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THE DIFFICULTY OF REDUCING INTRODUCED WASP (*VESPULA VULGARIS*) POPULATIONS FOR CONSERVATION GAINS

Summary: Introduced common wasps (*Vespula vulgaris*) are widespread, abundant pests in New Zealand. They compete for food with native birds and feed on native invertebrates. We poisoned wasps annually over 4 years to see if it was possible to reduce their abundance in two 30-ha beech forest sites. Two different poisons (sodium monofluoroacetate and sulfluramid) were used, mixed with sardine catfood. There was no evidence that one poison was more effective than the other. Between 82 and 100% of the colonies were killed in the poisoned sites, but reinvasion by foraging workers meant that cumulative wasp biomass (measured using Malaise traps) was reduced by only 55 - 70%. Individual wasps were about 16% heavier in the poisoned sites at the peak of the wasp season (March) than in the non-poisoned sites, although this had a minimal effect on cumulative biomass over the entire season. Conservation gains need to be quantified in order to assess whether the expense of such poisoning operations is warranted.

Keywords: wasp; *Vespula vulgaris*; invasions; 1080; sulfluramid.

Introduction

Throughout the world, social insects, such as wasps, ants and bees, have been highly successful invaders and can present a massive threat to native biota (Howarth, 1985; Wojcik, 1994; Moller, 1996). The reproductive and dispersal strategies of social insects means that they are formidable foes for conservation managers. In New Zealand, introduced common wasps (*Vespula vulgaris*) can reach very high densities in beech (*Nothofagus*) forests infested with honeydew scale insects (*Ultracoelostoma* spp.; Hemiptera: Margarodidae). The scale insects produce a sugary exudate called honeydew (Grant and Beggs, 1989) which the wasps harvest (Moller and Tilley, 1989). Wasps compete with native birds and invertebrates (Moller and Tilley, 1989; Beggs and Wilson, 1991; Moller *et al.*, 1991), and prey directly on a range of native invertebrates (Harris, 1991; Harris and Oliver, 1993; Toft and Beggs, 1995; Toft and Rees, in press).

For these reasons, conservation managers need to consider options for controlling wasp numbers. Biological control offers a long-term, widespread solution to the problem, but current efforts do not

offer any hope of reducing numbers to any great extent in the near future (Barlow, Moller and Beggs, 1996; Beggs, Harris and Read, 1996). Poison-baiting is currently the only viable technique for reducing wasp density, as finding and destroying nests is very labour intensive. Trials using poison-baiting have been carried out in relatively small sites (1.5 - 3 ha) (Spurr 1991; 1993). Most of these trials measured poisoning success by monitoring individual colonies. An earlier trial site which attempted to reduce wasp abundance (measured by counting wasps in baited traps) by poison-baiting in a 7.2 ha was unsuccessful (Thomas *et al.* 1990). The reasons suggested were poor bait acceptance and reinvasion of workers from neighbouring areas.

Given that the problems of reinvasion are likely to be smaller in larger areas, larger scale trials are required. Managers also need to know whether the costs and benefits of such an operation make it worthwhile.

In 1991, we started a study to manipulate wasp numbers experimentally in two 30-ha sites to measure the impact of wasps on a beech forest community. This paper reports on the impact of 4 years of annual poisoning on wasp populations.

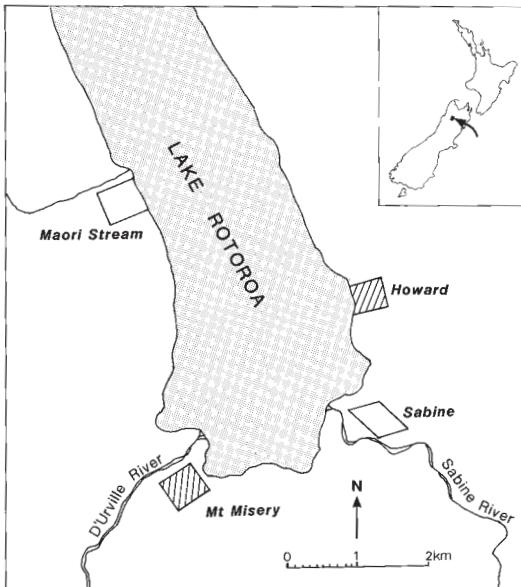


Figure 1: Map of study sites. Mt Misery and Howard were poisoned (hatched) and Sabine and Maori Stream were non-poisoned (open).

Methods

We selected four 30-ha (c. 500 x 600m) sites with an edge close to or bounded by Lake Rotoroa, Nelson Lakes National Park (41°54'S, 172°40'E; Fig 1) for the research and poisoned wasps in two of the sites (Mt Misery and Howard). We hoped to reduce the problem of reinvasion by wasps after poisoning by having the lake as one boundary. The sites were predominantly beech (*Nothofagus*) forest infested with honeydew producing scale insects.

We placed bait stations on a 30 m x 50 m grid (Mt Misery = 231 stations; Howard = 240 stations) that covered the entire 30ha. The area from which we reduced wasp numbers would have been much larger because wasps from further afield would have visited the bait stations. Bait stations were a plastic lid placed on the ground, covered with a wire mesh cage designed to exclude birds.

Table 1. Type of poison and differences in protocol used in different years.

	1991/92	1992/93	1993/94	1994/95
Poison	1080	1080	1080	Sulfluramid
Non-toxic baits	Twice	Twice	Once	Nil
Buffer line	No	Yes	No	No
Eary/late poisoning	Late	Late	Late	Both

For 3 years (1991/92, 1992/93, 1993/94) we poisoned with 1% sodium monofluoroacetate (1080) mixed with canned sardine in aspic jelly catfood (Spurr, 1991). In 1991/92 and 1992/93, we placed non-toxic baits out in the afternoon of the day before poisoning and again the morning before to attract the maximum number of wasps into the bait stations (Spurr 1991). In 1993/94, we only put out non-toxic bait the morning before poisoning (Table 1). We always put out toxic baits (about 40 g) in the afternoon because wasps remove more protein baits than in the morning (Barr *et al.*, 1996). Once there was an average of about 5 wasps feeding per non-toxic bait we poisoned both sites simultaneously (Spurr, 1991), and repeated the operation about 2 weeks later. We only put out baits on fine days because there is a dramatic drop in protein feeding by wasps after rain (Harris, Moller and Tilley, 1991). We removed any remaining baits the next morning.

In 1992/93, we attempted to increase the effectiveness of the poison operation by placing toxic baits along a buffer line 150 m from the edge of the poison grid (Table 1). These bait stations (Mt Misery n = 62, Howard n = 87) were 30 m apart. We placed toxic-baits on the buffer line about 2 weeks after the second poisoning of the main grid.

We changed from 1080 to sulfluramid (FinitronTM) when that became available in 1994/95 (Table 1) because sulfluramid is about 10 000 times less toxic to vertebrates than 1080 (Spurr, 1993). We poisoned wasps in the same two sites using 1% sulfluramid mixed with canned sardine in aspic jelly catfood (Spurr, 1993). We froze the toxic baits to keep them fresh, and then defrosted them before placing them in the bait stations in the afternoon. We did not use non-toxic baits because sulfluramid is much slower acting than 1080 and we reasoned that an individual wasp would be able to make many return trips to the bait before it was killed. Neither did we remove the toxic-baits from the bait stations, because sulfluramid is much less toxic to vertebrates than 1080 and the risk of accidentally killing vertebrates (including humans) was minimal. We laid toxic baits four times at approximately monthly intervals from early December 1994 to late February 1995.

In all years we measured wasp abundance using two techniques: Malaise traps (Townes, 1972) and nest searching in strip plots. We made collections from the Malaise traps (erected c. 20cm above the ground) about every 7 days from late October to late April/May each year. In order to avoid edge effects, the traps were positioned (randomly) at least 10m apart and no closer than 100m to a boundary. The directions the nets faced were evenly spaced around

Table 2: Comparison of wasp abundance (wasps trap⁻¹ year⁻¹) in poisoned and non-poisoned sites. We measured mean cumulative wasp abundance using Malaise traps set for a week each month. The average % reduction is the difference between poisoned and non-poisoned sites.

Treatment	Site	1991/92	1992/93	1993/94	1994/95
Poisoned	Mt Misery	800	1200	1300	500
	Howard	1200	1400	1600	900
Non-poisoned	Maori Stream	3300	2900	3500	2300
	Sabine	3000	3200	3600	2100
Average % reduction		68.9	56.4	59.4	66.7

the points of the compass. The number of traps set at each site increased as the study progressed: three in 1991 (first set in February), four in 1991/92, six in 1992/93 and 1993/94, and 12 in 1994/95 and 1995/96. There were not always the same number of traps in each site because traps were disrupted by events such as strong wind, heavy snowfall or tree fall. We computed the mean cumulative wasp numbers trap⁻¹ day⁻¹ by calculating the area under

the profile of the number of wasps caught per day for each trap separately. This method overcomes the problem of missing values.

We calculated the density of wasp nests from the number found in a strip plot 10 m x 500 m in each site. The same plot was searched each year at the peak of the wasp season in March/April (and sometimes in January before poisoning as well) by three people. For each nest found, we measured the

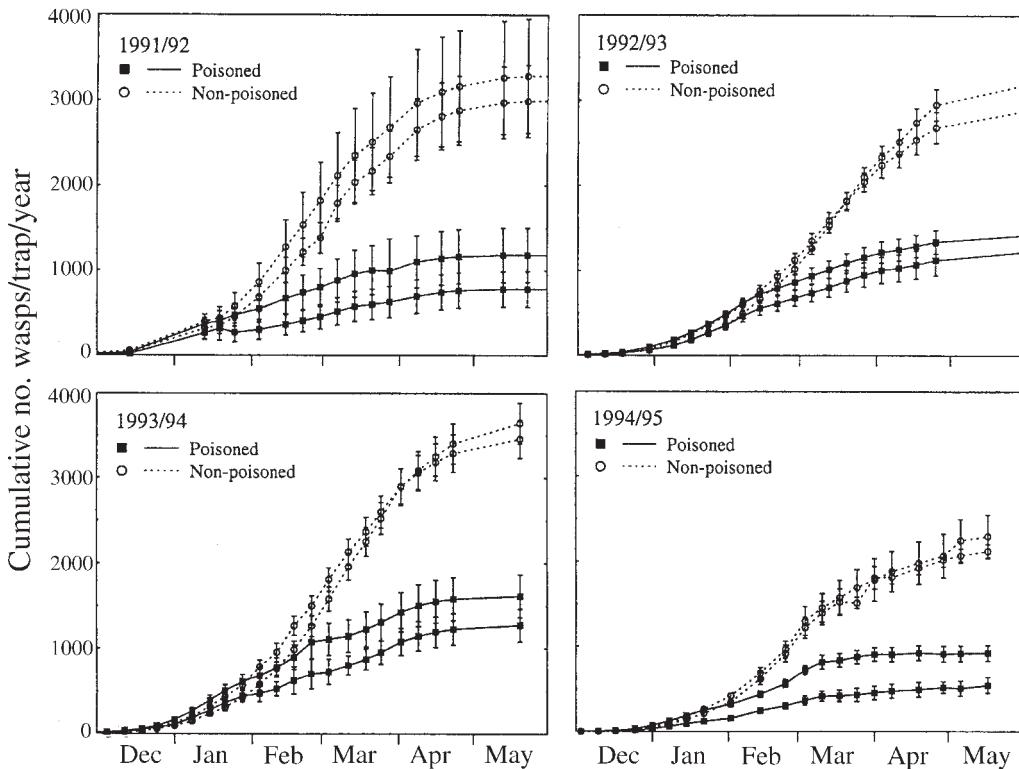


Figure 2: Cumulative number of worker wasps caught using Malaise traps. Vertical bars show ± one standard error.

Table 3. Comparison of nest density (nests ha^{-1}) in poisoned and non-poisoned sites. We measured nest density by locating all nests in a fixed strip plot (at least 500 m x 12 m) in March/April of each year. The average % reduction is the difference between poisoned and non-poisoned sites.

Treatment	Site	1991/92	1992/93	1993/94	1994/95
Poisoned	Mt Misery	0	6	5	0
	Howard	0	4	0	-
Non-poisoned	Maori Stream	16	22	34	8
	Sabine	22	22	32	16
Average % reduction		100	77.3	92.4	100

traffic rate (the number of wasps leaving or entering the nest $minute^{-1}$) and used this to calculate colony size (Malham *et al.*, 1991) and the density of wasps ha^{-1} . Traffic rate was also substituted into an equation to estimate the mass of wasps in a nest (Thomas *et al.*, 1990):

$$\text{wasp mass in nest (g)} = 109 + 7.5 \text{ traffic rate}$$

Biomass ($kg \ ha^{-1}$) was estimated using wasp weight per nest and multiplying by nest density.

Once a month in 1995 and once in March 1996, we collected a sample of up to 20 worker wasps from each Malaise trap in all sites. We dried the wasps to constant weight ($40^{\circ}C$ for 40 hours) and then weighed them. Results were analysed using residual maximum likelihood. The treatments (poisoned and non-poisoned) and date were considered to be crossed fixed effects, and the Malaise traps nested within site random and methodological effects. Lines were fitted using weighted least squares (using the inverse of the square of the standard error). We calculated the biomass of wasps caught in Malaise traps in each site using a derived relationship between number of wasps and weight of wasps. This curve was also fitted using weighted least squares.

Results

We caught large numbers of worker wasps in the non-poisoned sites - particularly in 1993/94 (3552 wasps $trap^{-1} \ year^{-1}$) (Table 2). Similar numbers of wasps were caught in all sites in any one season before the poison operations, but by late February/early March there were significantly fewer wasps caught in Malaise traps in the poisoned sites than in the non-poisoned sites (Fig. 2). The decline in standard errors reflect increased numbers of traps in later years. By the end of May, we had reduced the cumulative number of wasps caught in Malaise traps in the poisoned sites to between 55 and 70% of the numbers caught in the non-poisoned sites. The percentage reduction was similar in all years, even though the cumulative number of wasps varied (Table 2). This suggests that a buffer line or the type of poison or poisoning early in the season (Table 1) did not markedly alter the effectiveness of the poison operation.

Wasp abundance, as measured by nest density, in the non-poisoned sites followed the same trends as abundance measured using Malaise traps. For example, abundance was lowest in 1994/95 and

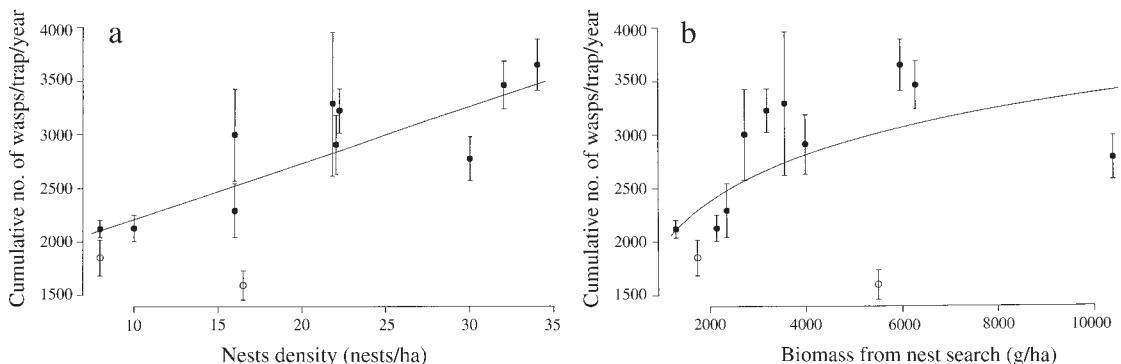


Figure 3: Relationships of nest density (a) and biomass (b) to wasp numbers (measured using Malaise traps). Biomass was estimated from nest density (estimated by nest searching in plots) and traffic rate. Three points at 22 nests ha^{-1} (a) were offset for clarity. The open circles are the two poison sites in 1996, a year after we last poisoned, and were not included when calculating the relationships. Vertical bars show \pm one standard error.

highest in 1993/94 (Table 2 and 3). There was a linear relationship between nest density (*d*) and the cumulative number of wasps caught in Malaise traps per year (*w*) (Fig. 3a., adjusted $r^2 = 0.86$; $p = 0.001$). Standard errors (*s.e.*) are given in parentheses underneath:

$$w = 1690 + 52.3d$$

$$s.e. \text{ (intercept)} = 133; s.e. \text{ (slope)} = 7.6$$

There was an approximately log relationship between biomass (*b*) estimated from the nest search and the cumulative number of wasps caught per year (*w*) (Fig. 3b., adjusted $r^2 = 0.63$; $p = 0.006$):

$$w = -2300 + 620 \times \ln(b)$$

$$s.e. \text{ (intercept)} = 1310; s.e. \text{ (slope)} = 168$$

The density of nests in the poisoned sites after poisoning ranged between 0 and 6 nests ha^{-1} and represented a reduction compared to non-poisoned sites of between 77% and 100% (Table 3).

In 1992/93 and 1993/94, we measured nest density both before and after the poison operations

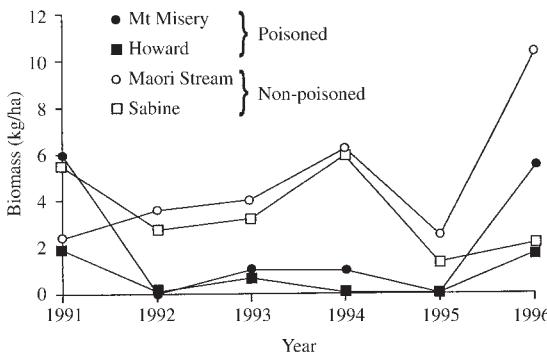


Figure 4: Reduction in resident wasp biomass ($kg\ ha^{-1}$) in two sites poisoned annually from 1992 to 1995 inclusive compared to two non-poisoned sites.

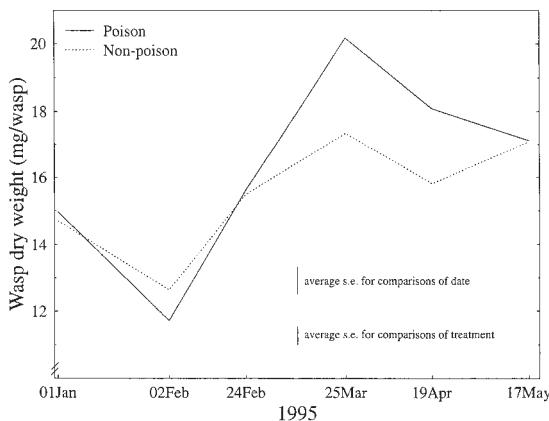


Figure 5: Change in the weight of worker wasps during the 1995 season in poison and non-poison sites.

and this indicated that between 82 to 100% of the nests in the poisoned sites were destroyed. This left an estimated resident wasp biomass (i.e. wasps from colonies within the 30-ha site) at the peak of the season of between 0 and $1.01\ kg\ ha^{-1}$, compared to densities of between 2.72 and $6.28\ kg\ ha^{-1}$ for the same years in the two non-poisoned sites (Fig. 4). The mean wasp biomass for all sites over 5 years (including the two poisoned sites the year before and the year after poisoning operations) was $3.60\ kg\ ha^{-1}$ ($s.d. = 2.76$).

In 1995, when wasp numbers peaked (March/April), individual wasps were heavier in the poisoned sites than in the non-poisoned sites (Fig. 5). The maximum differential was recorded at the end of March when wasps from the poison sites were approximately 16% heavier than those from the non-poisoned sites. However, earlier in the season (January/February) and at the end of the season (May) worker weights were similar in poisoned and non-poisoned sites (Fig. 5). In all sites, wasps were lighter in January/February than at the peak of the season. In 1996, when there was no poisoning, there was no difference in the weight of wasps in the poisoned and non-poisoned sites when wasp numbers peaked ($\bar{x} = 0.0153g\ s.e. = 0.0003$).

At the peak of the wasp season, wasps were heavier in sites where there were fewer wasps (i.e. number of wasps caught in Malaise traps per week), than in sites with more wasps ($p=0.013$; $r^2=0.67$; Fig. 6):

$$weight\ (mg) = 24.5 - 1.52 \times \ln(\text{number of wasps})$$

$$s.e. \text{ (intercept)} = 2.5; s.e. \text{ (slope)} = 0.04$$

Based on the number of wasps caught in Malaise traps, and the weight of wasps, the pattern of cumulative biomass (not shown) was similar to the pattern of cumulative worker numbers (Fig. 2).

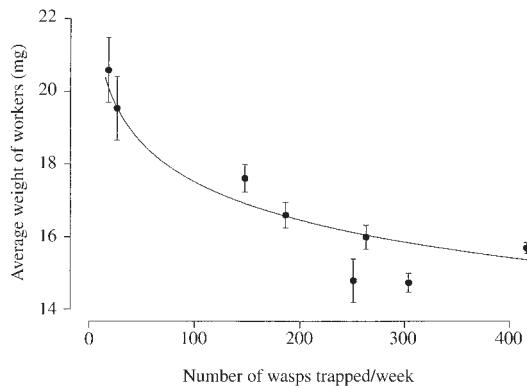


Figure 6: Relationship between worker weight and number of wasps caught in Malaise traps in one week at the peak of the wasp season (March). Vertical bars show \pm one standard error.

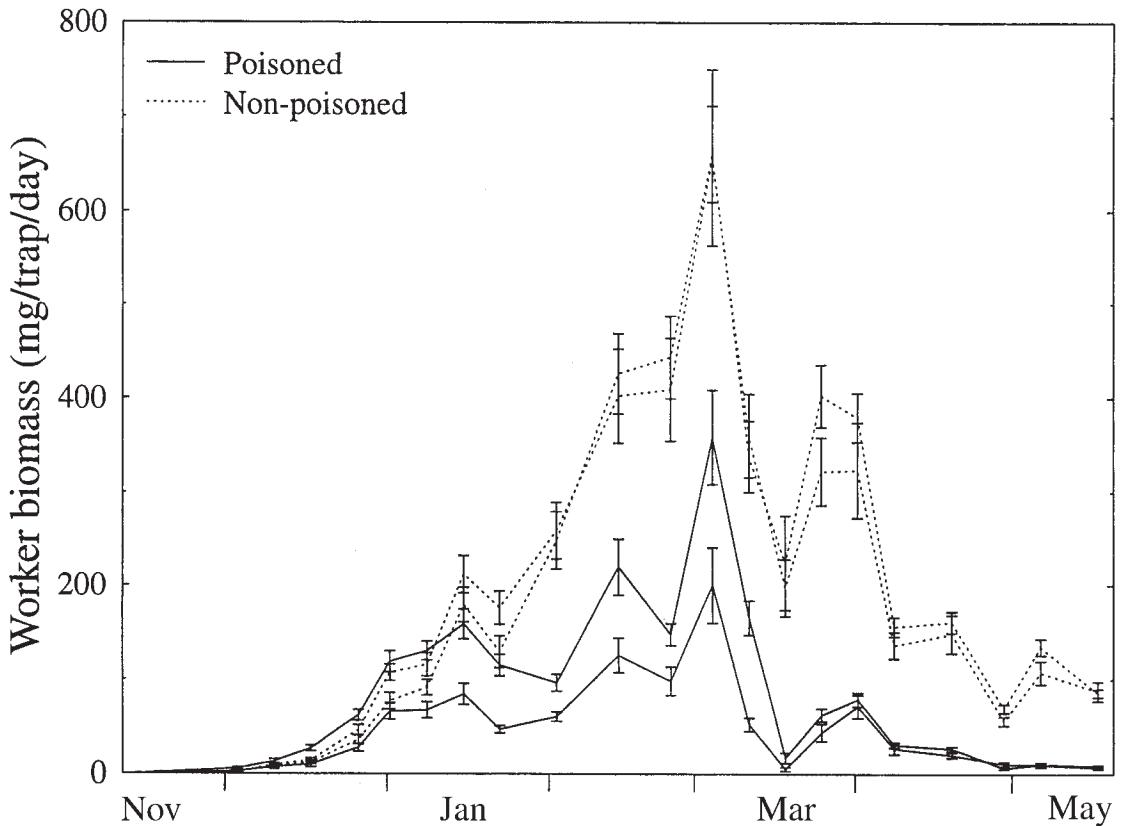


Figure 7: Instantaneous biomass of worker wasps in two poisoned and two non-poisoned sites in 1994/95. Biomass was calculated from number of wasps caught in Malaise traps and the weight of wasps. Vertical bars show \pm one standard error.

At the peak of wasp numbers in 1994/95, average instantaneous worker wasp biomass in poisoned sites was 58% lower than in non-poisoned sites (Fig. 7).

At all sites and in all years we caught too few queen wasps (max. 8 trap⁻¹ year⁻¹) or males (max. 3 trap⁻¹ year⁻¹) to distinguish any trends.

Discussion

The mean wasp biomass (3.60 kg ha⁻¹; *s.d.* = 2.76) for all sites over 5 years (including the two poisoned sites the year before and the year after poisoning operations) was similar to that measured at 19 northern South Island beech forest (with honeydew) sites (3.76 kg ha⁻¹; *s.d.* = 3.14) (Thomas *et al.*, 1990). Thus, the sites we worked in were fairly typical in terms of wasp density for beech forest with honeydew.

The biomass of introduced wasps in these forests has been estimated to be more than that of all the birds, rodents and stoats combined (Thomas *et al.*, 1990). Comparisons were made with birds because they potentially compete for food with wasps, and comparisons made with rodents and stoats because they are well recognised as predators of endemic biota. The biomass of wasps when compared to other predators in the forest indicates their potential to restructure both predator and prey communities (Thomas *et al.* 1990). Since the biomass of *Vespula* wasps in our study is similar to that in Thomas *et al.* (1990), it is likely that the ecological impact of wasps in our study sites is great.

We achieved a substantial reduction in numbers using both 1080 and sulfluramid poison. Given that both poisons reduced wasp numbers and the health risks associated with the high toxicity of 1080 to vertebrates (Spurr, 1993), we recommend that

sulfluramid is used for wasp control operations. Although we poisoned four times in a year with sulfluramid and only twice with 1080, we suggest the first two operations with sulfluramid were ineffective because it was too early in the season and no wasps were seen feeding on the toxic baits. In any case, we found sulfluramid much less time consuming to use because pre-baiting was unnecessary. Trials are required to determine the most effective method for applying the poison, particularly in terms of spacing of bait stations, timing of operation, and whether further reductions could be obtained by pre-baiting.

Poison-baiting effectively killed wasp colonies in two large (30 ha) sites. Between 82 and 100% of the resident wasp colonies were killed by the poison operations. We are confident that poisoning resulted in major changes in wasp abundance as resident wasp biomass remained high in both non-poisoned sites whilst it decreased in the two poisoned sites (Fig. 4).

Furthermore, there were reversals of rank order of resident biomass for the sites before, during and after poisoning (Fig. 4). Although poisoning was 82 to 100% effective against resident colonies, flying wasp densities were reduced by only 55 - 70%. This is not surprising given the size of the sites poisoned and the distance that foraging wasps can travel. Most wasp species have a similar foraging distance of only 50 - 400 m, but they will travel further when food is scarce (Edwards, 1980). Indeed, German and common wasps have been recorded flying 4 km to forage in bakeries and cafes (Coch, 1972). From the lake we could see wasps flying over the forest canopy to and from the poisoned sites.

Our 30-ha study sites were approximately 500 x 600 m wide and this was only increased to 650 x 750 m in buffer-zone treatments. Thus, there was substantial potential for workers from nests outside the poisoned sites to forage inside them, particularly when local intraspecific competition was reduced by the poisoning operation. We suggest the reduction in wasp numbers created a "vacuum" effect, increasing the abundance of food in poisoned sites and enticing wasps from further afield to forage there. Neither poisoning again about 2 weeks after the initial operation, nor buffer zones increased the effectiveness of the poison operation.

A disadvantage of the poison-baiting technique is that it is often not effective until there are numerous wasps feeding at a bait station (E. Spurr, pers. comm.); a rule of thumb is to wait until there are an average of about 5 wasps per non-toxic bait (Spurr, 1991). This level was not reached in our study sites until mid-January or later. If the aim of poisoning is to protect native invertebrate

communities, some of the damage will already have occurred by this stage. In 1995, we attempted to reduce wasp numbers earlier in the season by laying baits in November and December. As sulfluramid was slower acting than 1080, any wasp that located the sulfluramid baits could make more collecting trips than if feeding on 1080, and more toxin would enter the colony. However, we saw no wasps feeding on the baits placed out in November and December, and recorded no difference in the number of wasps caught in Malaise traps in poisoned and non-poisoned sites until early February when wasp numbers had built up. The early season poison operations with sulfluramid had undetectable effects on wasp numbers.

Wasps remaining in the poisoned sites were heavier than those in non-poisoned sites. This supports the idea that food resources are limiting – wasps are heavier when there are fewer wasps to compete for food. Variation in the quantity and quality of food is known to influence adult insect size and weight (Slansky and Rodriguez 1987; Gadagkar *et al.*, 1991). Harris (1995) demonstrated that experimental starvation of *V. vulgaris* larvae reduced survival rates of larvae and reduced the size of adults that did survive. There is considerable variation in the size of newly emerged queen wasps, but small queens are under-represented in the population that survive to establish their own colonies (Harris and Beggs 1995a). If reducing wasp numbers increases the availability of food, this may lead to better quality queens that therefore establish more nests. Thus, poisoning wasps in an area may result in an increase in wasp density the following year. Such an effect would be ameliorated by dispersal of queens and compounded if food availability increases in previously poisoned areas.

The cumulative biomass of wasps in a site was not greatly influenced by the change in wasp weight through the season. This was principally because the difference in weight occurred well after poisoning had affected wasp numbers, and then disappeared towards the end of the wasp season. However, a 16% increase in worker size in poisoned sites at the peak of the wasp season means that the instantaneous wasp biomass, and hence the impact of wasps, was not reduced by as much as the reduction in numbers would suggest. This may be of more relevance for species which are only exposed to wasp predation for a short time than for those with a longer exposure. For example, *Limonia (Discobola) tessellata* (Diptera: Tipulidae) is exposed as an adult to predation by wasps for only a few weeks in February and March (Toft and Beggs, 1995).

The costs of poisoning operations are quite substantial. In order to reduce wasp abundance in 60 ha by even the level we achieved, we required annually 12 person days plus NZ\$480 for the poison (at an estimated cost of NZ\$24 per ha per year (Harris and Beggs 1995b)), and an additional 70 person days plus \$500 materials to set up the bait stations (about NZ\$96 per ha (Harris and Beggs 1995b)). This was based on a labour charge of NZ\$10 per hour, and does not allow for indirect costs such as supervision and travel, nor for rugged terrain. Since wasps reinvaded the year following poisoning (Fig. 4), poisoning would have to be done annually. We estimate that a conservation manager would need about NZ\$200 per ha to reduce the impact wasps are having on the environment for 5 years.

Although we reduced cumulative wasp biomass (measured by Malaise traps) in the poisoned sites to 55 to 70% of the biomass at non-poisoned sites, we suggest this is not a large enough reduction to conserve some elements of the beech forest community. It is well below the 80-89.5% reduction required to protect populations of orb-web spiders (Toft and Rees, in press). Wasps reduce the standing crop of honeydew drops by over 92% for 5 months (Moller *et al.*, 1991), and native birds, such as kaka (*Nestor meridionalis*) have been shown to alter their behaviour when there is little honeydew available (Beggs and Wilson, 1991). It is likely that wasps have to be substantially reduced to protect the honeydew resource.

The estimated resident wasp biomass at the peak of the season in the poisoned sites (between 0 and 1.01 kg ha⁻¹) was quite variable between years, but the upper estimate suggests that the predation pressure of wasps was still quite substantial, at least in some years, and few conservation gains made. A larger scale operation may be of greater conservation value because reinvasion by wasps from outside the poisoned area would be reduced. Benefits need to be quantified to determine if the costs are warranted.

Despite these unknowns, the Department of Conservation is undertaking a Nature Recovery Project where they plan to poison wasps (and other introduced pests) in about 800 ha of beech forest. Not only do they hope to conserve native species already extant in the area, but eventually to reintroduce species such as kiwi (*Apteryx* spp.) and mohua (*Mohoua ochrocephala*) which were previously found in the area. The challenge is not only to remove sufficient numbers of predators and competitors from the beech forest community to make conservation gains, but to continue with the removals *ad infinitum*, or at least until other

measures (such as biological control) are found that permanently reduce the invasive threat these forests face. If achieved, we will have truly begun to turn the tide of homogenisation, impoverishment, and denaturing of biological communities.

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References

- Barlow, N.; Moller, H.; Beggs, J.R. 1996. A model for the effect of *Sphecophaga vesparum vesparum* as a biological control agent of the common wasps in New Zealand. *Journal of Applied Ecology* 33: 31-44.
- Barr, K.; Moller, H.; Christmas, E.; Lyver, P.; Beggs, J. 1996. Impacts of introduced common wasps (*Vespula vulgaris*) on experimentally placed mealworms in a New Zealand beech forest. *Oecologia* 105: 266-270.
- Beggs, J.R.; Harris, R.J.; Read, P.E.C. 1996. Invasion success of the wasp parasitoid *Sphecophaga vesparum vesparum* (Curtis) in New Zealand. *New Zealand Journal of Zoology* 23: 1-9.
- 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.
- Coch, F. 1972. Probleme der Wespenbekämpfung in Bäckereien und Konditoreien. *Bäcker Konditor* 26: 246-248.
- Edwards, R. 1980. *Social wasps, their biology and control*. East Grinstead, Rentokil Limited.
- Gadagkar, R.; Bhagavan, S.; Chandrashekar, K.; Vinutha, C. 1991. The role of larval nutrition in pre-imaginal biasing of caste in the primitively eusocial wasp *Ropalidia marginata* (Hymenoptera: Vespidae). *Ecological Entomology* 16: 435-440.

- Grant, W.D.; Beggs, J.R. 1989. Carbohydrate analysis of beech honeydew. *New Zealand Journal of Zoology* 16: 283-288.
- 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: 159-170.
- Harris, R.J. 1995. Effect of starvation of larvae of *Vespula vulgaris* (L.) (Hymenoptera: Vespidae) on subsequent survival and adult size. *New Zealand Journal of Zoology* 22: 33-38.
- Harris, R.J.; Beggs, J.R. 1995a. Variation in the quality of *Vespula vulgaris* (L.) queens (Hymenoptera: Vespidae) and its significance in wasp population dynamics. *New Zealand Journal of Zoology* 22: 131-142.
- Harris, R.J.; Beggs, J.R. 1995b (unpublished). Wasps in the Bay of Plenty. *Landcare Research Contract Report LC9495/160*.
- Harris, R.J.; Moller, H.; Tilley, J.A.V. 1991. Weather-related differences in attractiveness of protein foods to *Vespula* wasps. *New Zealand Journal of Ecology* 15: 167-170.
- 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.
- Howarth, F.G. 1985. Impacts of alien land arthropods and molluscs on native plants and animals in Hawaii. In: Stone, C.P.; Scott, J.M. (Editors) *Hawaii's terrestrial ecosystems preservation and management*, pp. 149-73. University of Hawaii Press, Honolulu.
- 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: 105-110.
- Moller, H. 1996. Lessons for invasion theory from social insects. *Biological Conservation* 78: 125-142.
- 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.; Tilley, J.A.V.; Thomas, B.W.; Gaze, P.D. 1991. Effect of introduced social wasps on the standing crop of honeydew in New Zealand beech forests. *New Zealand Journal of Zoology* 18: 171-179.
- Slansky, F. Jun.; Rodriquez, J.G. 1987. *Nutritional ecology of insects, mites, spiders and related invertebrates*. New York, John Wiley and Sons.
- 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.
- Spurr, E.B. 1993. The effectiveness of sulfluramid in sardine bait for control of wasps (Hymenoptera: Vespidae). *Proceedings 46th New Zealand Plant Protection Conference*. 307-312.
- Thomas, C.D.; Moller, H.; Plunkett, G.M.; Harris, R.J. 1990. The prevalence of introduced *Vespula vulgaris* wasps in a New Zealand beech forest community. *New Zealand Journal of Ecology* 13: 63-72.
- Toft, R.J.; Beggs, J.R. 1995. Seasonality of crane flies (Diptera: Tipulidae) in South Island beech forest in relation to the abundance of *Vespula* wasps (Hymenoptera: Vespidae). *New Zealand Entomologist* 18: 37-43.
- Toft, R.J.; Rees, J.S. (in press). Predation of orb-web spiders (Araneidae) by introduced common wasps (*Vespula vulgaris*) in a New Zealand beech forest. *Ecological Entomology* 23.
- Townes, H. 1972. A light-weight malaise trap. *Entomological News* 83: 239-247.
- Wojcik, D.P. 1994. Impact of the red imported fire ant on native ant species in Florida. In: Williams, D.F. (ed.) *Exotic ants biology, impact, and control of introduced species*, pp. 269-81. Westview Press, Boulder, CO.