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

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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.

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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

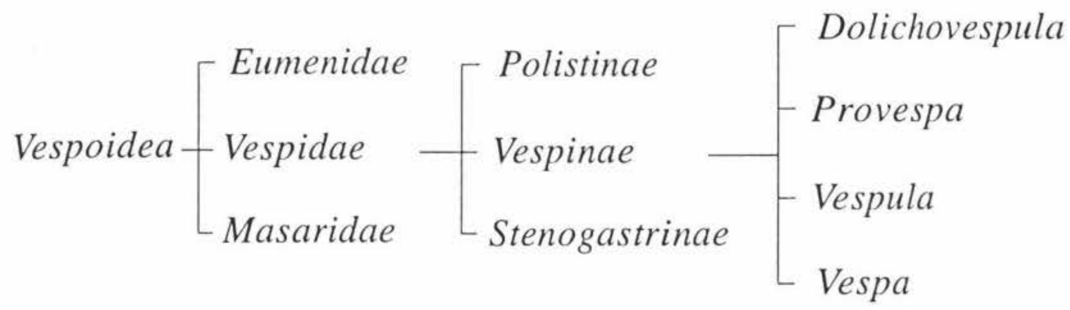

Figure 1 Classification of wasps (Hymenoptera) worldwide: only the connections between the family Vespidae and subfamily Vespinae are detailed because they specifically concern the wasps of this study.

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.