49 Margaret Avenue, Havelock North, New Zealand.

ABUNDANCE OF WASPS AND PREY CONSUMPTION OF PAPER WASPS (HYMENOPTERA, VESPIDAE: POLISTINAE) IN NORTHLAND, NEW ZEALAND

Summary: Polistine and vespine wasps were captured in Malaise traps in two fire-modified shrubland habitats of varying canopy height and composition at Lake Ohia, Northland, New Zealand. Prey consumption rates were calculated for the Asian paper wasp (Polistes chinensis antennalis) occupying these two areas of shrubland and a home garden in Whangarei, Northland. The sites were systematically searched for nests and wasp prey determined by intercepting foragers returning to nests. The Asian paper wasp predominated in the Malaise trap samples from the low-growing habitat while the German wasp (Vespula germanica) was more common in the taller vegetation type. The Asian paper wasp was more abundant than the German wasp in the samples in February and early March. Only four Australian paper wasps (Polistes humilis) and no common wasps (Vespula vulgaris) were caught. Asian paper wasps collected an estimated 15 000 prey loads per haper season from one of the shrubland areas, and 478 000 prey loads per haper season from the second area. These convert to estimates of 31 and 957 g per haper season of invertebrate biomass removed by paper wasps from each habitat, respectively. The estimate for the garden site was 79 g per ha per season. Wasp nest densities varied between 20 and 210 nests per hectare. The biomass estimates are similar to average figures calculated for vespine wasps in scrubland and pasture. Both Asian paper wasps and Australian paper wasps preyed mainly on lepidopteran larvae. The cabbage white butterfly (Pieris rapae) was the most commonly collected species. Noctuid species were also well represented. Both male and female Asian paper wasps collected nectar in late March and early April.

Keywords: Asian paper wasp; *Polistes chinensis antennalis*; Australian paper wasp; *Polistes humilis*; German wasp; *Vespula germanica*; abundance; prey consumption; biomass; diet.

Introduction

The temperate Asian paper wasp, *Polistes chinensis antennalis* Pérez (Vespidae, Polistinae) has become widespread in northern New Zealand, including Northland, Auckland, Waikato, Coromandel and Bay of Plenty since its arrival in the country in the late 1970s (Clapperton, Moller and Sandlant, 1989; Clapperton, Tilley and Pierce, 1996). It has recently become established in the top of the South Island. It is common in urban and rural habitats in warm, low-growing shrublands and salt meadows, and in forest clearings (Clapperton *et al.*, 1996). It co-exists with, or may be out-competing the Australian paper wasp, *Polistes humilis* (Fab.) (Clapperton *et al.*, 1996) which has been established in these habitats since the 1880s (Miller, 1984).

Paper wasps rely heavily on live lepidopteran larvae for their protein sources (Rabb and Lawson, 1957; Rabb, 1960). Paper wasps may attack native Lepidoptera, modify the structure of the invertebrate community, and compete with other insectivorous fauna. They may also compete with nectar-feeders at flowers and fruit, and for honeydew produced by homopterous insects (Douglas and Serventy, 1951; Rabb, 1960; Gillapsy, 1986), possibly affecting plant pollination.

In rural and garden environments, the paper wasps could have beneficial as well as adverse effects. While they are disliked because they prey upon monarch butterfly (*Danaus plexipus¹*) larvae (*pers. obs.*), they also take larvae of lepidopteran pest species. They have been viewed as valuable biocontrol agents of cabbage white butterfly (*Pieris rapae*) on cabbages in Japan (Morimoto, 1960b).

Little is known about the ecology and impact of Asian paper wasps in New Zealand. The aims of this study in shrubland and garden habitats were to quantify the abundance of paper wasps, to compare their abundance with that of vespine wasps, to quantify the biomass of invertebrates removed by

¹Lepidoptera nomenclature follows Dugdale (1988) for New Zealand endemics, and Nielson, Edwards and Rangsi (1996) for species shared with Australia.

Asian paper wasps and to report preliminary findings on the diet of Asian paper wasps and Australian paper wasps.

Methods

Study sites

In 1991 and 1992, wasp abundance and diet were studied in a rural garden on the outskirts of Whangarei (35°43'S, 174°22'E). The approximately one hectare garden comprised a mix of vegetable garden, ornamental shrubs, lawn, young native shrubs, and fruit trees.

In 1993, wasp abundance and dietary studies were carried out in two areas in shrublands around Lake Ohia, Karekare Peninsula, Northland (34°57'S, 173°22'E). One site (Tall Shrub) consisted of firemodified shrubland (1-2 m canopy height) dominated by *Leptospermum scoparium* (J.R. et G. Forst), *Kunzea ericoides* ((A. Rich) J. Thompson) and *Ulex europaeus* (L.), adjacent to coastal salt marsh containing damp reedy areas with islands of *Leptospermum* and other shrubs. The second site (Short Shrub) contained mainly low-growing vegetation (0-1 m canopy height), predominately *L. scoparium*, with a few taller exotic shrubs.

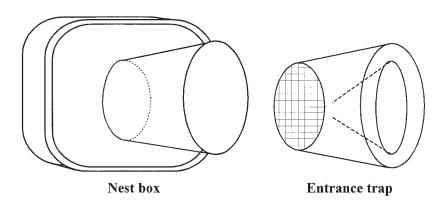
Estimates of wasp abundance

At the Garden site, nests were noted when found from October 1991 onwards, and the whole site was searched in early April 1992 to ensure all nests had been found. Numbers of wasps per nest for seven representative nests were counted 5-7 times during late February and early to mid March. At the two Lake Ohia sites, 10 plots measuring 10 m x 10 m were searched for wasp nests at least once between 25 February 1993 and 11 March 1993 to estimate the mean number of nests per hectare for each site. Nest abundances were compared using a two-sample t test. For each nest found, the number of wasps per nest was counted by direct observation and mean numbers of wasps per hectare calculated.

Six Malaise traps (Townes, 1972; Hutcheson, 1991) were operated at each of the Lake Ohia study sites. They were set with the base touching the ground cover, at least 100 m apart along a line, 0.25-1.5 km from nests used in the dietary studies. Orientation of the traps with respect to compass bearing was randomized along the lines. The traps were operated from 5 February to 14 May 1993, cleared weekly or fortnightly and numbers of each sex determined for vespine and polistine wasps caught. Catches were converted to a per 10 trap days rate. Two-way ANOVA was used to compare catch rates of the species for the two trap lines, with individual traps treated as replicates.

Pellet collection

Polistine nests used for diet sampling were collected either from or near the study sites, or transported in from Whangarei. They were glued into a 2 l plastic box with a funnel-shaped entrance (modified 1 l stackable container) inserted into the box lid (Fig. 1). A trap inserted into the funnel entrance was used to intercept returning foragers. Trapping occurred between 0900 h and 1600 h NZST. The trap was left in place for 10-30 minutes, during which time 0-15 wasps were caught and most released their pellet loads. The number of wasps caught in the trap was



recorded. The trap was then opened, the wasps released and the pellets recovered.

Six Asian paper wasp nests were repeatedly sampled at the garden site between 8 February and 8 March 1991. Three Asian paper wasp nests were used between 5 February and 16 April 1992, and another six between 24 and 27 March 1992. At Lake Ohia four Asian paper wasp and three Australian paper wasp nests were used at the Tall Shrub site, while eight Asian paper wasp nests and three Australian paper wasp nests were used at the Short Shrub site. Pellet collections were made on 14 days between 23 February and 31 March 1993.

Quantitative assessment

Prey consumption of Asian paper wasps, in terms of biomass per hectare per season, was calculated for the Garden in 1992 and both study sites at Lake Ohia in 1993 using equations based on those used by Harris (1991):

 mean daily prey consumption per nest = minutes of active foraging per day x proportion carrying prey x mean traffic rate

Mean traffic rates, or the mean number of wasps entering a nest per minute (Malham et al., 1991), were calculated from data collected in 1991 for seven nests in the Garden site. Nests were observed for 15-minute periods on warm, dry days in February and March, with each nest being observed between one and four times on different days during each hour between 0700 and 1700 NZST. The number of wasps present on the nest at the end of each 15-minute period was also noted. Counts per 15 minutes for individual nests were averaged for each hour and the estimated traffic rate used here is the grand mean of these 63 means divided by 15. The traffic rate estimate was also applied to the Lake Ohia study sites after adjusting for the difference in numbers of wasps per nest during the 25 February to 11 March period. A previous study (Hoshikawa, 1981) has shown that pellet collection rates are positively correlated with the numbers of foragers in the colony. The proportion of wasps carrying prey loads at each site was calculated from captures in the entrance traps, after adjusting for the percentage of loads comprising animal prey or plant material.

(2) mean daily prey consumption per hectare = mean daily prey consumption per nest x mean number of nests per hectare

The methods used to determine mean nests ha⁻¹ at each site are described above.

(3) mean seasonal prey consumption per hectare = mean daily prey consumption per hectare x number of days in the wasp season

The paper wasp foraging season was defined as all of

February and March. Nests have few (usually <10) wasps present before the end of January (Clapperton and Dymock, 1997) and foragers stop collecting pellets by early April (see below; Hoshikawa, 1981).

(4) mean biomass of prey consumed per season per hectare = mean seasonal prey consumption per hectare x mean prey biomass.

A subsample of 34 pellets from Asian paper wasps was weighed on the day of collection or the subsequent day (after cool storage overnight) and a mean fresh weight calculated.

Diet assessment

Pellets were collected and placed in 70% ethanol. They were macerated overnight in 10% potassium hydroxide, lightly stained with chlorazol black and examined under a binocular stereo-microscope.

Between 26 March and 16 April 1992, 46 captured Asian paper wasps (43 female, 3 male) at the Garden site were chilled until inactive and their crop content expressed by gently crushing the abdomen. This liquid was combined with one or two drops of rain water (to provide an assessable quantity). The presence of sugar was determined by measuring the refractive index with a hand-held refractometer.

Results

Wasp abundance and density

The Garden site had fewer nests than either site at Lake Ohia (Table 1), and mean wasps per nest in late February to mid-March for the seven regularly monitored nests was 15.1 ± 3.8 SE. This translates to only 302 wasps per hectare in the garden site.

Numbers of Asian paper wasp nests per hectare were more than four times greater in the Short Shrub at Lake Ohia than in the Tall Shrub (t=3.01, d.f.=12, P=0.011) (Table 1). Combined with a difference in mean number of wasps per nest (Short Shrub = 30.1±3.8; Tall Shrub = 20.4±10.4) this represents a significant difference in wasps per hectare of 6320 vs 1020 (t=3.77, d.f.=13, P=0.0024).

At Lake Ohia, only four Australian paper wasps and no common wasps (*Vespula vulgaris* L.) were caught in the Malaise traps. Catch rates of female Asian paper wasps did not vary significantly through the trapping period (Fig. 2a) but were higher in the Short Shrub than in the Tall Shrub ($F_{1,90}=28.7$, P<0.001). German wasp (*Vespula germanica* Fab.) females (workers) were scarce at the beginning of the trapping period (Fig. 2b), but their numbers increased from mid-March. German wasp females were more abundant in the Tall Shrub ($F_{1,180}=54.8$, P<0.001).

	Garden	Lake Ohia Tall shrub	Lake Ohia Short shrub
Nests hectare ⁻¹	20	50	210
Traffic rate (wasps minute ⁻¹)	0.23	0.31	0.46
Numbers of wasps trapped	302	44	293
Pellet wasp ⁻¹	0.38	0.29	0.25
Prey pellet ⁻¹	0.80	0.12	0.70
Foraging minutes day ⁻¹	480	480	480
Days season ⁻¹	59	59	59
Mean pellet weight (g)	0.002	0.002	0.002
Number of prey nest ⁻¹ day ⁻¹	33.6	5.2	38.64
Number of prey hectare ⁻¹ day ⁻¹	672	260	8114
Number of prey hectare ⁻¹ season ⁻¹	39 648	15 340	478 726
Biomass prey (g) hectare ⁻¹ season ⁻¹	79.3	30.68	957.4

Table 1: Estimates of daily and seasonal prey consumption by Asian paper wasps per nest and per hectare in the Whangarei garden in 1992 and in both sites at Lake Ohia in 1993.

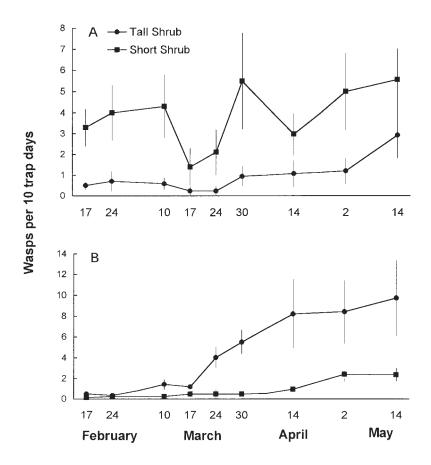


Figure 2: Mean (\pm 1S.E.) number of female (A) Asian paper wasps and (B) German wasps caught in Malaise traps at Lake Ohia in 1993.

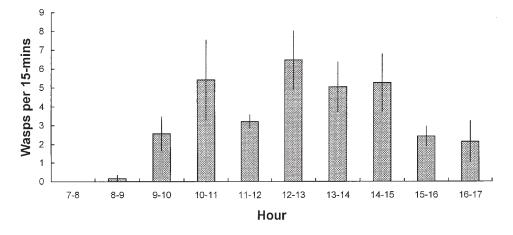


Figure 3: Mean (± 1S.E.) traffic rates (number of wasps returning to the nest per 15-min period) at seven nests at the rural garden site in February and March, 1991.

Asian paper wasp males were present from February but became abundant only from the end of March. Their highest mean catch rate was 10 per 10TD, in late March in Short Shrub. Male German wasps were caught in every month, but their catch rate never exceeded 1 wasp per 10TD.

Quantitative assessment

Traffic rates at the seven nests in the garden site varied between 0 and 20 wasps in the fifteen-minute observation periods (Fig. 3). The grand mean estimate of traffic rate used in the quantitative assessment was 3.5 wasps per 15 minutes, or 0.23 wasp per minute. Traffic rates were weakly correlated with numbers of wasps observed on the nests at the time (Fig. 4).

Per hectare prey consumption rates of Asian paper wasps varied by about 30 times between the two sites at Lake Ohia (Table 1). The consumption rate for this species at the Garden site was estimated to be about twice that of the Tall Shrub site. The proportion of wasps returning to the nest with prey pellets was as high at the Garden site as at the Short Shrub site, but this was offset by the low nest abundance at the former site.

Diet

A total of 402 female and five male Asian paper wasps were caught in entrance traps at the Garden nests between February and April (1991: 89 wasps; 1992: 318 wasps). They provided 147 pellets. Of these, 95 contained entire or coarsely fragmented prey (80%) or wood fibres (20%). The remainder were too finely masticated to allow determination of their composition. Pellet recovery rates were higher in February (70% and 50% in the two years, respectively) than in March (36% and 28%) ($P^2=9.1$, d.f. =1, *P*=0.005 for the two seasons combined). Fifteen wasps were caught in April and only one pellet was recovered. No pellets were collected from the male wasps.

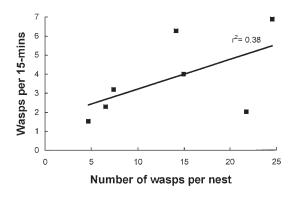


Figure 4: Relationship between number of wasps observed on a nest and traffic rate (number of wasps returning to the nest per 15-min period) for 7 nests at the rural garden site in February and March, 1991. Replicate counts for any one hourly period were averaged for individual nests, then the average over the hourly periods for each of the seven nests was calculated.

For Asian paper wasps foraging in the Garden lepidopteran larvae were the most common prey, accounting for 90% of the arthropods identified in the pellets (Table 2). The most common species identified in February was *Pieris rapae* (Pieridae) (52%). *Mythimna separata* (Noctuidae) predominated in March (41%). The remaining Lepidoptera were all members of the Family Noctuidae apart from one member of the family Geometridae. Other arthropod groups represented were Diptera, Coleoptera, Formicidae, Cicadelidae and Pholicidae.

Fifty-nine per cent of Asian paper wasps sampled (n=46) during late March and early April at the Garden site had full crops. Sugar was present in measurable amounts in the majority of these (81%). Two out of three of the male Asian paper wasps collected had full crops, as did one of the three females that also carried pellets.

One hundred and four pellets were collected from 378 polistine wasps at Lake Ohia during 1993 (86 from Asian paper wasps; 18 from Australian paper wasps). Pellet recovery rates in February (36%) and in March (25%) were not significantly different. Most (77%) of the pellets came from the Short Shrub site. Of 41 Asian paper wasp and 10 Australian paper wasp pellets examined, 24 contained prey, 17 contained plant material or fibrous dirt and the remaining 10 pellets contained material that could not be identified.

Table 2: The identity and numbers of prey items in pellets collected from Asian paper wasps at the Whangarei garden in 1991 and 1992 combined and from Asian paper wasps and Australian paper wasps at both sites at Lake Ohia in 1993.

Prey item	Whangarei garden	Lake Ohia	
	Asian	Asian	Australian
ARTHROPODA	-	1	-
INSECTA			
Lepidoptera	-	1	1
Pieridae			
Pieris rapae	20	6	-
Noctuidae			
Dasypodia sp.	7	-	-
Graphania sp.	11	-	-
Agrotis ipsilon	2	-	-
Mythimna separata	14	-	-
Heliothis armigera	5	2	-
unidentified	11	-	1
Geometridae			
Chloroclytstis sp.	1	-	-
Cleora scriptaria	-	-	1
Pterophoridae			
Pterophorus sp.	-	3	-
Lycaenidae			
Zizina labradus	-	1	-
Crambidae			
Uresiphita polygonalis maorialis	-	-	2
Diptera	1	-	-
Syrphidae	2	-	-
Sarcophagidae			
<i>Hybopygia</i> sp.	1	-	-
Coleoptera			
Chrysomelidae			
Paropsis sp.	1	-	-
Homoptera			
Cicadelidae	1	-	-
Hemiptera	-	1	-
Hymenoptera			
Formicidae	1	-	-
Sphecoidae	-	1	-
ARACHNIDA	-	1	2
Pholcidae	1	-	-
TOTAL	79	17	7

Pellets collected from Asian paper wasps at Lake Ohia most often contained larvae of *Pieris rapae* (Table 2). The other lepidopteran species present were *Helicoverpa armigera*, *Pterophorus* sp. and *Zizina labradus*. Other orders represented included Hemiptera and Hymenoptera. One arachnid was also collected.

The identifiable prey of the Australian paper wasp included several lepidopteran larvae (*Uresiphita polygonalis maorialis*, a geometrid larva, probably *Cleora scriptaria*), an unidentifiable noctuid larva, another comminuted caterpillar) and two arachnids (Table 2).

Discussion

Wasp abundance

Abundance of polistine foragers and nests, and of vespine foragers varied greatly between the two habitat types at Lake Ohia. That the Asian paper wasp was more abundant in the low-growing habitat is consistent with the broad habitat preferences of this species (Clapperton et al., 1996). The higher abundance of the German wasp in the Tall Shrub habitat may be because of the patchy distribution of nests (Harris and Oliver, 1993) rather than because of habitat preferences or competition between the species, as no German nests were found at either site. Numbers of individuals per nest are known to be much lower for Asian paper wasps than for vespine species (Malham et al., 1991; Clapperton and Dymock, 1997), but numbers of nests per hectare recorded at Lake Ohia were much higher than those reported for vespine wasps in similar habitat (Harris and Oliver, 1993). Under these conditions Asian paper wasps may have a similar level of impact on arthropods as that effected by foraging vespine wasps. Indeed their impact may be greater than that of vespines early in the season, when the trap data revealed that polistine foragers were more abundant than vespines. This assumes that there was no differential change in trappability over time between the species.

Few Australian paper wasps were caught in the traps at Lake Ohia. It is not clear whether the trapping results reflect a true low abundance of this species, or is an artefact of the trapping regime. Australian paper wasps nest at a higher average height than Asian paper wasps (Clapperton *et al.*, 1996) and thus may have been less abundant in the low-canopy site because of lack of nesting sites. Furthermore, Australian paper wasps may have been caught infrequently in the traps at either Lake Ohia site because the vertical zone at which they appear to

forage was higher than the trap entrance (*pers. obs.*): this vertical zonation of foraging has been observed in other wasp species (J.S. Dugdale, *pers. comm.*, Nelson). The common wasp has never been reported from Lake Ohia, so its absence from the Malaise trap data probably reflects its true absence from the study sites.

Quantitative assessment

Our assessment of the amount of prey collected by Asian paper wasps in the Garden and in the Short Shrub at Lake Ohia (34 and 39 prey items per nest per day, respectively) are comparable to that reported for the same species in Japan (29 prey items per nest per day) (Morimoto, 1960a), even though prey pellet collection rates were lower than those reported for Asian paper wasps in Japan (Suzuki, 1978). It is also similar to the average rate of 32 prey pellets collected per day by *Polistes* fuscatus Fab. in North Carolina (Rabb, 1960). In my study, as in those in Japan and North Carolina, the amount of prey removed by the wasps may have been underestimated as the wasps probably consumed some of the prey themselves rather than returning it all to the nest (Grinfel'd, 1978). This is offset, however, by the fact that the length of the foraging season may have been overestimated. No allowance was made for the fact that polistine wasps are much less active on cool, wet days (Rabb, 1960; pers. obs.). My failure to include the amount of prey material consumed early in the season (September to January), is not significant as early in the season each nest has only one foundress female (Clapperton and Dymock, 1997), which are less efficient hunters than their offspring (Hoshikawa, 1981) and the amount consumed during this period is small compared with the amount consumed during February and March (Suzuki, 1981, 1984). Morimoto (1960a) observed that a foundress female carried five prey loads to the nest per day before the emergence of the first brood.

We can compare the predatory impact of the Asian paper wasp on the invertebrate fauna with the impact of predation by vespine wasps. The estimated 31 and 957 g ha⁻¹ of insect biomass that Asian paper wasps removed from the shrublands of Lake Ohia are lower than the estimated 1.4-8.1 kg ha⁻¹ removed by common wasps in beech forest habitats (Harris, 1991). They are, however, closer to the amounts (50 and 470 g) removed by vespine wasps in scrubland-pasture habitat (Harris and Oliver, 1993). Asian paper wasps had large numbers of nests per hectare, but traffic rates are much lower than for the vespine species. I also used lower estimates of minutes and

days of active foraging than Harris and Oliver (1993), which produced conservative estimates of prey consumption.

Diet

Lepidoptera predominated in the diet of the Asian paper wasp in this study as in Japan (Suzuki, 1978), but less so than in other species of polistine wasps (Rabb and Lawson, 1957; Rabb, 1960). The garden pest species identified in the present study suggest that the Asian paper wasp plays a beneficial role in the garden environment. The diet of the Asian paper wasp in the shrubland habitat of Lake Ohia was similar to that in the rural garden site, with Lepidoptera making up the majority of prey items.

The Lepidoptera identified from the pellets recovered from Asian paper wasps were large species (e.g., *P. rapae* larvae are >8 mm long), and/ or exposed feeders in sunlight (J.S. Dugdale, *unpubl. data*). Although *Leptospermum* and *Kunzea* in the Lake Ohia area support the large (>20 mm long) caterpillars of several common endemic geometrid moths (Spiller and Wise, 1982), these species do not usually feed by day. They are thus unlikely to fall prey to paper wasps. However, the small leafrollers (Fortricidae) that live on *Kunzea* and *Leptospermum* and are likely prey of paper wasps were probably unrecognizable as such by the methods used in this study.

Although few items were identified from the pellets collected by the Australian paper wasps, Lepidoptera predominated. Both species also took Arachnida. This suggests competition for food resources between the two paper wasp species. There may also be overlap between the polistine and the vespine species. Harris and Oliver (1993) found that Lepidoptera were second only to Diptera in importance in the diet of both German wasps and common wasps in scrubland-pasture habitat. Diptera may have been underestimated in the samples of the present study if they were finely minced and thus unidentifiable. German wasps forage near the ground (*pers. obs.*), so their vertical foraging zone will overlap with that of Asian paper wasps.

Conclusions

The wasp abundances and prey consumption rates reported in this study suggest that the Asian paper wasp may have a significant impact on the fauna of New Zealand shrublands, similar to that of vespine species. The dietary studies indicated few species of native insects at risk of direct predation, but greater sampling is required, as are methods that identify the finely-minced prey species. The biomass estimates reported here probably represent a "worst-case scenario", the study being conducted in a year of high Asian paper wasp abundance (J.J. Dymock, *pers. comm.*, Ministry of Agriculture and Forestry, Auckland).

Acknowledgements

This research was funded by a contract from the Department of Conservation (Science & Research). I am grateful to Chris Locke for field assistance, and to John Dugdale for prey identifications and comments on an earlier draft of the manuscript. My thanks go also to Richard Harris and G.M. Barker for their comments on the manuscript.

References

- Clapperton, B.K.; Dymock, J.J. 1997. Growth and survival of colonies of the Asian paper wasp, *Polistes chinensis antennalis* (Hymenoptera: Vespidae), in New Zealand. *New Zealand Journal of Zoology 24:* 9-15.
- Clapperton, B.K.; Moller, H. Sandlant, G.R. 1989. Distribution of social wasps (Hymenoptera: Vespidae) in New Zealand in 1987. *New Zealand Journal of Zoology 16*: 315-323.
- Clapperton, B.K.; Tilley J.A.V.; Pierce, R.J. 1996.
 Distribution and abundance of the Asian paper wasp *Polistes chinensis antennalis* Pérez and the Australian paper wasp *P. humilis* (Fab.)
 (Hymenoptera: Vespidae) in New Zealand. New Zealand Journal of Zoology 23: 19-25.
- Douglas, A.; Serventy V.N. 1951. The establishment of the paper nest wasp in Western Australia. *The Western Australian Naturalist* 2: 169-174.
- Dugdale, J.S. 1988. Lepidoptera annotated catalogue and keys to family-group taxa. *Fauna* of New Zealand 14: 1-262.
- Gillapsy, J.E. 1986. Polistes wasps: Biology and impact on man. In: Vinson, S.B. (Editor), Economic impact and control of social insects. pp. 332-352. Praeger, New York, U.S.A.
- Grinfel'd, E.K. 1978. The feeding of the social wasp Polistes gallicus (Hymenoptera, Vespidae). Entomological Review 56: 24-29.
- Harris, R.J. 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.; 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.

- Hoshikawa, T. 1981. Some colony factors influencing the hunting activity of *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae). *Applied Entomological Zoology 16:* 395-405.
- Hutcheson, J.1991. Malaise trap collection jar: A cheap simple modification. *The New Zealand Entomologist 14:* 48-49.
- Malham, J.P.; Rees, J.S.; Alspach, P.A.; Beggs, J.R.; Moller, H. 1991. Traffic rates as an index of colony size in *Vespula* wasps. *New Zealand Journal of Zoology 18*: 105-109.
- Miller, D. 1984. *Common insects in New Zealand*. A.H. & A.W. Reed Ltd, Wellington, N.Z. 178 pp.
- Morimoto, R. 1960a. *Polistes* wasps as natural enemies of agricultural and forest pests. I (Studies on the social Hymenoptera of Japan X). *Science Bulletin of the Faculty of Agriculture, Kyushi University 18:* 109-116.
- Morimoto, R. 1960b. *Polistes* wasps as natural enemies of agricultural and forest pests. III (Studies on the social Hymenoptera of Japan XII). *Science Bulletin of the Faculty of Agriculture, Kyushi University 18:* 243-252.
- Nielson, E.S.; Edwards, E.D.; Rangsi, T.V. 1996. Checklist of the Lepidoptera of Australia. Monographs on Australian Lepidoptera 4: 1-529.
- Rabb, R.L. 1960. Biological studies of *Polistes* in North Carolina (Hymenoptera: Vespidae). *Annals of the Entomological Society of America* 53: 111-121.

- Rabb, R.L.; Lawson, F.R. 1957. Some factors influencing the predation of *Polistes* wasps on the tobacco hornworm. *Journal of Economic Entomology 50:* 778-784.
- Spiller, D.M.; Wise, K.A.J. 1982. A catalogue (1860-1960) of New Zealand insects and their hostplants. *In:* Dale, P.S.; Maddison, P.A. (Editors), Department of Scientific and Industrial Research Bulletin 231. DSIR, Wellington, N.Z. 260 pp.
- Suzuki, T. 1978. Area, efficiency and time of foraging in *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae). *Japanese Journal of Ecology* 28: 179-189.
- Suzuki, T, 1981. Flesh intake and production of offspring in colonies of *Polistes chinensis* antennalis (Hymenoptera, Vespidae) II. Flesh intake and production of reproductives. Kontyû, Tokyo 49: 283-301.
- Suzuki, T. 1984. Assessment of seasonal changes in the amount of flesh intake by colonies of a polistine wasp, *Polistes chinensis antennalis* (Hymenoptera, Vespidae). *Japanese Journal of Ecology* 34: 1-7.
- Townes, H. 1972. A light-weight Malaise trap. Entomological News 83: 239-247.