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THE PREVALENCE OF INTRODUCED *VESPULA VULGARIS* WASPS IN A NEW ZEALAND BEECH FOREST COMMUNITY

Summary: In honeydew beech forest in the South Island of New Zealand, introduced *Vespula vulgaris* wasps are now very abundant. Approximated biomass estimates indicate that *Vespula* (mostly *V. vulgaris)* biomass (mean estimate at peak = 3761 g ha^{-1}, averaged over the year = 1097 g ha^{-1}) is as great as, or greater than combined biomasses of birds (best estimate = 206 g ha^{-1}), rodents (up to 914 g ha^{-1} in some years, but usually much lower) and stoats (up to 30 g ha^{-1}). Relative *V. vulgaris* biomass is also estimated to be two orders of magnitude greater than native wasp biomass during the peak *V. vulgaris* season in one beech forest. Mean density of *Vespula* workers at the peak of the season was estimated to be 10,000 workers ha^{-1}, a greater density than the densities attained by other large wasp species when they have been used (with some success) at 'enhanced densities' as biological control agents overseas. The biological impacts of *Vespula,* and particularly *V. vulgaris,* in honeydew beech forest are likely to be great, but most of these impacts have not been documented.

Keywords: wasp; *Vespula vulgaris;* biomass; biological invasion; predation; competition; birds; rodents; stoats.

Introduction

Introduced species may become far more abundant than native species, potentially resulting in substantial restructuring of communities (e.g., Elton, 1958; Porter, van Eimeren and Gilbert, 1988). In New Zealand, the invasion of two species of *Vespula* wasps has led to fear that they may indeed be restructuring native communities. The German wasp *(Vespula germanica)* became established in New Zealand in 1945 (Thomas, 1960; Fordham, 1962). The common wasp *(Vespula vulgaris)* was established by 1978 (Donovan, 1984). *V. germanica* is now widespread in New Zealand, and *V. vulgaris* is firmly established in several regions, and is spreading rapidly (Moller *et al.,* 1987a; Clapperton, Moller and Sandlant, 1989). The invasion of *V. vulgaris* has reinforced concerns about wasps: the replacement of *V. germanica* by *V. vulgaris* in some habitats may have led to an overall increase in wasp density (Sandlant and Moller, 1989). Wasps compete for sugar resources with nectar-feeding birds and insects (e.g., Gaze and Clout, 1983; Moller *et al.,* 1987b; Beggs and Wilson, 1987; Moller and Tilley, 1989), are major predators of invertebrates (e.g., Cumber, 1961; Moller *et al.,* 1978a; Thomas, 1987), and they may compete for invertebrate prey with insectivorous birds and other predacious invertebrates.

Although the arrival of *Vespula* wasps in New Zealand has attracted comment because of the apparent large number of wasps, demonstration of their impact in native communities is limited to their effects on honeydew, a sugary secretion exuded by scale insects that infest the trunks and branches of beech trees. Wasps reduce the amount of honeydew that would otherwise be available to native nectar-feeding birds (Moller and Tilley, 1989).

The present paper is intended to broadly assess the ecological status of introduced wasps in New Zealand honeydew beech forest. The first aim was to quantify wasp abundances and biomasses, but such calculations on their own are of limited value. Comparisons of wasp abundance and biomass with those of other taxa are therefore necessary to put our calculations into perspective. Therefore, our second aim was to calculate the relative biomass of *V. vulgaris* with that of native wasps, and with estimated biomasses of birds and introduced rodents and stoats *(Mustela erminea).* Comparison with birds is made because they potentially compete for food with the introduced wasps.

Comparisons with rodents and stoats are made because they are well recognised as predators of endemic biota. We also compare the biomass of introduced and native wasps, since they potentially compete, and the latter may exert their own predation pressure on endemic insects. Our third aim was to compare *Vespula* wasp density with densities of predatory wasps overseas in instances where these wasps have been used at enhanced densities for biological control or in laboratory experiments. The effects of wasps on survival of Lepidopteran larvae in these other studies is then reviewed. This allows us to indirectly quantify the hypothesis that the ecological impacts of introduced social wasps on New Zealand's endemic insects could indeed be great.

Study areas and methods

Spooners Range Scenic Reserve is situated 38 km south-west of Nelson. It is an area of beech forest, dominated by hard beech *(Nothofagus truncata)* and

silver beech *(N. menziesii),* with a scattering of podocarps, especially rimu *(Dacrydium cupressinum)* and miro *(Prumnopitys ferruginea).* Locations of other honeydew beech forests surveyed are given in Table 1. These are in two general areas, central-northern South Island, and West Coast. The central northern South Island sites are from Nelson Lakes in the south to Nelson in the north, and from Owen River (Hope Ranges) in the west to Pelorus (W. Marlborough) in the east. The West Coast sites run from Oparara, north of Karamea, southwards to Hochstetter Lake, inland from Greymouth. Although all sites are honeydew beech forest (with large components of hard, red *(Nothofagus fusca)* and/or black beech *(N. solandri,),* many West Coast sites also have considerable proportions of podocarp species.

All 429 *Vespula* wasps swatted and identified at Spooners in the summer of 1989 were *V. vulgaris*. Most of the other central-northern South Island sites were also likely to be dominated by *V. vulgaris,* but some West Coast sites still possessed substantial proportions of *V. germanica* (Sandlant and Moller, 1989, unpublished data).

All assessments of abundance and biomass are approximate - they are intended only to give a rough evaluation of the biomasses of wasps, birds, rodents and stoats. Biases in the calculations are such that estimates of wasp biomass are minimised and those of birds and rodents are maximised. This is to avoid exaggerating the potential importance of wasps.

Abundance and biomass of introduced wasps

Transects along compass bearings, were searched for wasp nests at 19 sites during March and April 1989. The width of each transect ranged from 10 to 32 metres (depending on the personnel available), while the length ranged from 203 to 1160 metres (depending on the size of the forest patch). Because some nests would be missed, this gives minimum estimates of nest density along the transects. For each nest found, the traffic rate was measured (with the exception of 2 nests at Spooners which were modified for other experiments): traffic rate is the number of wasps leaving or entering the nest per minute.

Examination of 21 additional *V. vulgaris* nests from Pelorus Bridge and Nelson City, which were also measured for traffic rate in April and May 1988 and 1989, and then fumigated at night and excavated, revealed that there was a correlation between traffic rate and estimated number and weight of wasps in each nest:

$$\text{number of adults} = 481.42 + 37.187 \text{ traffic rate.} \quad (1)$$
(n=21, t=5.36, p=0.0001; r=0.776)

By substituting the mean traffic rates at each site into this equation, estimates of mean numbers of wasps per nest could be made, and hence estimates of the number of wasps per hectare.

Similarly, fumigation and excavation of the nests revealed that:
$$\text{wt of wasps in nest (g)} = 109.35 + 7.498 \text{ traffic rate} \quad (2)$$
(n=21, t=4.91, p=0.0001; r=0.748)

The weight of wasps in each excavated nest was assessed by adding together the separate values estimated for workers, drones, queens, larvae and pupae. Mean weight of a worker was taken as 0.0607 g (n = 57), a drone as 0.0856 g (n = 22), a queen as 0.2250 g (n = 24), and a larva as 0.0428 g. Larval weight was calculated as half the weight of an adult drone (by that stage in the season most filled cells contained prospective sexuals, and drones are the lighter of the two sexes). Pupal weight was taken to be 0.0607 g for worker cells that contained pupae (using the weight of an adult worker; many or even most of these cells would have contained heavier drone pupae), and 0.2250 g for queen cells (the weight of an adult queen). This provides a minimum estimate of weight of wasps associated with a nest because it ignores workers that died away from the nest and sexuals that had already departed the nest. Biomass (g ha^{-1}) was estimated by substituting mean traffic rate at each site into the above equation to obtain an estimate of mean wasp weight per nest, and multiplying by nest density.

Relative numbers and biomasses of introduced and native wasps

Relative abundance of native and introduced wasps were monitored with 15 sticky traps at Spooners. These were sheets of transparent plastic stapled over 30 cm x 30 cm metal frames, with adhesive gum on one side of each trap. Each trap presented a sticky surface of 0.09 m^2. Traps were hung vertically, as close as possible to randomly chosen points within a 50 m x 50 m block in the centre of the study site. Sampling periods were (i) four weeks ending 7 February 1989, (ii) 7 February to 9 March, (iii) 9 March to 4 April, and (iv) 4 April to 5 May 1989.

When sheets were collected, GLAD^{TM} wrap was stretched over the sticky surfaces, and the sheets were stored in a freezer. At the end of the field season, the numbers of introduced and native wasps were counted through the transparent GLADTM wrap. The 'native'

wasp category included all non- *Vespula* wasps trapped, including parasitoids and predatory wasps, such as the native spider-hunting wasps. In the 'native' wasps category, some of the smaller parasitoids could have been introduced species, but they were too small to have had much influence on relative biomass estimates. The length of each wasp was measured. Length[3] was then calculated as a measure that is proportional to weight, and these values summed for introduced and for native wasps in each of the four sampling periods. These gave values of up to several hundred thousand, so the values were divided by 10^5 to give a manageable index of relative biomass.

Abundance and biomass of vertebrate taxa

Birds

The total density of all birds in beech forest was taken as that recorded at Nelson Lakes by Kikkawa (1966). An estimated density for each species at Spooners was then calculated by multiplying overall density from Nelson Lakes by the relative abundance of each bird species at Spooners (as measured by the "five minute bird count technique" (Clout and Gaze, 1984». Scientific names for birds are given in Clout and Gaze (1984). Bird counts over-record some species of visible or noisy birds, so this will produce some inaccuracies in estimates of relative densities. Because the most obvious birds (especially bellbirds and tui) are also relatively heavy, this is likely to produce an overestimate of bird biomass. The estimated density of each bird species was multiplied by its average weight, from data in Robertson, Whitaker and Fitzgerald (1983). For species not given by Robertson *et al*. (redpoll, goldfinch, greenfinch), weights were calculated by interpolating from the relationship between body length and body weight. Inaccuracy due to this interpolation will have very little effect on the final estimate of biomass because these three species accounted for only 3% of estimated bird biomass.

Thus, the biomass (g ha^{-1}) for bird species A was calculated to be:

$$\text{total bird density at Nelson Lakes} \times \frac{\text{mean bird count for species A}}{\text{summed mean count for all spp.}} \times \text{mean wt of sp. A} \qquad (3)$$

These values were calculated for each bird species, and total bird biomass was estimated by summing all of the values.

Rodents

Daniel (1972) estimated that black rat *(Rattus rattus)* biomass was 221 g ha^{-1} in part of the Orongorongo valley, where there was an average of 2.13 rats caught per 100 trap nights. Data on numbers of black rats caught per 100 trap nights are available for Mt Misery beech forest in Nelson Lakes National Park (R.H. Taylor, in Daniel, 1978). Mice *(Mus musculus)* densities from the Orongorongo valley (0.55 to 3.3 per hectare) were multiplied by 16 g to give estimated of 8.8 to 52.8 g ha^{-1} during a period when snap trapping varied from 0.2 to 8 captures per 100 trap nights (Fitzgerald, Karl and Moller, 1981). Capture rates of mice are available from Mt Misery beech forest (R.H. Taylor, in Fitzgerald, 1978). Rat and mouse biomasses were calculated as:

$$\text{Rat/mouse biomass} = \frac{\text{Mt Misery trap rate}}{\text{Orongorongo trap rate}} \times \text{Orongorongo biomass} \qquad (4)$$

Stoats

A stoat trap rate of 16 per 100 trap nights was equivalent to a density of 0.11 stoats/ha on Adele Island (Taylor and Tilley, 1984). Average adult stoat weight was taken as 265.8 g (the mean for males and females, King and Moody, 1982). Stoat trap rates from other sites (King, 1983) were then calibrated by the Adele Island study to give estimated biomasses:

$$\text{Stoat biomass (Y)} = \frac{\text{trap rate at Y}}{\text{Adele Island trap rate}} \times \text{Adele Island biomass} \qquad (5)$$

Results

Abundance and biomass of introduced wasps

Eleven *V. vulgaris* nests were found along a 500 m, 32 m wide transect at Spooners, giving an estimate of 6.875 nests per hectare. The nest densities for 19 honeydew beech forest sites in the northern half of the South Island are given in Table 1. These ranged from 1.31 nests/ha to 32.88 nests/ha. West Coast sites had lower densities (mean = 4.89 nests/ha, s.d. = 3.34) than did central-northern sites (mean = 15.98 nests/ha, s.d. =9.54; t=2.81, d.f. = 17, p=0.012). For all 19 sites, mean density was 11.9 nests/ha (s.d. = 9.8). At Spooners and nearby sites, wasp density in late summer of 1989 was higher than at the same time in 1988, but similar to or lower than in the previous two years (H. Moller, unpublished data).

The mean traffic rate at nine nests at Spooners was 28.1, which gave an estimated mean wasp abundance of 1549 adult wasps per nest, and hence a density of 10649 wasps per ha (by substitutions into equation 1). Mean estimated density was 24836 wasps/ha (s.d. = 14199) for central-northern South Island sites, and 6090 wasps/ha (s.d. =2985) for West Coast sites (t = 3.26, d.f. = 17, p =0.005). For all 19 sites, mean density was 17930 wasps/ha (s.d. = 14973) with a total range of 2277 to 48035 wasps/ha.

Table 1: *Wasp densities and biomasses in honeydew beech forest at sites in the northern half of the South Island.*
Calculations are given for March and April because this is the time of peak wasp abundance.

	Map Grid Reference	Date (1989)	No. of nests found	Area searched (ha)	Nests per ha	Mean traffic rate	Biomass (g per ha)	Wasps per ha	Workers per ha
CENTRAL NORTHERN									
Spooners Range	N28 032712	10/3	11	1.60	6.88	28.1	2231	10649	5974
Winns	N28 996789	8/3	11	1.70	6.47	33.3	2323	11127	6242
Pelorus Bridge	027 578896	1/3, 3/3 & 26/4	28	1.77	15.82	31.8	5502	26324	14768
Tinline	027524919	2/3	29	1.30	22.31	29.7	7402	35381	19848
Pretty Bridge	N28 013784	6/3 & 9/3	6	2.45	2.45	40.0	1003	4824	2706
Watson Creek	S33924415	4/4	36	1.82	19.78	33.5	7131	34164	19166
Matakitaki	S33 917459	5/4	31	2.20	14.09	27.9	4488	21402	12007
Tiraumea	N29 775211	6/3	122	3.71	32.88	26.3	10089	48035	26948
Mt Misery	N29 812214	30/3	25	2.12	11. 79	20.1	3070	14506	8138
Loop, St Arnaud	N29 980320	20/3 & 31/3	66	2.12	31.13	26.7	9637	45895	25747
Howard	N29 857397	22/3	13	2.24	5.80	34.3	2126	10190	5717
Owen River	N28 715544	23/3	39	1.74	22.41	29.7	7441	35539	19937
WESTERN									
Oparara	L27 423086	11/4	8	1.67	4.79	28.3	1538	7338	4117
Corbyvale	L28 306694	12/4	8	0.65	12.31	11.0	2361	10962	6150
Charming Creek	L28 221573	13/4	1	0.77	1.31	39.5	531	2555	1433
Hochstetter Lk	K32 058574	14/4	3	1.27	2.36	13.0	488	2277	1277
Hochstetter Dam	K32 975595	14/4	6	1.11	5.41	29.1	1772	8459	4745
Merrijigs	LJO 143934	15/4	4	0.79	5.06	23.7	1452	6896	3869
Slab Hut	L31 175897	15/4	3	1.00	3.00	24.2	872	4144	2325

Only workers are likely to be foraging actively. For the 21 nests excavated, 56% of all wasps were workers. Thus, the density estimates become 5974 workers/ha for Spooners, 13933 workers/ha (s.d. = 7966) for central-northern sites, and 3416 workers/ha (s.d. = 1675) for West Coast sites. The mean was 10059 workers/ha (s.d. = 8400) for all 19 sites, with a total range of 1277 to 26948 workers/ha (Table 1).

At a density of 6.875 nests per hectare and traffic rate of 28.07 wasps per minute, the biomass of *V. vulgaris* at Spooners is estimated at 2231 g ha^{-1} at the peak of the wasp season (by substitution into equation 2). Wasp biomass estimates for all 19 sites are given in Table 1. These estimates ranged from 488 g ha^{-1} at Hochstetter Lake to 10089 g ha^{-1} at Tiraumea. Mean wasp biomass was 1288 g ha^{-1} (s.d. =639) for West Coast sites, and 5204 g ha^{-1} (s.d. = 3111) for central-northern South Island sites (t = 3.25, d.L = 17, P =0.005). The mean for all 19 sites was 3761 g ha^{-1} (s.d. = 3137).

Wasps reach peak abundance during late summer and autumn. To give a very rough estimate of the average wasp biomass throughout the year, we assume that wasps are at peak for two months, and at half peak for three further months, giving an equivalent of 3.5 months of wasps at peak (see Moller and Tilley, 1989; Sandlant and Moller, 1989). Over the year, average biomass can then be calculated to be 3.5/12 x 2231 = 651 g ha^{-1} at Spooners. At all 19 sites in Table 1, mean biomass over the year can then be estimated to be 1097 g ha^{-1} (s.d. = 915), with a range of 142 to 2943 g ha^{-1}.

Relative densities and biomasses of introduced and native wasps

Numbers of *V. vulgaris* and other wasps caught at Spooners in sticky traps are shown in Fig. la. Numbers of native wasps per trap differed significantly between sampling periods (ANOVA, $F_{3,56}$ = 13.39, p<0.0005), as did number of *V. vulgaris* (ANOVA, $F_{3,56}$ = 8.21, p<0.0005), indicating that there are statistically significant seasonal changes in abundance. The percentage of wasp individuals that were native declined from 71 % in the four weeks up to 7 February 1989 to 26% between 9 March 1989 and 4 April 1989 (Fig. la). Over the whole sampling period, 51 % of individual wasps sampled were native.
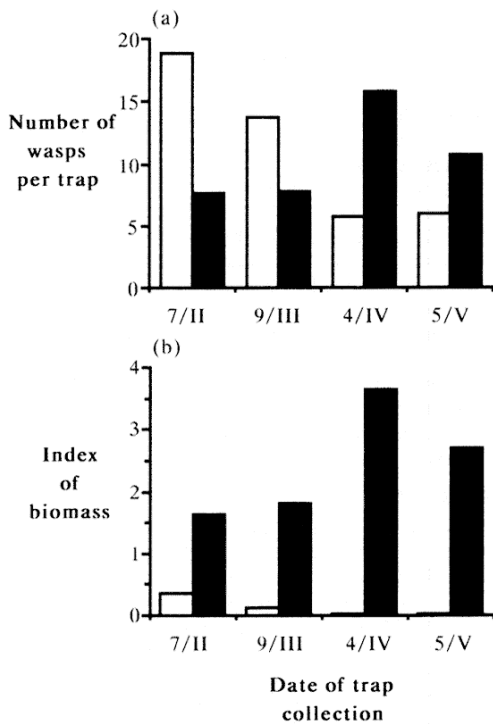
Figure 1: *Native wasps (open) and introduced* V. vulgaris *(solid) caught in sticky traps at Spooners in 1989. (a) Mean numbers of wasps per trap. (b) Estimated relative biomasses of wasps, summed for all traps. Dates given are the days on which traps were brought in.*

Introduced *V. vulgaris* wasps were much larger than most native wasps (Fig. 2). An index of relative biomass was then calculated (see methods) for native and introduced wasps for each of the four sampling periods (Fig. 1b). Comparison of these values showed that an estimated 81.5%, 98.0%, 99.0% and 99.1% of wasp biomass was *V. vulgaris* for the sampling periods ending 7 February, 9 March, 4 April and 5 May 1989 respectively.

Abundance and biomass of vertebrates
Birds
Bird density was taken as 2.69 pairs per hectare (109 pairs per 100 acres) from honeydew beech forest in Nelson Lakes (Kikkawa, 1966). Counts of bird species at Spooners are given in Table 5 of Clout and Gaze

(1984). These counts are representative of honeydew beech forest in general: the counts at Spooners (Clout and Gaze, 1984) are correlated with the summed counts at 23 honeydew beech forest sites where counts were made in 1988 (Appendix 2 in Moller *et al.,* 1988) (we gave a value of 0.01 to bird species scored as trace by Clout and Gaze; n = 18, r^2 =0.86, p<0.00l). Substituting Spooners count values into equation 3, a value of 132 g ha^{-1} is obtained for the sum of all bird species except New Zealand pigeon, the only bird species with no real diet overlap with *V. vulgaris*. Including pigeon, total biomass is estimated at 206 g ha^{-1}. Of this 206 g ha^{-1}, 29.35 g ha ha^{-1} (14%) is estimated to be of introduced birds (counting silvereye as native), although this may be a slight underestimate because blackbirds (10.65 g ha^{-1}) are relatively poorly recorded on bird counts (M.N. Clout pers. comm.). Excluding pigeons, this leaves only about 100 g ha^{-1} of native birds.
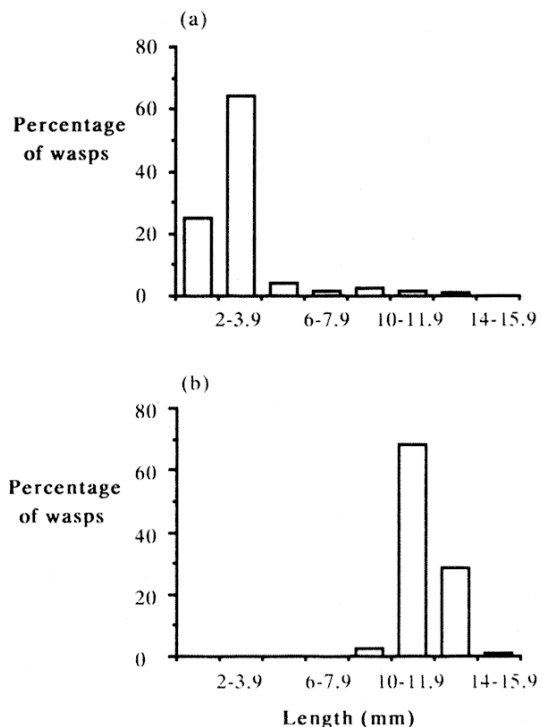

Figure 2: *Size distributions of (a) native wasps and (b) introduced* V. vulgaris *captured in sticky traps at Spooners in 1989. Data for the four sampling periods are pooled.*

Because the bird count adjustment has various problems, it is useful to estimate a range of potential biomasses. If all 2.69 pairs were tui, the heaviest bird apart from pigeons, the estimate would be 577 g ha^{-1}. If all 2.69 pairs were grey warblers, the lightest species, the estimate would be 35 g ha^{-1}. Kikkawa (1966) gave a range of densities for beech forest, from 70 to 170 pairs per 100 acres (1.73 to 4.32 pairs per hectare). If the actual density was 4.32 pairs per hectare, and using the relative counts given by Clout and Gaze (1984), as above, an estimate of 331 g ha^{-1} is obtained for all birds including pigeons. If they were all tui, we obtain an estimate of 927 g ha^{-1} or if they were all grey warblers, 56 g ha^{-1}. If the actual density was 1.73 pairs per hectare, the estimates would be 133 g ha^{-1} for all birds including pigeons, 371 g ha^{-1} if they were all tui, and 22 g ha^{-1} if they were all grey warblers. Reasonable estimates for all birds are from about one hundred to a few hundred grams per hectare, with a maximum range of 22 to 927 g ha^{-1}.

Rodents

Rodent densities vary greatly in beech forest in response to mast fruiting of beech trees (periodic heavy fruiting) (e.g., Daniel, 1972; Fitzgerald, 1978). At Mt Misery beech forest, 0 to 2.3 black (ship) rats were caught per 100 trap nights (R.H. Taylor, in Daniel, 1978). However, the trap line was an elevational transect, and black rats were restricted to the bottom third (R.H. Taylor, pers. comm.), so trap rates were equivalent to 0 to 6.9 rats per 100 trap nights at lower elevations. Daniel (1972) found that an overall black rat trap rate of 2.13 per 100 trap nights was equivalent to a mean biomass of 221 g ha^{-1}. Therefore, maximum black rat biomass at Mt Misery can be estimated to be 716 g ha^{-1} (by substitution in equation 4). No Norway rats *(Rattus norvegicus)* were present.

Mice trap rates at Mt Misery were 1 to 15 per 100 trap nights (R.H. Taylor, in Fitzgerald, 1978). Mice were present throughout the transect, but more abundant in the lower half (R.H. Taylor, pers. comm.), so the figures have been doubled to give an estimated 2 to 30 per 100 trap nights at lower elevations. A capture rate of 8 per 100 trap nights was equivalent to 52.8 g ha^{-1} at Orongorongo, so the maximum biomass at Mt Misery is estimated to have been 198 g ha^{-1} and the minimum 15 g ha^{-1} from equation 4).

Using these values, maximum rodent biomass, after beech masting, may have reached about 914 g ha^{-1} if rats and mice peaked at exactly the same time.

Normally rodent biomass would be much lower, and as low as 15 g ha^{-1} during population troughs.

Stoats

On Adele Island, density was 0.11 stoats/ha (Taylor and Tilley, 1984), which was equivalent to 29.2 g ha^{-1}. Trap rates per 100 trap nights were 0 to 5.66 at Eglinton, 0.17 to 9.28 at Hollyford, 0.07 to 3.68 at Craigieburn, and 0.19 to 2.97 at Mt Cook (King, 1983). Calibrating these data by the Adele Island trap rates (by substituting into equation 5), biomass estimates are obtained of 0 to 10.3 g ha^{-1} at Eglinton, 0.3 to 17.0 g ha^{-1} at Hollyford, 0.1 to 6.7 g ha^{-1} at Craigieburn, and 0.3 to 5.4 g ha^{-1} at Mt Cook. Stoat biomasses range from 0 to 29 g ha^{-1} at these sites. Craigieburn is beech forest with honeydew, but Craigieburn is at higher elevation than Spooners and is likely to have a lower stoat biomass than at Spooners.

Discussion

Problems surround any estimate of biomass, and the above estimates and ranges are probably no more accurate than to an order of magnitude. However, the maximum and minimum estimates are probably sufficiently robust to permit qualitative comparisons among groups. These comparisons show that wasp biomass appears to be as great as, or greater than, bird, rodent and stoat biomasses (Table 2). If the estimates are taken at face value, it seems likely that (with the exception of years following beech mast fruiting) the biomass of introduced *Vespula* (mostly *V. vulgaris)* wasps exceeds the total biomass of birds plus rodents plus stoats, even when biomasses are averaged throughout the year. When rodent and stoat biomasses peak after beech fruiting, the combined biomass of birds, rodents and stoats is still unlikely to exceed the peak biomass that wasps attain each season in honeydew beech forest.

We do not know why West Coast sites had lower wasp numbers. Several possible explanations exist. *V. vulgaris* has not yet completed its invasion of the West Coast, and total wasp numbers may increase with the arrival of *V. vulgaris* (Sandlant and Moller, 1989). West Coast weather conditions may also be less suitable for wasps, and the vegetation compositions of West Coast and central-northern sites are not identical.

The relative biomasses in Table 2 may not hold in other habitat types. In non-honeydew beech forest, wasp densities appear to be lower (Moller *et al.,* 1988; Sandlant and Moller, 1989), and in other types of

Table 2: *Comparative biomasses (g/ha) of* Vespula *wasps, birds, rodents and stoats in honeydew beech forests. A few estimates of stoat densities from habitats other than honeydew beech forests are included.*

	Mean (or best estimate)	Range Min.	Max.
Vespula peak	3761	488	10089
Vespula (average over year)	1097	142	2943
All birds	206	22	927
Rats		0	716
Mice		15	198
Stoats		0	29
Vertebrates (cumulative)		37	1870

forest, bird and rodent densities may be higher. For example, Innes and Skipworth (1983) report the presence of five black rats in a non-beech forest fragment of only 0.22 ha, giving a biomass estimate of nearly 3000 g ha^{-1}, and higher densities still have been recorded for rats on some offshore islands (Beveridge and Daniel, 1965; Daniel, 1969). However, such high densities may occur only in real and habitat islands.

If relative biomass is at all correlated with predation pressure on invertebrates due to wasps, then almost all predation pressure exerted by wasps at Spooners is by introduced *V. vulgaris* over the months of peak *V. vulgaris* abundance (Fig. 1). During peak periods, introduced *V. vulgaris* biomass is one or two orders of magnitude greater than biomass of all native wasps together. Of course, different sizes and species of wasps hunt in different ways and pursue different prey, but these biomass estimates indicate that *V. vulgaris* has the potential to restructure both predator and prey communities.

Mean (for all our honeydew forest sites) *Vespula* density at peak was about 10,000 workers/ha, with a maximum of about 27,000 workers/ha. A North American wasp (*Mischocyttarus flavitarsus*), attained densities equivalent to between 800 ha^{-1} and 5000 ha^{-1} in a greenhouse (Bernays, 1988). *Polistes wasps* (another genus of Vespulid wasp, two species of which are established in the North Island of New Zealand; Clapperton *et al.,* 1989) have been used as biological control agents at densities encouraged by the provision of nesting sites. These wasps attained densities of 2722 ha^{-1} and 3389 ha^{-1} (Gould and Jeanne, 1984), 3781 ha^{-1} (Nakasuji, Yamanaka and Kiritani, 1976), and 540 ha^{-1} (with an exceptionally low site of 108 ha^{-1}) and 864 ha^{-1} (Lawson *et al.,* 1961). In the study by Lawson *et al.* (1961), the sizes of individual wasp nests were not given, so a value of 7.2 wasps per nest is assumed here. This is the mean value given for *Polistes*

fuscatus nests by Gould and Jeanne (1984); this value was used because *P. fuscatus* was the commonest wasp species in the study area used by Lawson *et al*.

These published densities are mostly well below the densities attained by *Vespula* in honeydew beech forest. However, beech forest is structurally more complex and occupies a greater volume than a comparable area of crop or greenhouse, even though much of the forest is empty space. Therefore, different wasp or worker densities and biomasses in different habitats are not automatically correlated with different predation pressures exerted on prey species or honeydew drops. Nonetheless, *V. vulgaris* densities are clearly very high.

Lepidoptera are the most common prey item gathered by *Vespula* wasps in honeydew beech forest (R.J. Harris, unpublished data). Lepidopterans were the main prey items eaten by the wasps in the studies (cited above and below), and in some cases the impact of the wasps on them has been measured directly. Morimoto (1960a, b) observed wasp predation on caterpillars at a rate of 14.0 to 88.2% in a 10 hr foraging period, reaching a mean of 81.2% after five days. Lawson *et al.* (1961) reported 50 to 98% predation on moth larvae over a whole brood, with average larval populations reduced by 60% in 'enhanced' wasp areas compared to 'control' areas, which presumably still had some wasp predation. Ito and Miyashita (1968) estimated that there was an additional 67% mortality due to wasp predation in a comparison of 'coarse mesh' and 'fine mesh' treatments. Morris' (1972) study of predation on *Hyphantria cunea* larvae gave an estimate that average larval mortality was reduced by 97% in an area with very few *Vespula* wasps (his CDA site) compared to areas with denser *Vespula* populations. Introduced *V. vulgaris* was the principal wasp predator at one site where predation on fourth and fifth instar larvae was 100%. Gould and Jeanne (1984) found that caterpillar populations were reduced by 63% and 34% by wasps in different years, by comparison of 'control' and 'wasp enhanced' treatments, and that caterpillar numbers were reduced by 40% due to wasp predation in a comparison of a 'wasp enhanced' treatment and a 'wasp exclosure' in the same field. In Bernays' (1988) greenhouse study, 12 out of 27 (44%) species of caterpillar suffered greater than 25% predation within 6 hours. Bernays stopped her studies at 6 hours (or before that if more than 50% predation was reached). In a field study, Stamp and Bowers (1988) observed 97.4% wasp predation of *Hemileuca lucina* caterpillars in 24 hrs.

If the predation rates observed by Bernays (1988) and by Stamp and Bowers (1988) continued over a 15 day development period, then 17 of the 28 species concerned (61%) could be expected to suffer 95% or greater mortality due to wasp predation. In a review of Lepidoptera life tables, Dempster (1983) reported that larval predation (disappearance of a kind consistent with, but not necessarily caused by, wasp predation) was the key factor in 5 of 14 species, and possibly also important in a further 5 species.

The above studies demonstrated major impacts on insect prey by wasps at much lower (but often artificially enhanced) densities than are attained by *V. vulgaris* in New Zealand. Therefore it seems extremely likely that *V. vulgaris* is a major mortality factor for many of those Lepidoptera species that develop during periods of high wasp densities. However, without further ecological information it is not possible to assess whether *Vespula* predation results in increased Lepidoptera mortality rates, or whether overall Lepidoptera mortality is relatively unchanged but that the source of mortality is changed. In the latter case the impact is borne by competitors that can no longer obtain adequate Lepidoptera prey for themselves (e.g., insectivorous birds, parasitoids and native wasps). Furthermore, parasitoids may fall indirect prey themselves if *Vespula* wasps prey on parasitised Lepidoptera larvae: this has been recorded (R.J. Harris, unpublished data).

None of the above measures of biomasses or comparative abundances prove any specific impact of *V. vulgaris* on particular components of the beech forest community, but all of the figures suggest that impacts are likely to be significant. Introduced wasps probably now playas important a role in honeydew beech forest communities as do birds, rodents and stoats, and considerably more research is required to assess wasp impact.

Acknowledgements

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