflect the impact that males have on the larval stage, where excessive trophallaxis can hasten the death of the larvae (Spradbery 1973).

The percentage of cells containing larvae was considerably higher than those containing eggs. Spradbery (1973) suggests that because the development time of the larval stage is longer than the incubation period of the egg, the number of larvae continues to accumulate.

6.4.2.4 Queen brood

The percentage of common wasp queen egg cells was high in the nest taken in early April, because it had only just begun queen rearing and few larvae had hatched. This dropped in nests by mid-April and both species showed similar percentages throughout the remainder of April. The steady percentage in queen egg cells of around 20-25% indicates that there is some form of constraint on oviposition in queen cells at this time. For both species queen cells take around 1.5 times as much woodpulp as other caste cells to produce (Chapter 5), and because the steadily declining worker force returns with fewer woodpulp loads (Chapter 7), these cells probably take longer to build than worker/male cells. If this is so, the low percentage of empty queen cells implies that they will be in demand, and that the availability of queen cells may be the factor limiting oviposition during this period.

Queen larvae and pupae rose to similar peak percentages as those seen in the worker/male cells, but over a much shorter time frame. This is probably because the greater proportion of attention given to the queen larvae enables them to develop more quickly and pupate sooner.

However, the upper limit to larvae production remained, and peaked for a shorter period of time, because the number of workers required to maintain adequate care were declining rapidly.

6.4.3 Climax and decline of the colony

The departure of reproductives from nests in Manawatu was first noticed in early May, but may have occurred earlier, because observations took place during diet sampling which was often days apart. Thomas (1960) records mating flights in German wasp nests as early as March 16, but such instances are likely to be exceptions.

For the 3 study nests, estimating the time between the initiation of queens (Chapter 7) and the first observation of their departure, gives 43 days, 31 days, and 21 days respectively, for the Ring Rd, Limbrick St, and Acacia St nests. Gaul (1951, cited in Spradbery 1973) and Matsuura (1990) state that reproductives leave the nest as they mature, and may only stay in the nest for 1-2 weeks. If we assume the development of queens from an egg to an adult is 34 days (Archer 1980), then these data suggest that calculated dates of departure of queens from the Limbrick St and Acacia St nests are too early. However, this may be explained in the following way. Because queen development varies with nest temperature and food availability, both of which are directly related to the number of workers, the development estimate varies with time of season. Also, the estimates of queen initiation in the above nests were based solely on the rise in protein return, hence reflecting demands of the larval stage, and not the building of the first queen cells. Archer (1980) says the biggest gains in larval weight do not occur until the fourth or fifth instar, which is not reached until around 12 days after oviposition. Considering all the above, the initiation of queen cell building may have a margin of error of more than two weeks. This would support my earlier data on the appearance of the reproductives, and bring my conclusions on their departure into line with past research.

The period between the first and last sighting of queens leaving the nest was 25 days, 13 days, and 57 days for the above nests. This fits in with the observations of Spradbery (1973), where he notes that the flight activity of the reproductives could be up to 8 weeks or more. It is unlikely that my estimates include the very first and last mating flights, therefore these data represent a minima of flight activity.

Records of mating between vespulid wasps are few, but Thomas (1960) has described it for German wasps in New Zealand. He reports that copulation usually takes less than 5 minutes, but this does not appear to be so in the two cases I observed. When found, both were already in copulation, and it is unknown how long they had been so. Richards (1937, cited in Spradbery 1973) records an eyewitness account of a German wasp queen *in copula*, and mentions that the union lasted around half an hour. These data indicate that mating in German wasps probably takes longer than five minutes.

Thomas (1960) records that males leave the nest in mid morning, and are soon followed by the queens. Although I also observed the majority of reproductives leaving during the morning period, I saw no pattern between the males and queens exiting the nest. The departure of both castes appeared random, with queens and males leaving intermittently. My observation of mating occurring close to the nest is supported by eyewitness accounts in Spradbery (1973). Thomas (1960) records that after mating, queens and males return to the nest for a short period of time, but no explanation as to why they may do this is given. I did not observe such behaviour, but in both cases, watched queens and males fly away from the nest. Presumably the queens sought hibernation sites shortly afterwards.

With the departure of the reproductives, the social organisation in the colony disintegrates, and production in the nest declines rapidly. The seasonal pattern of empty worker/male cells and queen cells is similar in both species, but the timing of decline is later in German wasp nests. This same trend is apparent in the percentages of egg and larval cells as well. The active but declining annual German wasp nest taken on July 23 1993 gives further support to this. Moller et al. (1991a) found that German wasp colonies in Nelson go into decline slightly later than common wasp colonies, which supports my observation.

6.4.4 Overwintering brood

The abundance of functional queens in overwintering German wasp nests causes oviposition to be less ordered than that seen in annual nests (Thomas 1960; Spradbery 1973; plates 6.7 & 6.8). Multiple eggs are often laid in single cells; I counted 21 in one worker/male cell of the overwintering nest (pers. obs.), and Spradbery (1973) has record 20 eggs in one cell. In other cases, eggs were laid in cells that already contained larvae. Spradbery (1973) believes this indicates considerable pressure on the functional queens to oviposit, but cannibalism of these extra eggs and larvae may prevent wastage.

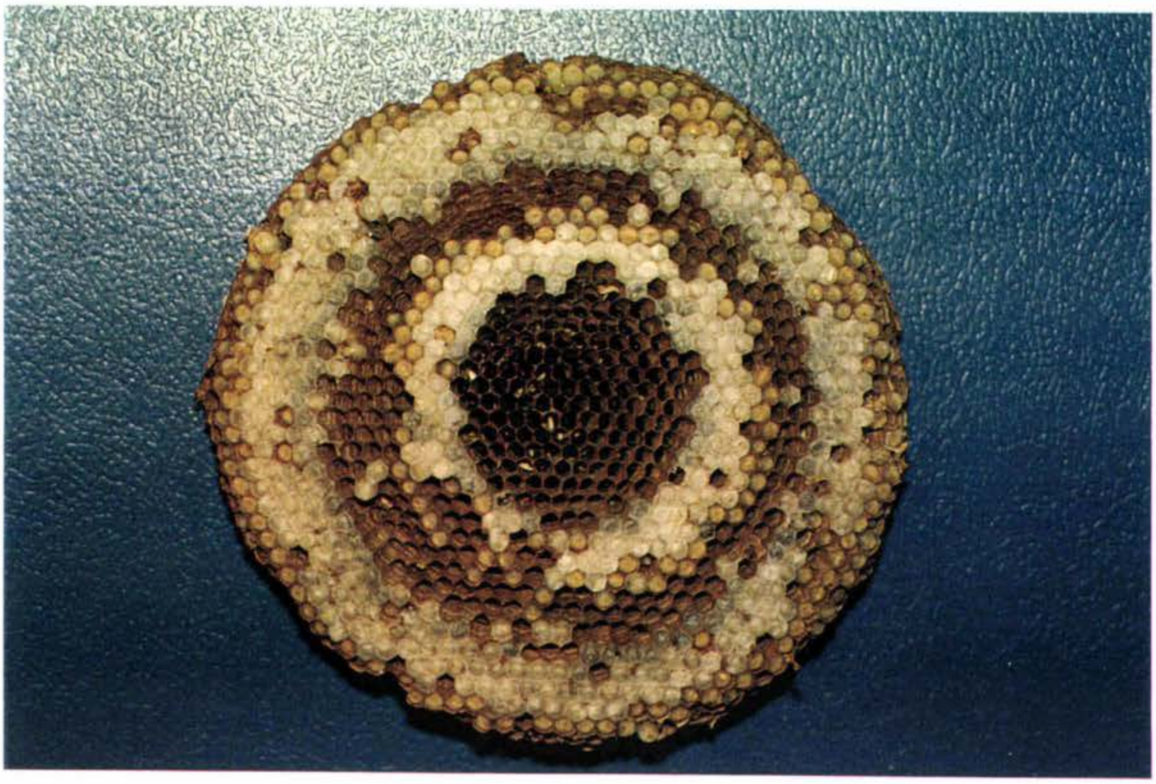
The percentages of empty cells, and of cells with eggs or larvae, were similar to those found during their respective peaks in annual nests, which implies that the production of queens may continue at high levels during the winter months. Thomas (1960) found that the majority of production in winter was queen brood, which supports this conclusion. The large numbers of queens that such nests produce could be expected to affect the balance of *Vespula* species where

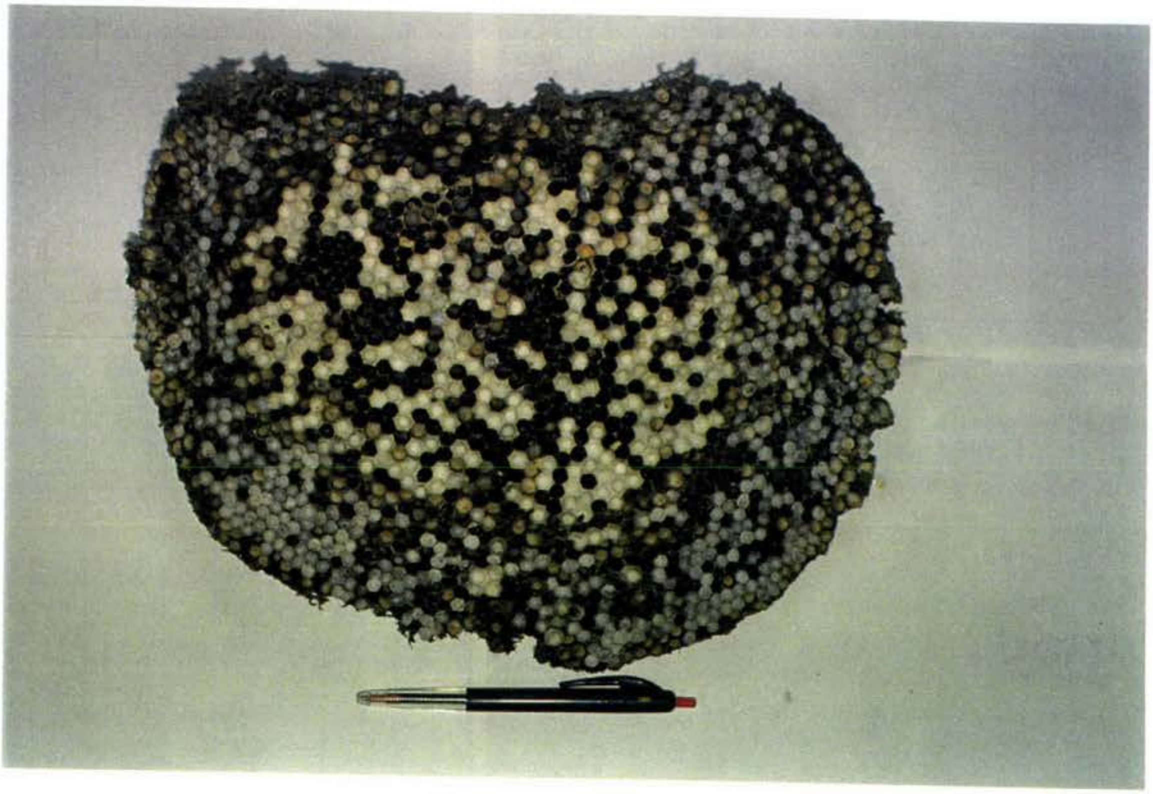
PLATE 6.1 ANNUAL COMMON WASP NEST COMB

The strict order of oviposition found in an annual *Vespula vulgaris* nest is here typically displayed in the fourth comb layer of the Clifton nest taken on April 15 1993 (see Appendix 2). Two generations had already been produced in the inner empty area, with a second generation coming through in the inner pupal ring, and a first generation pupating in the oute pupal ring. Size: 1336 cells.

PLATE 6.2 PERENNIAL GERMAN WASP NEST COMB

Oviposition chaos is seen in the 11th comb layer of an overwintering *Vespula germanica* nest extracted on July 23 1993. The disorder results because the multiple fertile queens compete for the vacant oviposition sites. Note the band of worker/male cells encompassing the central queen cell area, indicating that worker/male cell building had been reinstated for the winter season. Size: 2028 cells.





overwintering nests occur. However, Moller et al (1991a) query why common wasps can outnumber German wasps in some habitats, and have caused localised extinction of German wasps in honeydew beech forests. It has been determined that competition for this limited resource has been the principal factor in driving this displacement (Harris et al. 1994). Harris & Beggs (in press) found that small queens were under-represented in the reproductive population sampled during spring. This indicated that small queens were less likely to survive through winter. Harris (in press) found that starving larvae produced smaller adults, as long as a threshold weight allowing pupation to occur was reached. If protein sources become scarce during winter, natural starvation may result and queens produced in overwintering nests during this time may be smaller. The higher mortality associated with their size may reduce the population considerably, and negate much of the winter production. Research similar to that of Harris & Beggs (in press), but for overwintering nests would be invaluable.

The percentage of pupae in all three castes also appear to be maintained at levels similar to the peaks in annual nests. This indicates that there is still some control present in the nest, even though the phenology and dynamics have markedly changed. Overwintering nests no older than 18 months have been discovered (Spradbery 1973; R. J. Harris, pers. comm.; pers. obs.), and it is not known how long such nests could continue if left alone. Studies of the individual behaviour and interactions between functional queens could provide answers on why the complex social structure of an overwintering nest remains viable for so long.

Queens which leave perennial nests through winter to early summer, and successfully initiate nests, may illustrate a different phenology to a nest founded by a queen from an annual nest. Donovan (1991) records small German wasp nests in late summer, attributing this to queens leaving overwintered nests around this time. It is known that queens do not need to hibernate before initiating nests (D. M. Leathwick, pers. comm.). If the physiological age of the queen helps to determine the phenology of the colony, then the outcome in such late initiated nests would be instructive. If such nests could be followed through to the climax of the season, they could provide further information on vespulid phenology.

Chapter 7 WASP DIET

7.1 INTRODUCTION

The diet of a vespulid wasp colony centrally concerns the supply of protein, carbohydrates and water (Edwards 1980). Foraging wasps scavenge, and prey upon many species, returning with provisions which are fed to the colony's inhabitants. Protein is given solely to the larvae but, by means of trophallaxis, non-foraging nurse wasps share the regurgitated carbohydrates and water (Spradbery 1973).

The dietary preferences and predatory skills of foraging workers from *Vespula* colonies have been recorded in several overseas studies (Potter 1965; Free 1970; Archer 1977; Gambino 1986). The division of labour between foraging workers, their individual behaviour when foraging, and load capabilities have all been studied in northern hemisphere ecosystems. However, apart from a few observations where general estimates of wasp predation have been made (Barrington 1896; Watson 1922, cited in Edwards 1980), no overseas research has focused on the potential impact these wasps can have on invertebrate communities in different habitats.

There have been general records of wasp predation in New Zealand (Fordham 1961; Gibbs 1980, Kleinpaste 1980; Little 1981), but these are surprisingly few considering the time that has passed since the German wasp was declared established (Thomas 1960). As early as 1952 alarm was raised about possible competition between German wasps and native birds (Anon. 1952), but it was about 35 years before any relevant research was undertaken (Moller et al. 1988; Moller & Tilley 1989; Beggs & Wilson 1991).

Further concerns were expressed when the common wasp was found to be established in Wellington in 1978 (Donovan 1984). Their rapid spread and colonisation of diverse habitats prompted a flurry of wasp research in the late 1980s. Dietary studies of both wasp species in a honeydew beech forest south-west of Nelson (Harris 1991) and in scrubland-pasture near Hamilton (Harris & Oliver 1993) have quantified wasp impact on invertebrates in these two habitats.

This study complements those findings by describing the diet and foraging ecology of vespulid wasps in urban and rural habitats. Estimates of the prey provision and woodpulp collected are made, to quantify their role in colony development and nest building.

7.2 METHODS

Vespula wasp nests were located in Manawatu between January and August 1993. This was achieved through contact with pest control services, the Manawatu-Wanganui Regional Council, and members of the public. Nests of both species in urban and rural habitats were selected for diet trap attachments (see Harris 1991). One rural and two urban common wasp nests were used, but only one urban German wasp nest was suitable. Two suitable rural German wasp nests were found too late in the season to be of any use. Nests found between January and March were sampled regularly through the season, by means of diet traps, until the nest failed in late autumn or winter. On each day of sampling, the date, time of day (NZST), general weather conditions and 'traffic rate' (average number of wasps leaving and returning to the nest in 10 min) were recorded. Returning foragers were caught in the entrance trap and anaesthetised with CO_2. Sampling duration ranged from 4 min (colony peak) to 17 min (colony death), with individual samples taking 2-3 min each. The number of wasps captured, total sampling time, and number of prey fragments were recorded. All fragments were kept for identification and fresh weights recorded.

Chi-square analysis was used to investigate the effect habitat and species had on relative prey abundance. Analysis of variance (ANOVA) evaluated the effect habitat and species had on the weight of prey returned.

Estimates of prey loads and woodpulp returned to the four nests during March-April 1993 were made, using NZST daylight data (Gerlach 1974), and an adjusted form of Harris' (1991) daily prey consumption equation, where:

prey/woodpulp consumption during March-April = mean (±SE) traffic rate × mean (±SE) mins of daylight × proportion carrying prey/woodpulp × 61 days.

The period of March-April was chosen as this contained the seasonal peaks of all four nests and therefore would illustrate their foraging potential. The amount of daylight for this 61 day period averaged 698±17 minutes.

Estimates of the prey biomass consumed during this same interval were derived from the following equation:

biomass of prey consumed during March-April = mean (±SE) prey weight returned per minute × mean (±SE) minutes of daylight × 61 days.

Meteorological data (daily windrun and rainfall) were obtained from AgResearch Grasslands, Palmerston North, to complement the temporal weather observations.

7.3 RESULTS

7.3.1 Wasp diet

Between February and July 1993 a total of 5902 common wasps and 2400 German wasps were sampled (Table 7.1). Of these, 656 common wasps (11.1%) and 381 German wasps (15.9%) were carrying protein items. Woodpulp was returned by 5.6% common- and 3.4% German wasp foragers respectively. Fruitpulp foraging occurred in only one nest of each species, the overall return coming from less than 0.3% of foragers for both species.

The overall period of colony observation ranged between 66 days (Morris St) and 114 days (Acacia St), averaging an interval of 5.4 days (Acacia St) to 8.3 days (Morris St/Ring Rd) between samples (Table 7.1). The total sampling duration of common wasp diets was 4 hours 43 minutes, with German wasps at 3 hours 31 minutes. This averages the traffic rate of common wasps at 20.9 wasps minute^{-1} and German wasps at 11.4 wasps minute^{-1}.

7.3.2 Relative prey abundance

Statistical analysis of total prey abundance was inappropriate as the opportunity for extra harvesting resulted in biased samples. However between February and April comparisons of prey abundance between colonies for a combined interval of 24 minutes was possible, showing that the relative abundance of the four main prey groups caught by both species and between habitats were significantly different (Table 7.2: $\chi^2 = 69.405$, df = 9, $P < 0.001$).

Chi-square tests for the species and habitat combinations revealed significant differences. The Limbrick St common wasp colony caught more Hemiptera but fewer spiders than the Morris St colony (Table 7.2: $\chi^2 = 29.127$, df = 3, $P < 0.001$). More Hemiptera and Lepidoptera were caught at Limbrick St than both the rural and German wasp nest (Table 7.2: $\chi^2 = 15.995$, df = 3, $P < 0.001$; $\chi^2 = 27.664$, df = 3, $P < 0.001$).

The Morris St common wasp colony caught more Hemiptera, Lepidoptera, and spiders in comparison to both the rural and German wasp colonies (Table 7.2: $\chi^2 = 22.456$, df = 3, $P < 0.001$; $\chi^2 = 17.506$, df = 3, $P < 0.001$). The rural common wasp and German wasp colonies did not differ significantly.

Due to low counts and zero values for some Diptera families in this period a χ^2 analysis of all families could not be performed. However a χ^2 comparison of the two most frequently caught Diptera between habitats showed significant differences.

Table 7.1 Summary of wasp diet data collected from *V. vulgaris* (V.v) and *V. germanica* (V.g) nests in urban and rural habitats, Palmerston North, between February and July 1993.

		LOCATION		
	Limbrick St **V.v urban**	Morris St **V.v urban**	Acacia St **V.g urban**	Ring Rd **V.v rural**
Total wasps	3025	1678	2400	1199
Total protein	320	216	381	120
Total woodpulp	181	72	82	75
Total fruitpulp	4	-	7	-
First day sampled	19 Feb	26 Feb	31 Mar	30 Mar
Last day sampled	3 Jun	12 May	3 Jul	22 Jun
No. days sampled	14	9	21	8
Total sample time (min)	122	94	67	211

Table 7.2 Number of prey items in the four main prey groups returned by foragers to *V. vulgaris* (V.v) and *V. germanica* (V.g) nests, in urban and rural habitats, Palmerston North. The data represents combined samples totalling 24 minutes each, taken between February 26 - April 23 1993.

		LOCATION		
	Limbrick St **Vv urban**	Morris St **Vv urban**	Acacia St **Vg urban**	Ring Rd **Vv rural**
Diptera	54	68	67	55
Hemiptera	30	17	6	5
Lepidoptera	41	47	17	20
Araneae	10	55	19	7

The rural common wasp colony caught significantly more syrphids than any other location (Table 7.3: Morris St: $\chi^2 = 19.166$, df = 1, $P < 0.001$; Limbrick St: $\chi^2 = 23.610$, df = 1, $P < 0.001$; Acacia St: $\chi^2 = 6.346$, df = 1, $P < 0.05$) but significantly more tipulids were returned to the urban common wasp colonies. There was no significant difference between the relative abundance of tipulid and syrphid items returned to the two urban common wasp colonies.

7.3.3 Seasonal prey abundance

The relative seasonal abundance of different prey groups for both species and habitats is shown in Fig. 7.1. Between February and July Diptera remained the most important prey item for all colonies. It was the most abundant item in the Morris St and Ring Rd colonies, peaking at 75% in April and 85% in May respectively.

Lepidoptera larvae were the second most important item throughout the Limbrick St colony's season, providing between 26% and 34% of all diet items. In contrast Araneae were the German wasp nest's secondary item, supplying between 19% and 32% throughout the season. Unsynchronized nest sampling initiation and different harvesting rates throughout the season made statistical analysis of the prey groups inappropriate.

7.3.4 Overall prey abundance

Total prey abundance figures were very similar to the proportions of the prey groups caught during the February-April period. Diptera remained the most frequently returned item for all nest locations regardless of habitat or species (Table 7.4). The two urban common wasp colonies returned very similar proportions whilst a higher proportion was returned to the rural common and urban German wasp colonies. Lepidoptera and Araneae fragments were in the top 3 contributors for 3 of the 4 colonies.

Tipulids were the most frequently returned Diptera item in all urban colonies (Table 7.5). Nearly half of all Diptera returned to the rural colony were of syrphid origin. Calliphorids were at least twice as often brought back in the rural habitat, making up only 3-9% in other situations. Sarcophagids provided over 25% of all Diptera items returned to the German wasp colony, but less than 10% for all other situations (Table 7.5).

7.3.5 Prey weight

German wasp foragers returned with the heaviest mean fresh weights in 5 of the main prey groups (Table 7.6). Diptera, Hemiptera, Lepidoptera, Araneae, and 'other' (which includes vertebrate muscle) were all significantly heavier than those carried by common wasp foragers (ANOVA $P <$

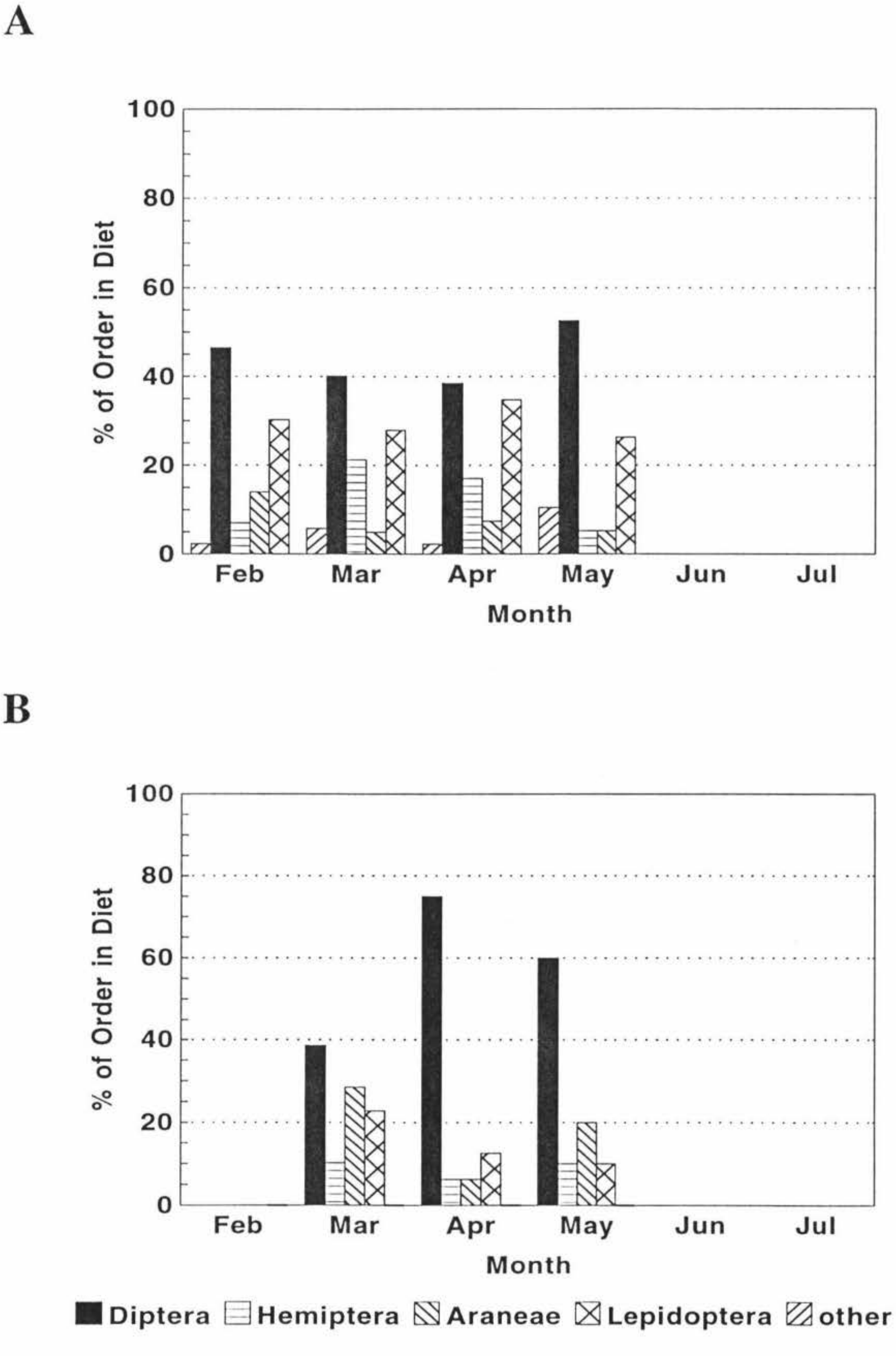
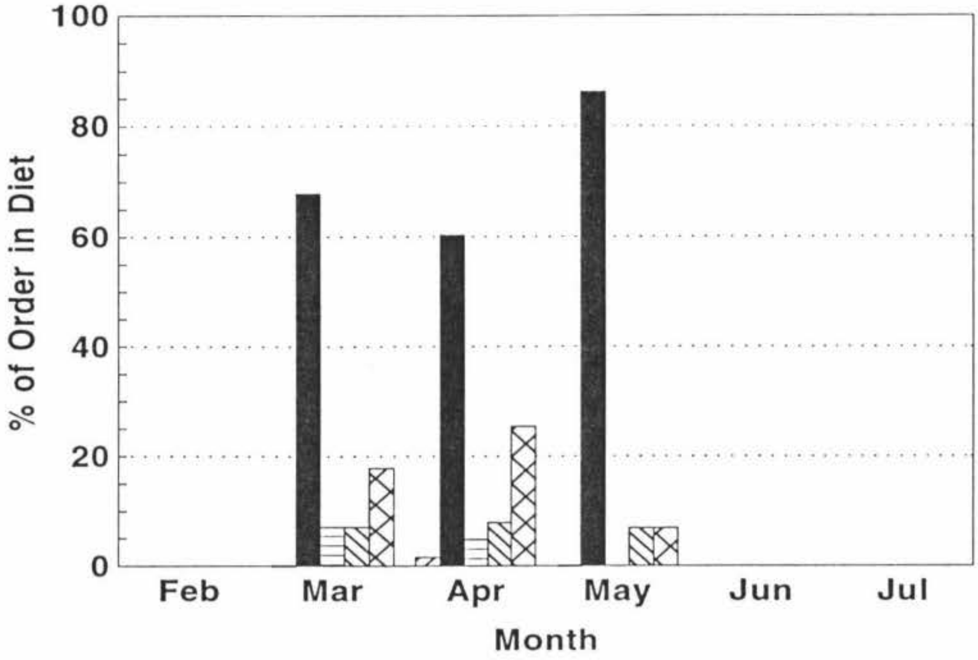


Figure 7.1 Relative seasonal abundance of arthropod prey items returned to *Vespula vulgaris* (V.v) and *V. germanica* (V.g) nests in urban and rural habitats in Manawatu, between February - July 1993. (**A**), (**B**) Limbrick / Morris St - **urban V.v** (**C**) Ring Rd - **rural V.v** (**D**) Acacia St - **urban V.g**.

C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% of Order in Diet
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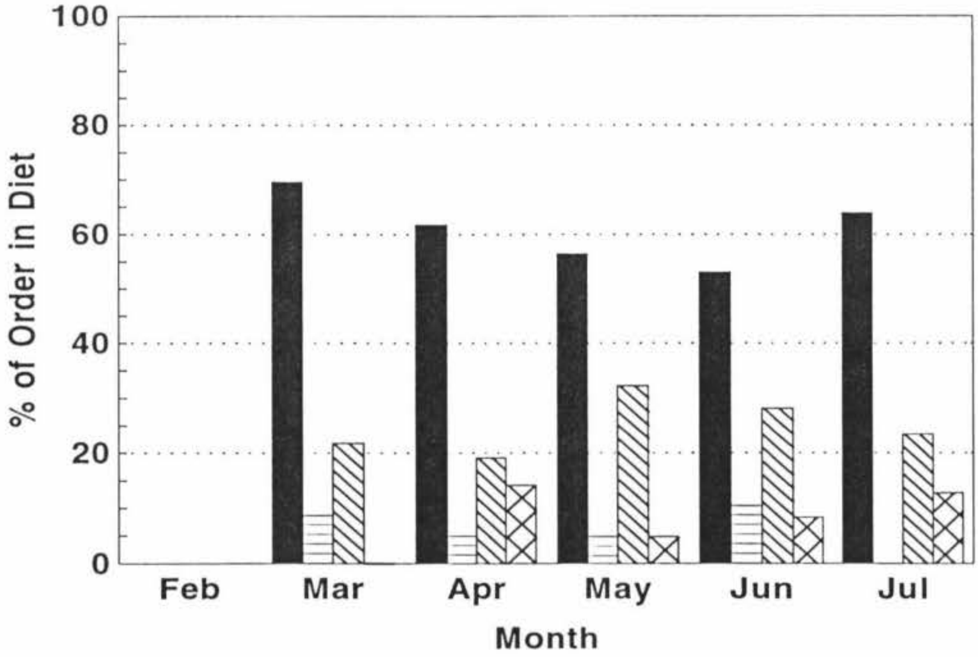
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% of Order in Diet
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Table 7.3 Number of Diptera prey items of the two main families returned by foragers to *V.vulgaris* (V.v) and *V. germanica* (V.g) nests, in urban and rural habitats, Palmerston North. The data represents combined samples totalling 24 minutes each, taken between February 26 - April 23 1993.

	LOCATION			
	Limbrick St **Vv urban**	Morris St **Vv urban**	Acacia St **Vg urban**	Ring Rd **Vv rural**
Tipulidae	34	30	18	13
Syrphidae	6	7	11	28

Table 7.4 Ranked proportions of insect Orders in the total protein samples taken from *V. vulgaris* (V.v) and *V. germanica* (V.g) nests in urban and rural habitats, Palmerston North, between February-July1993.

LOCATION			
Limbrick St **V.v urban**	Morris St **V.v urban**	Acacia St **V.g urban**	Ring Rd **V.v rural**
Diptera 0.4094	Diptera 0.4000	Diptera 0.5748	Diptera 0.6833
Lepidoptera 0.3094	Araneae 0.2651	Araneae 0.2362	Lepidoptera 0.1917
Hemiptera 0.1656	Lepidoptera 0.2326	Lepidoptera 0.0997	Araneae 0.0750
Araneae 0.0718	Hemiptera 0.0884	Hemiptera 0.0656	Hemiptera 0.0417
Other 0.0218	Other 0.0139	Other 0.0211	Coleoptera 0.0083
Orthoptera 0.0063	-	Orthoptera 0.0026	-
Phasmatodea 0.0063	-	-	-
Hymenoptera 0.0063	-	-	-
Homoptera 0.0031	-	-	-

Table 7.5 Ranked proportion of Diptera families returned to *V. vulgaris* (V.v) and *V. germanica* (V.g) nests in urban and rural habitats, Palmerston North, between February-July 1993.

LOCATION			
Limbrick St **V.v urban**	Morris St **V.v urban**	Acacia St **V.g urban**	Ring Rd **V.v rural**
Tipulidae 0.4198	Tipulidae 0.4186	Tipulidae 0.3333	Syrphidae 0.4756
Syrphidae 0.2443	Other 0.1511	Sarcophagidae 0.2511	Calliphoridae 0.1829
Other 0.0993	Stratiomidae 0.1163	Syrphidae 0.1142	Tipulidae 0.1707
Stratiomidae 0.0916	Syrphidae 0.1047	Calliphoridae 0.0913	Sarcophagidae 0.0976
Calliphoridae 0.0534	Muscidae 0.0698	Stratiomidae 0.0731	Other 0.0488
Muscidae 0.0534	Sarcophagidae 0.0581	Muscidae 0.0685	Muscidae 0.0244
Bibionidae 0.0153	Bibionidae 0.0465	Other 0.0502	-
Anthiomidae 0.0153	Calliphoridae 0.0349	Bibionidae 0.0183	-
Sarcophagidae 0.0076	-	-	-

Table 7.6 Mean fresh weight (mg±1SE) and number of prey loads returned by *V. vulgaris* (V.v) and *V. germanica* (V.g) foragers in urban and rural habitats, Palmerston North, between February and July 1993.

	LOCATION							
	Limbrick St **V.v urban**	n	Morris St **V.v urban**	n	Acacia St **V.g urban**	n	Ring Rd **V.v rural**	n
INSECTA								
Diptera	7.2±0.6	131	5.5±0.6	86	13.1±0.8	219	7.7±0.9	82
Sarcophagidae	5.2	1	9.0±4.7	5	18.9±1.2	55	10.5±2.0	8
Muscidae	6.3±1.2	7	4.6±0.7	6	10.2±1.6	15	13.3±3.1	2
Tipulidae	7.5±0.5	55	7.1±1.0	36	5.6±0.4	73	4.6±1.1	14
Stratiomidae	14.9±4.0	12	5.6±1.2	10	28.1±3.1	16	-	-
Calliphoridae	18.5±4.4	7	11.6±5.3	3	29.8±3.3	20	20.7±1.9	15
Syrphidae	4.8±0.5	32	3.3±0.3	9	8.3±2.4	25	3.4±0.3	39
Bibionidae	0.6±0.4	2	0.7±0.1	4	0.8±0.1	4	-	-
Anthiomidae	3.5±0.8	2	-	-	-	-	-	-
Other	1.0±0.2	13	1.3±0.3	13	2.7±0.8	11	2.9±1.9	4
Hemiptera	6.8±0.5	53	4.0±0.7	19	7.7±0.7	25	3.0±1.0	5
Ricanidae	7.0±1.3	50	4.3±0.7	17	7.7±0.7	25	2.6±1.6	3
Pentatomidae	2.4±1.3	2	1.3±0.3	2	-	-	-	-
Flatidae	8.0	1	-	-	-	-	-	-
Cercopidae	-	-	-	-	-	-	3.7±1.3	2
Lepidoptera (larvae)	11.0±1.0	99	6.5±1.1	50	15.9±2.3	38	7.3±1.3	23
Orthoptera	16.4±8.2	2	-	-	6.4	1	-	-
Tettigonidae	16.4±8.2	2	-	-	6.4	1	-	-
Phasmatodea	11.5±7.8	2	-	-	-	-	-	-
Phasmatidae	11.5±7.8	2	-	-	-	-	-	-
Coleoptera	-	-	-	-	-	-	7.2	1
Homoptera	1.0	1	-	-	-	-	-	-
Hymenoptera	0.4±0.2	2	-	-	-	-	-	-
Formicidae	0.4±0.2	2	-	-	-	-	-	-
ARACHNIDA								
Araneae	3.8±0.9	23	2.6±0.5	58	9.2±1.3	90	6.2±3.2	9
Other	7.2±1.9	7	5.1±3.2	3	16.6±4.9	8	-	-
Woodpulp	1.3±0.3	181	1.2±0.2	72	1.6±0.1	82	1.7±0.3	75

0.001). Overall German wasps carried loads 2.2 times heavier than common wasps (ANOVA $P < 0.001$), but no significant difference was found between the weight of woodpulp carried back by foragers of both species. Foragers from both the urban and rural common wasp nests returned with similar mean prey weights, though slightly heavier Hemiptera were returned to the urban colonies (ANOVA $P = 0.0608$) and spiders to the rural colony (ANOVA $P = 0.0533$) (Table 7.6).

Diptera prey items provided the majority of total prey weight in 3 of the 4 colonies (Table 7.7). Lepidoptera larvae were also major contributors of prey weight for the common wasp colonies. However the grouped weights of Lepidoptera larvae pieces differed significantly between the German and common wasp nests (Table 7.8; $\chi^2 = 7.425$, df = 1, $P < 0.01$). Common wasp foragers returned more often with lighter Lepidoptera fragments than did German wasps, 56% returning with pieces less than 0.1mg. Araneae weight was the second most important for the German wasp colony. Total Tipulidae and Stratiomidae weight provided the majority of Diptera protein in the two urban common wasps colonies (Table 7.9). Almost half of the total Diptera weight in the rural nest was of Calliphoridae origin. Sarcophagidae items provided the greater proportion of Diptera weight in the German wasp colony.

7.3.6 Prey biomass and woodpulp return

Traffic rates and protein demands for the 4 colonies are shown in Fig. 7.2. The 3 common wasp colonies traffic rates peaked between day 69 and 97 (10 March-7 April), with the German wasp colony peaking around day 130 (10 May). Just prior to these peaks the percentage of wasps carrying prey items more than doubled for all 4 colonies (Fig. 7.2.). The Morris St and Limbrick St nests show that this increase in protein return lasted between a minimum of 9-24 days, and up to a maximum of 26-38 days (Fig. 7.2.). The duration of the German wasp nest lasted only a maximum of 13 days before returning to pre-peak levels. Previously common wasp colonies averaged between 8-9% of foragers returning with prey whilst the German wasp colony averaged 14%. Fluctuations in this measurement occurred after the decline of the colony. This is probably due to the fact that as the traffic rate decreases so too does the accuracy of measuring the percentage of wasps carrying protein.

The temporal increase in protein weight and quantity of woodpulp pellets returned to the 4 colonies is shown in Fig. 7.3. The 3 common wasp colonies peak protein returns ranged between 5.672 ghr^{-1} to 7.272 ghr^{-1} (Ring Rd-Limbrick St), on 2 April and 23 March respectively, with the

Table 7.7 Ranked proportion of insect Order weight in the total protein weight taken from *V .vulgaris* (V.v) and *V. germanica* (V.g) nests in urban and rural and habitats, Palmerston North, between February-July 1993.

LOCATION			
Limbrick St **V.v urban**	Morris St **V.v urban**	Acacia St **V.g urban**	Ring Rd **V.v rural**
Lepidoptera 0.4209	Diptera 0.4251	Diptera 0.6205	Diptera 0.7193
Diptera 0.3664	Lepidoptera 0.2940	Araneae 0.1779	Lepidoptera 0.1911
Hemiptera 0.1400	Araneae 0.1383	Lepidoptera 0.1300	Araneae 0.0641
Araneae 0.0340	Hemiptera 0.1288	Hemiptera 0.0417	Hemiptera 0.0172
Other 0.0194	Other 0.0138	Other 0.0285	Coleoptera 0.0083
Orthoptera 0.0127	-	Orthoptera 0.0014	-
Phasmatodea 0.0089	-	-	-
Homoptera 0.0004	-	-	-
Hymenoptera 0.0003	-	-	-

Table 7.8 Frequency and weight classes of Lepidoptera larval pieces returned by foragers from *Vespula* wasp colonies in Manawatu 1993.

	Lepidoptera larvae	
	0.00 - 0.15mg	>0.15mg
Vespula vulgaris	78	27
Vespula germanica	15	16

Table 7.9 Ranked proportion of family weight in the total weight of Diptera taken from *V. vulgaris* (V.v) and *V. germanica* (V.g) nests in urban and rural habitats, Palmerston North, between February-July 1993.

LOCATION			
Limbrick St	Morris St	Acacia St	Ring Rd
V.v urban	**V.v urban**	**V.g urban**	**V.v rural**
Tipulidae	Tipulidae	Sarcophagidae	Calliphoridae
0.4363	0.5487	0.3605	0.4925
Stratiomidae	Stratiomidae	Calliphoridae	Syrphidae
0.1893	0.1196	0.2069	0.2114
Syrphidae	Sarcophagidae	Stratiomidae	Sarcophagidae
0.1614	0.0961	0.1558	0.1327
Calliphoridae	Calliphoridae	Tipulidae	Tipulidae
0.1375	0.0738	0.1409	0.1029
Muscidae	Syrphidae	Syrphidae	Muscidae
0.0471	0.0623	0.0717	0.0422
Other	Muscidae	Muscidae	Other
0.0143	0.0582	0.0530	0.0183
Anthiomidae	Other	Other	-
0.0073	0.0351	0.0102	
Sarcophagidae	Bibionidae	Bibionidae	-
0.0055	0.0062	0.0011	
Bibionidae	-	-	-
0.0013			

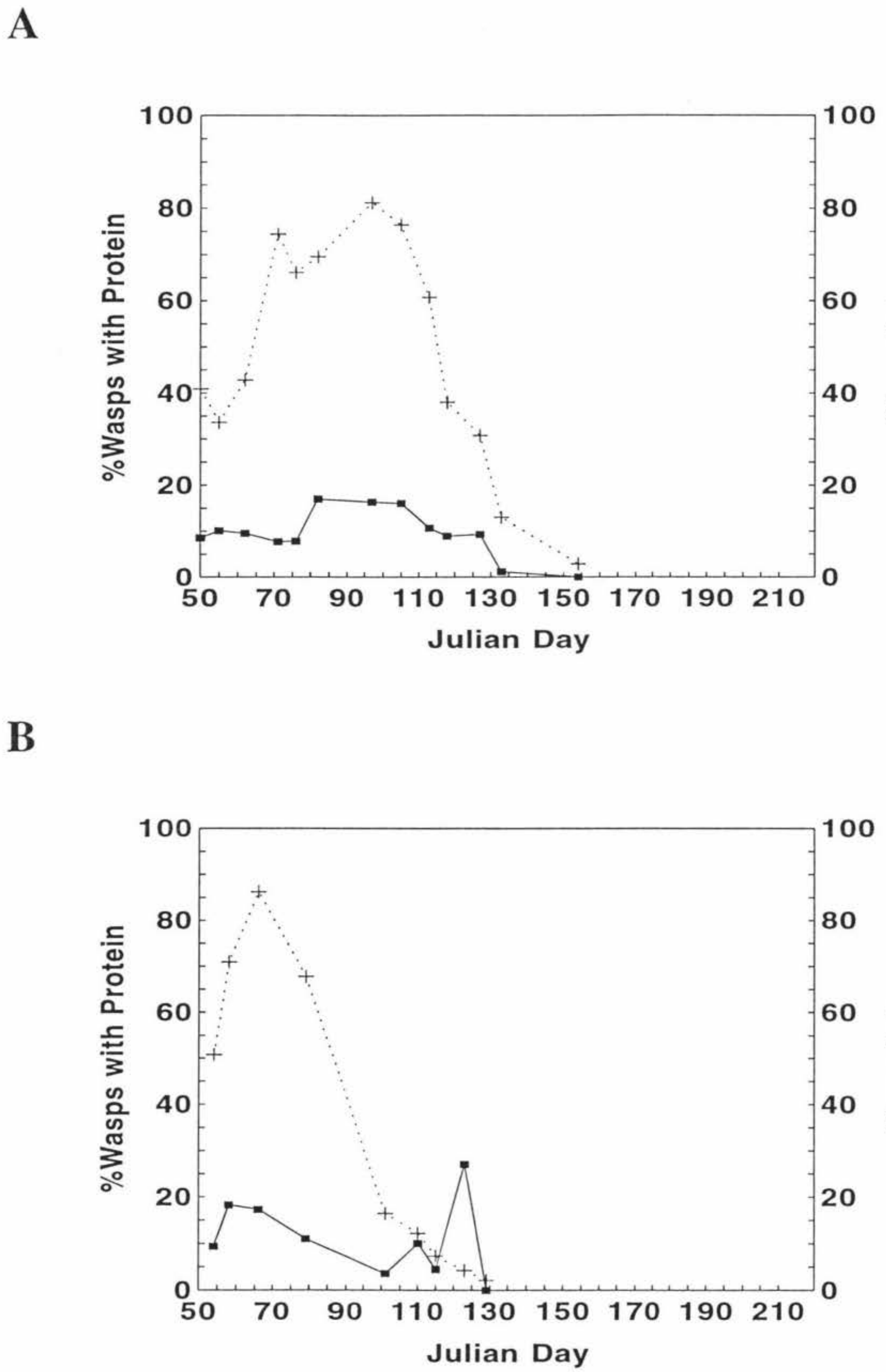
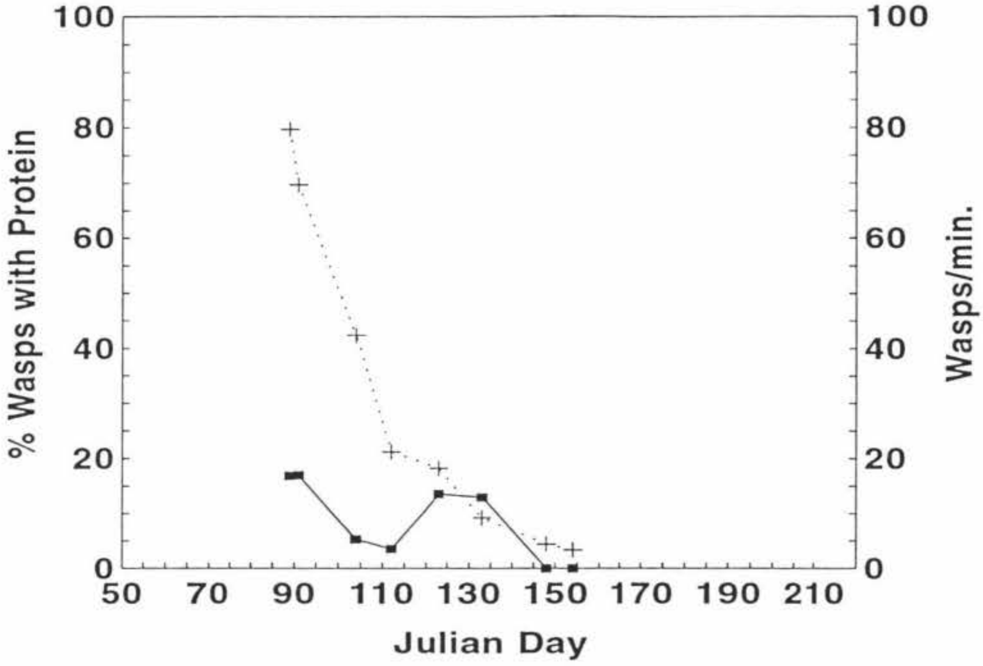


Figure 7.2 Seasonal traffic rate and percentage of wasps carrying protein items in *Vespula vulgaris* (V.v) and *V. germanica* (V.g) nests in urban and rural habitats in Manawatu, between February - July 1993. (**A**) , (**B**) Limbrick / Morris St - **urban V.v** (**C**) Ring Rd - **rural V.v** (**D**) Acacia St - **urban V.g.** (■) = protein carriers (+) = traffic rate. Day 50 = February 19, Day 90 = March 31, Day 110 = April 20.

C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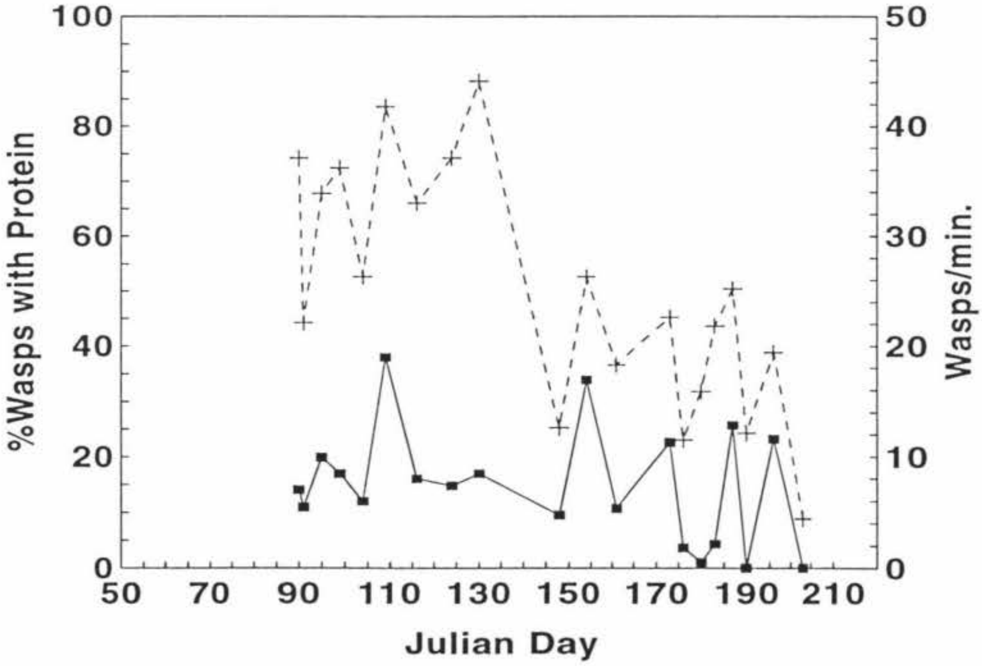
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Julian Day

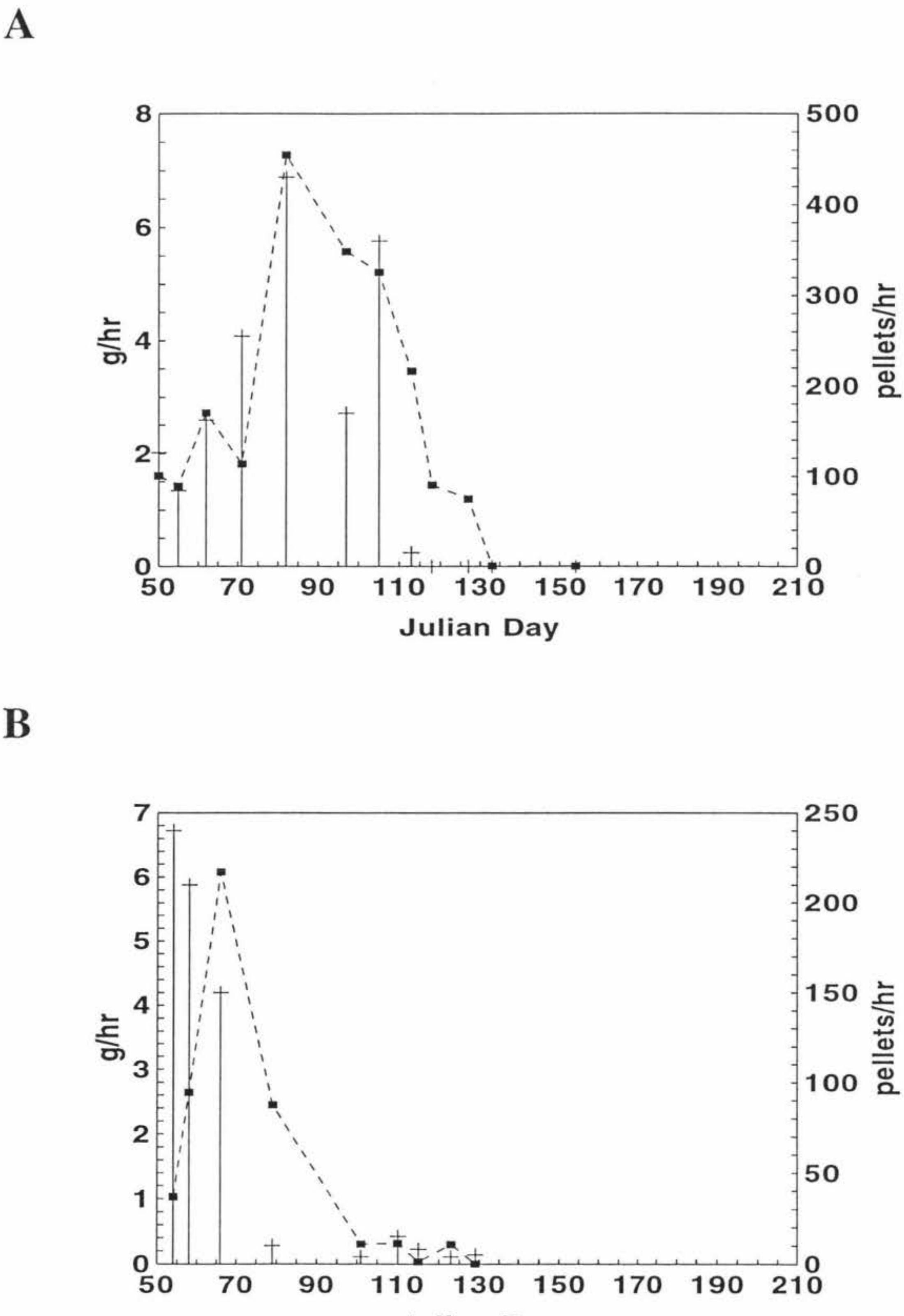
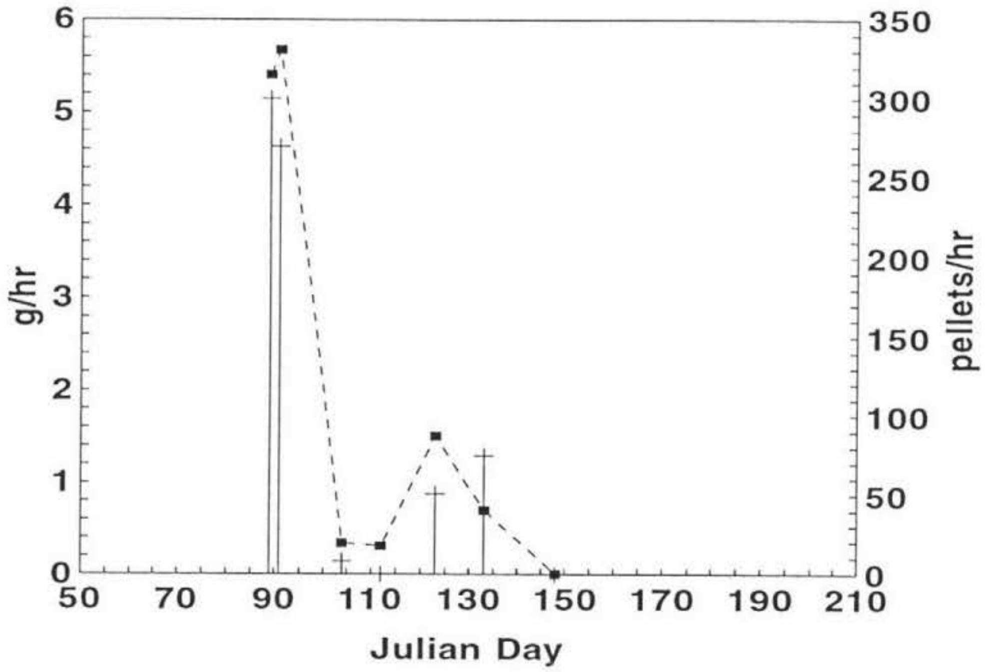


Figure 7.3 Rate of protein and woodpulp returned to *Vespula vulgaris* (V.v) and *V. germanica* (V.g) nests in urban and rural habitats in Manawatu, between February - July 1993. (**A**) , (**B**) Limbrick / Morris St - **urban V.v** (**C**) Ring Rd - **rural V.v** (**D**) Acacia St - **urban V.g**. (■) = protein (+) = woodpulp. Day 50 = February 19, Day 90 = March 31, Day 110 = April 20.

C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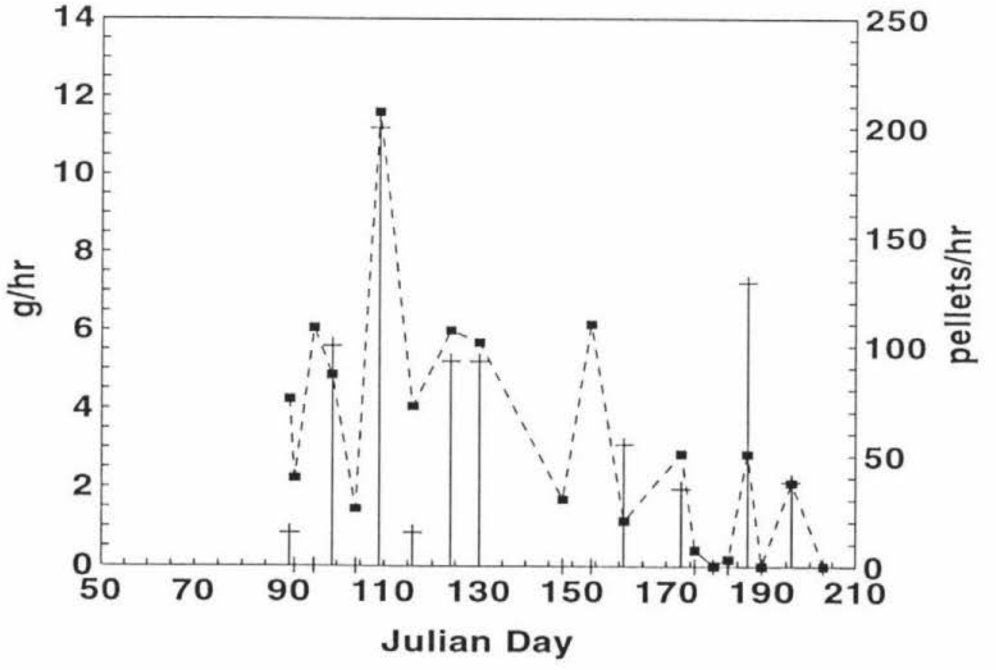
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Julian Day

Morris St colony peaking at 6.079 ghr^{-1} on 10 March. The German wasp colony nearly doubled this, providing 11.6 ghr^{-1} on 19 April (Fig. 7.3.).

Woodpulp return to the four nests also appeared to follow the respective protein peaks. The highest overall rate was found at the Limbrick St nest where it returned a rate of 430 pellets hr^{-1} on 17 March. In comparison the German wasp nest's highest rate was 200 pellets hr^{-1} on 19 April. The earliest woodpulp peak occurred on 26 February at the Morris St nest, with a rate of 240 pellets hr^{-1} (Fig. 7.3). The percentage of wasps returning with woodpulp were similar between both species throughout the season (*Appendix 3*).

Using the earlier data, estimates of prey biomass consumed, the number of prey caught, and the quantity of woodpulp pellets returned during March-April 1993 were made (Table 7.10). The Limbrick St and German wasp nests had a similar biomass consumption, as did the rural common wasp and Morris St nest. All three common wasp nests returned more prey items during this period than the German wasp nest, with woodpulp return also matching this result.

7.4 DISCUSSION

7.4.1 Wasp diet

The invertebrate diet of vespulid wasp colonies in rural and urban habitats of the Manawatu region are broadly similar to those recorded in the honeydew-beech forest of the South Island (Harris 1991), and scrubland-pasture around Hamilton (Harris & Oliver 1993). Diptera, Lepidoptera, Araneae, and Hemiptera were the main components of the 4 Manawatu nests studied. Diptera were the most commonly returned prey item regardless of species or habitat, which mirrors the result of Harris & Oliver (1993). They found that Diptera were the most common prey item for both species in the rural scrubland-pasture habitat. In rural and urban Manawatu Hymenoptera were noticeably absent in contrast with the honeydew-beech forest habitat where hymenopterans (71%-83% Formicidae) were the dominant prey of both the German and common wasp (Harris 1991). This absence suggests that there is a direct relationship between habitat type and wasp diet.

The variation in the relative prey abundance between February and April indicates that there are differences between the species and habitat combinations. Significant differences in the relative predation on Diptera families in the rural and urban habitats illustrate this. For example the dominance of Sarcophagidae ('grassflies') items caught at Acacia St was probably due to the location of a stock grazing area near the nest. Even within the urban habitat the two common wasp nests had significantly different levels of predation on the same arthropod groups. Harris & Oliver

Table 7.10 Prey biomass, numbers, and woodpulp returned to *V. vulgaris* (V.v) and *V. germanica* (V.g) nests in urban and rural habitats, Palmerston North, between March-April 1993.

	Biomass of prey caught (Kg nest^{-1}) mean±SE	Prey caught (10^3 items nest^{-1}) mean±SE	Woodpulp return (10^3 pellets nest^{-1}) mean±SE
URBAN			
Limbrick St V.v	2.063±0.623	332.5±58.4	122.1±25.8
Morris St V.v	1.297±0.428	288.3±126.7	50.5±24.5
Acacia St V.g	2.003±0.548	265.4±67.9	15.5±4.4
RURAL			
Ring Rd V.v	1.286±0.491	304.0±142.1	160.1±46.6

(1993) found that the majority of Diptera prey items returned to German and common wasp nests in a rural habitat were of syrphid origin. The study nest in a Manawatu rural habitat produced very similar results. Harris & Oliver (1993) suggest that local prey abundance and availability rather than a specific prey preference has the major role in determining a colony's diet. My results support the conclusion that wasps are opportunistic predators.

Different habitats can provide a variety of resources for invertebrates to utilise and these can have an effect on a habitat's invertebrate diversity and abundance. It may be spurious therefore to allocate wasp nests to the broad category of 'urban' nests since in reality the surrounding biota are not usually homogenous. The Limbrick St nest was in an area with a diversity of plants and well maintained properties, whilst the Morris and Acacia St nests were in a locality containing sections of long grass. The Limbrick St nest returned a greater range of insects than the Morris St and Acacia St nests, but this does not necessarily indicate that this habitat supported a greater species richness. Instead, it may indicate an abundance of certain species in the long grass habitats. If the demands for the diet provision were met by an abundance of invertebrates in the long grass habitat, then these foragers would return with more similar items, hence offering a lower species diversity. Conversely, a similar species richness but lesser abundance at the Limbrick St habitat would force their workers to forage over a wider range to meet their colony's requirements. Continuing investigations into the vespulid diet in the urban habitat will have to address the problem of nest habitat heterogeneity if further comparisons are to be made.

7.4.2 Prey weight

Manawatu German wasps carry overall a significantly heavier mean prey weight which Harris (1991) suggests may be possible because of the large size of the workers. However, Archer (1977) found no correlation between common wasp worker size and the flesh loads they carried, but did note a significant correlation for earth loads. There is no comparative work on the German wasp to clarify these results. Harris (1991) further suggested the difference between German and common wasp prey weight in the honeydew-beech forest was due to the difference in diets, where German wasps preyed upon larger invertebrates.

Compared to common wasps, German wasp foragers returned with significantly heavier prey items over all comparable prey groups. This suggests that either different and bigger prey items were more abundant, or these foragers carry back more of their prey.

Results here show that dietary difference does have an effect on the weight of prey items returned by common and German wasps. Although tipulids were the most common dipterans returned to the German wasp nest, they rated only fourth in importance as contributors to total protein weight. In contrast tipulids were also the most common Diptera item in the urban common wasp nests and ranked highest as suppliers of Diptera protein. This indicates that fewer, but heavier, Diptera items from different families were actually more important for the German wasp nest in terms of total protein weight. Since habitat type affects what invertebrates are available and their level of abundance, it appears the German wasp's habitat supported different and heavier Diptera items which contributed to their heavier mean prey weight.

However, even when both species are sampled in the same habitat, German wasps will return with heavier prey items (Harris 1991; Harris & Oliver 1993), which means some other factor is having an effect. This may be explained by the way wasps handle their prey.

Observing the manipulation of taxonomically similar prey caught by both species confirms they can have different methods of preparing their prey. Small flies such as tipulids are treated similarly by both species where their legs and wings bitten off and are macerated into a ball-like shape, possibly to aid transport whilst in flight (pers.obs.). Larger flies like calliphorids and sarcophagids are often returned by common wasps with their heads and abdomens removed as well, leaving just the thorax. German wasps appear to differ, returning more frequently with less dismembered specimens (pers. obs.). Matsuura (1990) states that the thorax would be the prime part to retrieve because of its high concentration of flight muscles. This suggests that common wasps may carry a lighter but more protein-rich load, because it will provide a more efficient return for their expended energy.

Conversely German wasps may carry back heavier items because, either they are more physically able to, or by being less efficient carriers, return with heavier loads which contain proportionately less protein.

Investigation of Lepidoptera larvae prey confirms that German wasps can carry heavier loads and may be just as efficient at carrying prey as common wasps. Significantly lighter sections of Lepidoptera larvae were returned to common wasp nests. The majority of these weighed less than 0.10mg and were pieces, rather than whole larvae, indicating that common wasps prefer to bite off smaller parts and carry back lighter items. In contrast with this over 50% of Lepidoptera pieces returned by German wasps weighed more than 0.15mg. It seems likely that the combination of a difference in diet and an ability to carry heavier items explain why Manawatu German wasp foragers return with heavier prey loads.

7.4.3 Biomass

Comparison of the prey return of both species showed that a higher proportion of German wasps returned with prey items, presumably because of a greater colony requirement. Before the colony reached its peak an average of 14% of returning German wasps carried protein items. Since they carry on average 2.2 times as much as the common wasp, in real terms this equates proportionately to an actual protein return of over 30%. In contrast common wasps returned only 9%.

Although the traffic rate of the urban German wasp nest (Acacia St) was about 50% lower than the 3 common wasp nests I assume that the needs of the colony were still being met. The lower traffic rate just denotes a smaller nest (Malham et al. 1991). The above calculation indicates that protein requirements for German wasp larvae are much higher than that of common wasp larvae. If it is assumed that this colony's performance is similar to that of other German wasp nests, then German wasp larvae need 3 times as much protein as common wasps in order to develop successfully. Spradbery (1973) remarks that German wasp adults are generally larger than their common wasp equivalents and this has been quantified by other research (D. M. Leathwick, pers. comm.). My study (Chapter 5) shows that cells of all German wasp castes are almost twice the size of their common wasp counterparts. This indicates that it is the German wasp's larger size and hence higher dietary needs that necessitate a higher protein return.

The seasonal switch from the production of workers and males to queens probably explains why in all 4 nests protein return doubled between March-April 1993. Again the size of the caste may explain why the protein requirements increased two-fold. In both species virgin queen adults weigh approximately twice that of the workers (D. M. Leathwick, pers. comm.). From this we can infer that the protein requirements of queen larvae are twice that of worker wasps. The high protein return dropped to pre-peak levels 12-18 days before virgin queens were observed leaving their nests (Chapter 6), which may provide further evidence that an increase in protein return was due to queen production.

The difference in the duration of the protein increase between the German and common wasp colonies may bare significantly on each colony's future production. Richards (1971) divides the productivity of a wasp colony into two components: (1) the reproductive performances of the individual colony, and (2) the successful establishment of new colonies by young queens. The young queens' reproductive success depends heavily on the care they received whilst in the 'mother' colony. The difference I observed in the attention given to each species' queen larvae indicates they have different durations of brood care. The flow on effect should be an interspecific difference in each species component productivity.

Once queen rearing is under way worker production becomes heavily reduced and mortality without further recruitment causes worker numbers to decline. The size of the worker population prior to queen production will determine how long a colony can sustain higher levels of protein foraging. Large nests will be more capable of extending their foraging duration because of their well established worker force. Since the Acacia St nest had a traffic rate around half that of the common wasp nests, it may explain why the length of their protein peak was much shorter. Archer (1985) states that a larger worker force can produce a greater number of queens. Since the 3 common wasp nests had higher traffic rates and longer periods of high protein return, they should have produced more queens than the German wasp nest. The total number of queen cells constructed by the common wasp nests gave a mean of 2131±346 cells. In comparison, the German wasp nest with a lower traffic rate produced significantly fewer queen cells, building only 1424 cells by the season's end, which suggests they produced fewer queens (*Appendix 2*).

7.4.4 Foraging impact

Although the German wasps had a greater relative need for protein, they caught fewer prey than the common wasps to meet their demand. Foragers from all 3 common wasp nests caught between 8-25% more prey between March-April 1993, however, all but one returned a lower biomass. This implies that common wasps will have a heavier impact on an invertebrate community by consuming a greater number of insects, albeit for a lower return. This may bare heavily on invertebrate communities in upper forest and sub-alpine habitats, where Fordham (1991) and Beggs (1991) both record the presence of common wasp nests. Overwintering of German wasp nests have been recorded in New Zealand and Tasmania (Thomas 1960; Plunkett et al 1989; Spradbery 1973). Harris & Oliver (1993) report that winter consumption of invertebrates add greatly to a colony's biomass estimates, with large overwintering nests placing very heavy pressure on the surrounding invertebrate community. For the urban German wasp nest (Acacia St), biomass estimates for the March-July period indicate consumption of prey was 5.6±1.5 kg. Such long living German wasp nests will impact more on the surrounding invertebrate fauna than annual nests of either species.

7.4.5 Woodpulp foraging

The collection of woodpulp varied between all 4 colonies, possibly due to the seasonal level of colony demand, and as well as the time of day when each nest was sampled. Meteorological data suggested no direct interaction between the weather and woodpulp return. Spradbery (1973) from

Potter (1965) noted that pulp collection was principally a morning activity. In this study it also appeared to be so with most of the highest woodpulp rates occurring in morning samples. A few high rates were recorded in the early afternoon (pers. obs.). Most of the urban German wasp samples took place in the afternoon and combined with a lower traffic rate, may explain why the estimate of woodpulp gathered was much lower than the 3 other nests. The highest recorded rates for all 4 nests occurred around the period of the protein peak and illustrate the increased demand for colony expansion. This similar increase in woodpulp demand supports the view that queen rearing occurs around this time. High woodpulp return in afternoon samples at this time indicate that any previous diurnal fluctuation is now superseded by the colony demand for queen rearing.

Queen cells of both species are much larger than those which rear workers and males, requiring more than twice as much woodpulp to make (Chapter 5). Furthermore German wasp queen cells take almost double the amount of woodpulp needed to build a common wasp queen cell. This in effect means that each German wasp queen cell requires twice as much effort to produce. Archer (1977) found that there was no correlation between common wasp worker size and the weight of woodpulp returned. He explained this by arguing that because woodpulp has a low density, it is volume, and not weight that becomes the limiting factor. This could imply that German wasps are disadvantaged when it comes to building cells because, although they appear able to carry heavier protein loads, they cannot carry a larger volume of woodpulp to compensate for their larger cell building requirements. The carriage of similar woodpulp weights by both species supports this idea. (Harris 1991) obtained a similar result. Woodpulp was carried by a similar percentage of foragers from both species throughout the season, which implies that German wasps do not compensate for their large cells by allocating more workers to that task. Common wasps should therefore have an advantage in nest building and the rearing of new wasp generations, because they can build cells using only half as much effort as the German wasp. Chapter 5 discusses this in more detail.

Chapter 8 GENERAL DISCUSSION AND FUTURE RESEARCH

8.1 General discussion and conclusions

This study describes the relative abundance of German and common wasp colonies in Manawatu, but not the densities of their colonies. It is therefore unclear whether the German wasp has been affected demographically by the invasion of the common wasp. For the future it would be useful to quantify and monitor wasp nest densities . Such measures are feasible, but would require a campaign in the news media, and the cooperation of pest control companies.

The study described for common wasps a potential competitive advantage in nest building. This advantage could have directly affected relative production of queens by both species, and may help to explain the displacement of German wasps in the honeydew beech forests of the South Island. The honeydew resource is unique to that area and the differences between the species in their foraging efficiency for this food appear to have caused the displacement (Harris et al. 1994). Flow-on effects from the German wasps' inferior ability to gather honeydew may have further influenced their displacement. Exploitation competition for the honeydew probably acted as a catalyst, and emphasised the ecological differences between the two species. Although German wasps appear to be more efficient than common wasps at removing nest cavity debris, a reduced level of carbohydrates moving through their colonies would soon slow down the growth of their nests. Results show that smaller nests do produce fewer queens and, being in direct competition with common wasps for the honeydew over a number of years, it is feasible that a dramatic decline in the reproductive potential of German wasp colonies in beech forests may have caused their displacement. Honeydew is not a crucial resource in Manawatu and so probably does not play a significant role in colony dynamics.

Results from this research suggest that the initiation of nests, the onset of male rearing, the timing of queen production, and the nature of the nest substrate all play major roles in the ultimate productivity of the colony. Colonies which begin earlier, are built in a soft substrate, and begin male production much later in the season than other colonies (ie. just prior to queen production), will produce more queens. Although more common wasp colonies than German wasp colonies showed these tendencies, the sample size was small. It would, therefore, be interesting to determine whether these traits were expressed more often in common wasp colonies than German wasp colonies, as it could further suggest why the common wasp has been so successful in New Zealand.

The phenology of German and common wasps are broadly similar but this study and others have shown that variability does occur geographically, as well as within and between the two species. The phenology of overwintering nests is different again and its uniqueness warrants separate study.

Sample sizes in urban and rural habitats were uneven, so complete phenological comparisons between these broad habitats could not be made. However, there was a large difference between Apiti German wasp worker cell : queen cell ratios in April (April 16) and those in German wasps nests taken earlier in Palmerston North (April 5-15). This suggests that habitat may affect wasp phenology, possibly through localised climatic factors, or availability of protein foods (R. D. Akre, pers. comm., cited in Fordham et al 1991). The diets of German and common wasps in Manawatu were similar, with Diptera being the overall main prey taken. However, the habitat in which the colonies were located most influenced the prey returned. For example, the type of Diptera families caught most often differed between habitats. Differences were even apparent within urban areas, which suggests that care must be taken when allocating nests to such broad habitat classes as 'urban' and 'rural'.

The discovery that common wasps kill more invertebrates to maintain their colonies than German wasps implies that they pose a substantial threat to our native invertebrate fauna. Moller et al. (1990) and Fordham (1991) have already expressed concern at the impact of common wasps in various habitats, and this recent finding can only increase the concern.

8.2 Key areas for future wasp research

A number of key areas for future wasp research developed from this study.

1. The effects of seasonal rainfall on nest abundance need closer investigation. While heavy rain in spring appears to promote nest abundance in the following year, high rainfall between January and June seems to suppress nest abundance during that time. It is unclear why this switch occurs. At least two avenues of work are important. First, the relationships between seasonal nest abundance and major meteorological

parameters must be clarified. Any such relationship could vary between main habitat types. Second, flow on ecological effects between major meteorological parameters and significant wasp resources (prey, water, woodpulp, nest cavities) needs to be quantified. Such work will help determine what causes high wasp years, and provide a predictive model.

2. Common wasps are well established in Manawatu but how long their dominance over German wasps will continue is unknown. Long-term monitoring of nest densities would allow valuable comparisons of the invasive ability of the two species in Manawatu. Further, the question of whether the social wasp nuisance in Manawatu is increasing could be addressed.

3. Calculations suggest that the two species have different nest building abilities. However, in unrestricted ground sites they do not produce nests of different size. Closer examination of the diurnal removal of nest debris and the weight of debris removed throughout the season may help explain the similarity of nest sizes. A similar investigation of diurnal woodpulp return through the season would reveal whether the rate of woodpulp collection by German wasps is higher than that of common wasps.

4. Harris & Beggs (in press) found that large queens were more likely to survive winter and initiate nests in spring, than smaller, malnourished queens. The type of nest producing these queens was unknown. An investigation of the weights of queen wasps leaving overwintered nests may allow prediction of the 'success' of this type of nest. Are queens from perennial nests as successful at producing new nests as queens originating from annual nests?

5. Some aspects of the phenology of wasp colonies need further study. The timing of male production and the proportion of males produced can negatively affect the number and quality of queens produced. This needs to be quantified, in both species, to determine its significance role in the invasive success of common wasps. A pertinent question to be answered is how badly is queen production hindered in nests that do not start until mid-summer?

Chapter 9 SUMMARY

1) Common wasps are the most abundant wasp species in both urban and rural habitats in Manawatu.

2) Spring rainfall appears to be positively correlated with wasp nest abundance the following year. High rainfall over 600 mm during the first half of the year may reduce wasp nest abundance by causing many ground nests to drown.

3) The reporting of wasp nests is greatest in January, but high numbers are also recorded in February and March.

4) Wasp nests in roof/eaves or in walls of buildings become larger more quickly than those in other sites because the nest cavity is already formed and well insulated.

5) German wasps appear to prefer building nests in ground sites (81%), while common wasps are more opportunistic on their selection.

6) Traffic rates from nests of both species rose to a peak in late-March, before declining and dying around May-June. Significantly higher rates in common wasp nests during January-February may be due to an earlier nest initiation.

7) Diurnal traffic rates were highest in the early afternoon and increased as queen rearing neared. After this point the seasonal decrease in day length appeared to cause foraging activity to increase in the late afternoon period.

8) Colonies that constructed high numbers of worker/male cells to their 'peak' produced significantly more queen cells than those that had built fewer worker/male cells. This may be due to an early nest initiation, a late change to male rearing, or due to a differential rate of substrate extraction.

9) The weights of nest components (cells, struts) differed between the two species; to build a German wasp nest of a similar size to a common wasp nest would require more than twice the amount of woodpulp to be gathered.

10) Worker cell : queen cell ratios in nests taken from one location differed between the two species probably because of an earlier switch to queen rearing in the German wasp nests.

11) In Manawatu male production appeared to occur earlier (early-February) in German wasp colonies than in common wasp colonies (early-March). As a result proportionally more males were found in German wasp nests.

12) Queen rearing begins earlier (March 12) in common wasp colonies than in German wasp colonies (March 20). However, variation does occur within and between the species.

13) In both species the percentage of worker/male and queen cells containing eggs remained fairly constant after peaking, suggesting a limiting factor is involved. In worker/male cells it appears to be the egg-laying ability of the queen; in queen cells it appears to be the number of cells available for oviposition.

14) A similar upper limit to both species percentage of worker/male and queen cells containing larvae, is related to the number of workers available to tend them.

15) Queens were first seen leaving German and common wasp nests in early May. The majority of these pre-nuptial flights were in the morning, with the highest rate of departure being 24 wasps minute^{-1}. Queens continued leaving the nests until the death of the colony. Mating of German wasps was observed to take around 20-30 minutes.

16) The percentage of cells containing all life stages in an overwintering German wasp nest was similar to the respective peaks found in annual nests.

17) Between 11% (common wasp) and 16% (German wasp) of wasp foragers returned with protein items. Only 3-6% of wasp foragers returned with woodpulp.

18) Diptera, Lepidoptera, Araneae, and Hemiptera were the main diet items returned to colonies in urban and rural Manawatu.

19) Prey availability, rather than a particular prey preference, appears to be more important in determining each colony's diet.

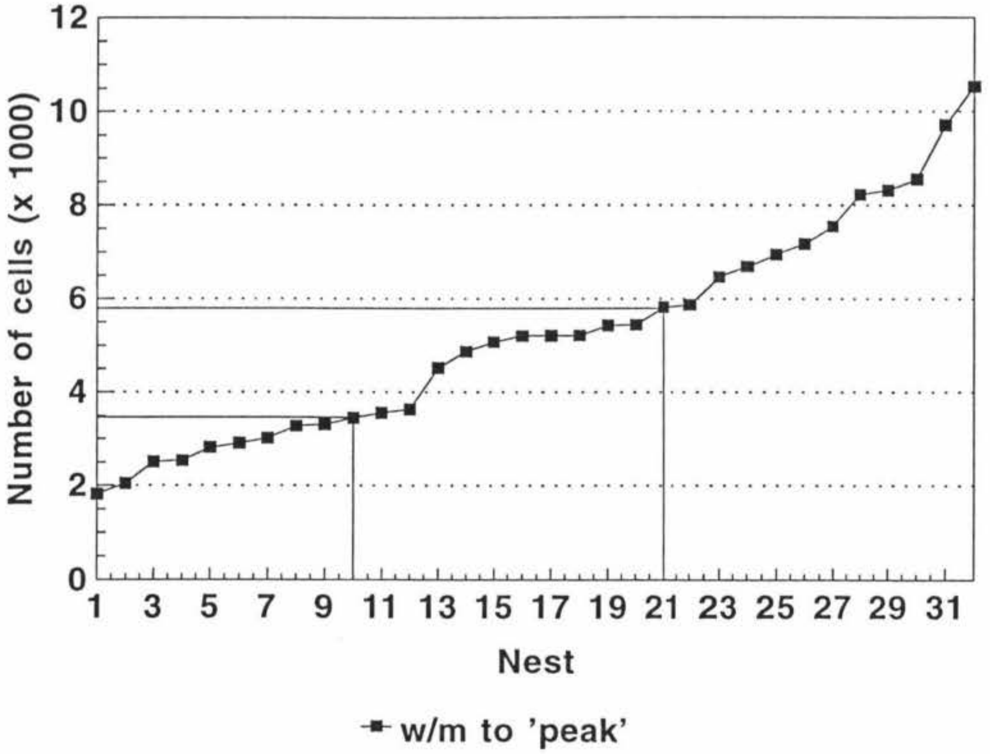
20) German wasps return overall with a mean protein weight 2.2 times heavier than common wasps. This is because German wasp larvae need around 3 times as much protein as common wasp larvae.

21) Size again determines why protein return to colonies of both species doubles during queen rearing. Queen larvae need around twice the amount of protein of worker/male larvae. The number of workers available at the beginning of queen production determines the duration of this protein peak.

22) Although German wasp foragers return with heavier prey weights, common wasp colonies kill more invertebrates to meet their needs. They may, therefore, have more of an impact on a habitat's invertebrate community than that of a German wasp colony.

23) Similar weighing woodpulp pellets are returned by foragers of both species. Woodpulp return increases around the time of queen production to match the woodpulp requirements of the larger queen cells.

Appendix 1 Ranked total number of worker / male cells built to the 'peak' of each *Vespula* spp. wasp nest extracted in Manawatu 1993. For definition of nest 'peak' see Chapter 5 methods. The straight lines at nest 10 and 21 relate to the 33% and 66% percentiles. Corresponding cell counts are 3508 and 5819 respectively.



Appendix 2 Data derived from German and common wasp nests extracted in Manawatu, between January 23 and August 20 1993. w/m = worker / male; q = queen.

V. germanica	Date	Habitat	w/m cells	queen cells	Total cells	w/m:q ratio
Tilbury	6 Feb	urban	5657	0	5657	0
Buick	10 Feb	urban	471	0	471	0
Baker	5 Apr	urban	10109	2242	12351	4.5
Kentucky	10 Apr	urban	7404	949	8353	7.8
POH 1	11 Apr	rural	8004	2358	10362	3.4
POH 2	11 Apr	rural	4798	994	5792	4.8
Apiti 1	16 Apr	rural	4765	940	5705	5.1
Apiti 2	16 Apr	rural	8829	869	9698	10.2
Apiti 3	16 Apr	rural	11612	777	12389	14.9
POH 3	24 Apr	rural	2813	676	3489	4.2
FH 3	7 May	rural	4188	336	4524	12.5
Colyton	17 May	rural	10624	1308	11932	8.1
Acacia	23 Jul	urban	9819	1424	11243	6.9
Amberley	23 Jul	urban	19259	6193	25452	3.1
V. vulgaris						
Firth Place	23 Jan	urban	5919	0	5919	0
Heretaunga	4 Feb	urban	9715	0	9715	0
Wyndham	4 Feb	urban	8567	0	8567	0
Dittmer	11 Feb	urban	1680	0	1680	0
Hughes Ave	17 Mar	urban	11302	195	11497	58
Matamau	6 Apr	urban	4166	206	4372	20.2
Russell St	8 Apr	urban	7827	979	8806	8
Fergusson 1	13 Apr	rural	6816	644	7460	10.6
Fergusson 2	13 Apr	rural	7669	494	8163	15.5
Clifton	15 Apr	urban	7644	863	8507	8.9
Apiti 4	16 Apr	rural	6124	140	6264	43.7
Apiti 5	16 Apr	rural	10252	512	10764	20
Apiti 6	16 Apr	rural	3821	70	3891	54.6
Apiti 7	16 Apr	rural	3230	174	3404	18.6
Apiti 8	16 Apr	rural	5267	197	5464	26.7
Apiti 9	16 Apr	rural	4303	47	4350	91.6
Apiti 10	16 Apr	rural	2320	64	2384	36.3
Apiti 11	16 Apr	rural	5778	289	6067	20
FH 1	23 Apr	rural	10546	2287	12833	4.6
POH 4	24 Apr	rural	12701	3645	16346	3.5
Gibbs	24 Apr	rural	6698	1247	7945	5.4
FH 2	27 Apr	rural	10307	2353	12660	4.4
Anzac Park	5 May	rural	9451	1055	10506	9
Morris St	31 May	urban	18696	1460	20156	12.8
Ring Rd	16 Jun	rural	11053	2615	13668	4.2
Limbrick St	16 Jun	urban	12523	2317	14840	5.4
Feilding	20 Aug	urban	7748	2037	9785	3.8

Appendix 3 Percentage of foragers returning with woodpulp pellets to *V. vulgaris* and *V. germanica* nests in urban and rural habitats, Palmerston North. Sampling occurred between February and July 1993.

Limbrick St		Morris St		Acacia St		Ring Rd	
V.v **urban**		V.v **urban**		V.g **urban**		V.v **rural**	
19 Feb	8.5	26 Feb	10	31 Mar	1.2	30 Mar	18.1
24 Feb	6.4	2 Mar	5.7	1 Apr	0	2 Apr	8
3 Mar	11.2	10 Mar	3.3	5 Apr	0	15 Apr	0.3
12 Mar	9.3	23 Mar	0.3	9 Apr	5.3	23 Apr	0
17 Mar	14.7	14 Apr	0.9	14 Apr	0	3 May	6.7
23 Mar	5.6	23 Apr	3.3	19 Apr	8.6	13 May	27.8
7 Apr	9.1	28 Apr	2.9	26 Apr	2.3	28 May	0
15 Apr	0.4	6 May	2.7	4 May	8	3 Jun	0
23 Apr	0	12 may	14.3	10 May	2.7	-	-
28 Apr	0	-	-	28 May	0	-	-
5 May	0	-	-	3 Jun	0	-	-
11 May	0	-	-	10 Jun	0	-	-
28 May	0	-	-	16 Jun	7.3	-	-
3 Jun	0	-	-	22 Jun	7.5	-	-
-	-	-	-	25 Jun	0	-	-
-	-	-	-	29 Jun	0	-	-
-	-	-	-	2 Jul	0	-	-
-	-	-	-	6 Jul	14.3	-	-
-	-	-	-	9 Jul	0	-	-
-	-	-	-	15 Jul	6.1	-	-
-	-	-	-	22 Jul	0	-	-

REFERENCES

Akre, R. D.; Myhre, E.; Chen, Y. 1993: A huge nest of the common yellowjacket, *Paravespula vulgaris* (Hymenoptera: Vespidae), in California. *Entomological News 104 (3)*: 123-128.

Anon. 1952: European wasp. *Notornis 4*: 23.

Archer, M. E. 1972: Studies of the seasonal development of *Vespula vulgaris* (L.) (Hymenoptera: Vespidae) with special reference to queen production. *Journal of entomology (A) 47*: 45-59.

--------------1977: The weights of forager loads of *Paravespula vulgaris* (Linn.) (Hymenoptera: Vespidae) and the relationship of load weight to forager size. *Insectes sociax 24*: 95-102.

--------------1980: Population dynamics. *In* Edwards, R. *ed.*, Social wasps, their biology and control. East Grinstead, Rentokil Limited. pp. 172-207.

--------------1981: Successful and unsuccessful development of colonies of *Vespula vulgaris* (Linn.) (Hymenoptera: Vespidae). *Ecological entomology 6*: 1-10.

--------------1985: Population dynamics of the social wasps *Vespula vulgaris* and *Vespula germanica* in England. *Journal of animal ecology 54*: 473-485.

Barrington, R. M. 1896: Wasps catching flies on cattle. *Irish Nature 5*: 272.

Beggs, J. R. 1991: Altitudinal variation in abundance of common wasps (*Vespula vulgaris*). *New Zealand journal of zoology 18*: 155-158.

Beggs, J. R.; Wilson, P. R. 1991: The Kaka (*Nestor meridionalis*), a New Zealand parrot endangered by introduced wasps and mammals. *Biological conservation 56*: 23-38.

Beggs, J. R.; Harris, R. J.; Read, P. E. C. in prep: Invasion success of the wasp parasitoid *Sphecophaga vesparum vesparum* (Curtis) in New Zealand.

Brian, M. V.; Brian, A. D. 1952: The wasp *Vespula sylvestris* Scopoli: feeding, foraging and colony development. *Trans. R. ent. soc. Lond. 103*: 1-26.

Burgess, S. M. 1988: The climate and weather of Manawatu. *New Zealand Meteorological Service 115 (18)*. 47 pp.

Clapperton, B. K.; Lo, P. L.; Moller, H.; Sandlant, G. R. 1989a: Variation in colour markings of German wasps *Vespula germanica* (F.) and common wasps *Vespula vulgaris* (L.) (Hymenoptera: Vespidae) in New Zealand. *New Zealand journal of zoology 16*: 303-313.

Clapperton, B. K.; Moller H.; Sandlant G. R. 1989b: Distribution of social wasps (Hymenoptera:

Vespidae) in New Zealand in 1987. *New Zealand journal of zoology 16*: 315-323.

Clapperton, B. K.; J. A. V. Tilley; J. R. Beggs; H. Moller 1994: Changes in the distribution and proportions of *Vespula vulgaris* (L.) and *Vespula germanica* (Fab.) (Hymenoptera: Vespidae) between 1987 and 1990 in New Zealand. *New Zealand journal of zoology 21*: 295-303.

Clary, M. S.; Fordham, R. A.; Godfrey, P. L. 1993: How does nest maintenance activity in *Vespula vulgaris* (Hymenoptera: Vespidae) vary on a daily basis? Zoology degree project requirement, Massey University, New Zealand.

Crawley, M. J. 1986: The population biology of invaders. *Phil. Trans. R. Soc. Lond. B* 314: 711-731.

Crawley, M. J. 1989: Chance and Timing in Biological Invasions. *In* Biological Invasions: a Global Perspective. John Wiley & Sons. 525 pp.

Crosland, M. W. J. 1993: The spread of the social wasp, *Vespula germanica*, in Australia. *New Zealand journal of zoology 18*: 375-388.

Donovan, B. J. 1983: The common wasp is here. *New Zealand beekeeper 180*: 9-10.

Donovan, B. J. 1984: Occurrence of the common wasp, *Vespula vulgaris* (L.) (Hymenoptera: Vespidae) in New Zealand. *New Zealand journal of zoology 11*: 417-427.

---------------1991: Nest initiation by German and common wasp queens (Hymenoptera: Vespidae) and nest fate at Christchurch, New Zealand. *New Zealand journal of zoology 18*: 95-99.

Donovan, B. J.; Read, P. E. C. 1987: Attempted biological control of social wasps, *Vespula* spp., (Hymenoptera: Vespidae) with *Sphecophaga vesparum* (Curtis) (Hymenoptera: Ichneumonidae) in New Zealand. *New Zealand journal of zoology 14*: 329-335.

Donovan, B. J.; Howie, A. M. E.; Schroeder, N. C. 1992: Comparative characteristics of nests of *Vespula germanica* (F.) and *Vespula vulgaris* (L.) (Hymenoptera: Vespinae) from Christchurch City, New Zealand. *New Zealand journal of zoology 19*: 61-71.

Edwards, R. 1980: Social wasps, their biology and control. East Grinstead, Rentokil Ltd. 398p.

Esler, A. E. 1978: Botany of the Manawatu. *New Zealand Department of Scientific and Industrial Research information series no 127.*

Fechney, K. J. 1989: Analysis of the establishment and seasonal development of *Vespula vulgaris* and *Vespula germanica* (Hymenoptera: Vespidae) colonies in Wellington City, New Zealand. Unpublished BSc (Hons) dissertation, Victoria University, Wellington, New

Zealand.

Fordham, R. A. 1961a: Notes on the German wasp *Vespula germanica. Tuatara 1*: 24-31.

--------------------1961b: Spread of the German wasp in New Zealand. *Tuatara 9*: 129-130.

--------------------1991: Vespulid wasps at the upper forest margin in Tongariro National Park - a threat to the native biota? *New Zealand journal of zoology 18*: 151-153.

Fordham, R. A.; Craven A. J.; Minot E. O. 1991: Phenology and population structure of annual nests of the German wasp *Vespula germanica* (Fab.) in Manawatu, New Zealand, with particular reference to late summer and autumn. *New Zealand journal of zoology 18*: 127-137.

Fox-Wilson, G. 1946: Factors affecting populations of social wasps, *Vespula* species, in England. *Proc. R. ent. soc. Lond. 21*: 17-27.

Free, J. B. 1970: The behaviour of wasps (*Vespula germanica* L. and *V.vulgaris* L.) when foraging. *Insectes sociax 17*: 11-19.

Gambino, P. 1986: Winter prey collection at a perennial colony of *Paravespula vulgaris* (L.) (Hymenoptera: Vespidae). *Psyche 93*: 331-340.

Gaul, A. T. 1951: Additions to vespine biology. VII. Orientation flight. *Bull. Brooklyn ent. soc. 46*: 54-56.

Gerlach, J. C. 1974: Climatographs of New Zealand. *Ruakura Agricultural Research Centre Bulletin 74* - 1.

Gibbs, D. R. 1980: Predation of the spider *Araneus pustulosa* by the German wasp *Vespula germanica. Weta 4*: 17.

Gibbs, D. R. 1983: The German wasp super predator. *Weta 6*: 66-67.

Harris, R. J. 1989: An entrance trap to sample foods of social wasps (Hymenoptera: Vespidae). *New Zealand journal of zoology 16*: 369-371.

--------------1991: Diet of the wasps *Vespula vulgaris* and *V.germanica* in honeydew beech forest of the South Island, New Zealand. *New Zealand journal of zoology 18*: 159-169.

Harris, R. J. in press: The effect of starvation of larvae of *Vespula vulgaris* (L.) (Hymenoptera: Vespidae) on subsequent survival and adult size. *New Zealand journal of zoology.*

Harris, R. J.; Thomas C. D.; Moller H. 1991: The influence of habitat use and foraging on the replacement of one introduced wasp species by another in New Zealand. *Economic entomology 16*: 441-448.

Harris, R. J.; Oliver, E. H. 1993: Prey diets and population densities of the wasps *Vespula vulgaris* and *V.germanica* in scrubland-pasture. *New Zealand journal of ecology 17*: 5-12.

Harris, R. J.; Beggs, J. R. in press: Variation in the quality of *Vespula vulgaris* (L.) queens (Hymenoptera: Vespidae) and its significance in wasp population dynamics. *New Zealand journal of zoology*.

Harris, R. J.; Moller, H.; Winterbourne, M. J. 1994: Competition for honeydew between two social wasps in South Island beech forests, New Zealand. *Insectes sociax 41*: 379-394.

Heerdegan, R. G. 1987: Manawatu River: A Region's Identity. *In* Manawatu and its neighbours. Massey University, New Zealand. 169pp.

Holy Bible (King James Version). Oxford University Press. 1506pp.

Horwood, M. A.; Toffolon, R. B.; Brown, G. R. 1993: Establishment and spread of *Vespula germanica* (F.) (Hymenoptera: Vespidae) in New South Wales and the influence of rainfall on its abundance. *Journal of the Australian entomological Society 32*: 241-248.

Ishay, J. 1975: Caste determination by social wasps: Cell size and building behaviour. *Animal behaviour 23*: 425-431.

Kleinpaste, R. 1980: Food of the German wasp. *Weta 3*: 17.

Little, C. 1981: Predation of a caterpillar and other insects by *Vespula germanica. Weta 4*: 17.

Madden, J. L. (1981): Factors affecting the abundance of the European wasp (*Paravespula germanica* (F.)). *Journal of the Australian entomological Society 20*: 59-65.

Malham, J. P.; Rees J. S.; Alspach P. A.; Beggs J. R.; Moller H. 1991: Traffic rate as an index of colony size in *Vespula* wasps. *New Zealand journal of zoology 18*: 105-109.

Manawatu-Wanganui Regional Council 1993: Regional Land Management Discussion Document June 1993. 51 pp.

Matsuura, N.; Yamane, S. 1990: Biology of the Vespine wasps. Hokkaido University Press. 323pp.

Moller, H.; Tilley, J. A. V. 1989: Beech honeydew: Seasonal variation and use by wasps, honey bees and other insects. *New Zealand journal of zoology 16*: 289-302.

Moller, H.; Beggs J. R.; Tilley J. A. V.; Toft R. J.; Wilson N. J.; Alspach P. A. 1990: Ecology and control of wasp populations in New Zealand. Unpublished Contract report to Department of Conservation.

Moller, H.; Clapperton B. K.; Alspach P. A.; Tilley J. A. V. 1991a: Comparative seasonality of *Vespula germanica* (F.) and *Vespula vulgaris* (L.) colonies (Hymenoptera: Vespidae) in urban Nelson, New Zealand. *New Zealand journal of zoology 18*: 111-120.

Moller, H; Tilley J. A. V.; Plunkett G. M.; Clapperton B. K. 1991b: Nest sites of common and German wasps (Hymenoptera: Vespidae). *New Zealand journal of zoology 18*: 121-125.

Moller, H. in press: Lessons for Invasion Theory from Social Insects. Proceedings of the Invasion Workshop. University of California, Davis, May 1994.

Parker, N. 1992: Comb structure and traffic rate in one colony of the German wasp (*Vespula germanica*), in the Bay of Plenty, New Zealand. Zoology degree project requirement, Massey University, New Zealand.

Perrott, D. C. F. 1975: Factors affecting use of mirex-poisoned protein baits for control of European wasp (*Paravespula germanica*) in New Zealand. *New Zealand journal of zoology* 2: 491-508.

Pimm, S. L. 1989: Theories of Predicting Success and Impact of Introduced Species. *In* Biological Invasions: a Global Perspective. John Wiley & Sons. 525 pp.

Plunkett, G. M.; Moller, H.; Hamilton, C.; Clapperton, B. K.; Thomas, C. D. 1989: Overwintering colonies of German (*Vespula germanica*) and common wasps (*Vespula vulgaris*) (Hymenoptera: Vespidae) in New Zealand. *New Zealand journal of zoology 16*: 345-353.

Potter, N. B. 1965: A study of the biology of the common wasp, *Vespula vulgaris* (L.), with special reference to foraging. Ph.D. Thesis (unpublished), Bristol University.

Ratnieks, F. L. W.; Miller, D. G. 1992: Two polygyne overwintered nests of *Vespula vulgaris* from California. *Psyche 100*: 43-49.

Richards, O. W. 1937: The mating habits of species of *Vespa* (Hymenoptera). *Proc. ent. soc. Lond. 12*: 27-29.

Richards, O. W. 1971: The biology of the social wasps (Hymenoptera: Vespidae). *Biological Review of the Cambridge Philosophical Society 46*: 483-528.

Sandlant, G. R.; Moller H. 1989: Abundance of common and German wasps (Hymenoptera: Vespidae) in the honeydew beech forests of New Zealand in 1987. *New Zealand journal of zoology 16*: 333-343.

2

Saunders, B. G. R. 1987: Agriculture: Strength from the Land. *In* Manawatu and its neighbours. Massey University, New Zealand. 169 pp.

Simberloff, D.1989: Which Insect Introductions Succeed and Which Fail? *In* Biological Invasions: a Global Perspective. John Wiley & Sons. 525 pp.

Spradbery, J. P. 1971: Seasonal changes in the population structure of wasp colonies (Hymenoptera: Vespidae). *Journal of animal ecology 40*: 501-523.

-----------------1973: Wasps, an account of the biology and natural history of solitary and social wasps. Seattle, University of Washington Press. 408pp.

-----------------1991: An orphaned colony of the European wasp *Vespula germanica* (F.) (Hymenoptera: Vespidae) in Australia resulting from repeated usurpation. *New Zealand journal of zoology 18*: 101-103.

Spurr, E. B. 1991: Reduction of wasp (Hymenoptera: Vespidae) populations by poison-baiting; experimental use of sodium monofluoroacetate (1080) in canned sardine. *New Zealand journal of zoology 18*: 215-222.

Strambi, A. 1990: Physiology and Reproduction in Social Wasps. *In* Social Insects: An Evolutionary Approach to Castes and Reproduction. Springer-Verlag, New York. pp. 59-75.

The New Zealand Official Yearbook 1994. Statistics New Zealand. 587pp.

Thomas, C. R. 1960: The European wasp (*Vespula germanica* Fab.) in New Zealand. *New Zealand Department of Scientific and Industrial Research information series no 27.*

Townsend, C. R. 1991: Exotic species management and the need for a theory of invasion ecology. *New Zealand journal of ecology 15*: 1-3.

Watson, E. B. 1922: The food habits of wasps. *Bulletin of Chamber Horticulture 1*: 26-31.

Wilson, E. O. 1971: The insect societies. Harvard University Press, Cambridge. 548 pp.