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## COMPETITION BETWEEN HONEY BEES (*APIS MELLIFERA*) AND WASPS (*VESPULA* SPP.) IN HONEYDEW BEECH (*NOTHOFAGUS SOLANDRI* VAR. *SOLANDRI*) FOREST

**Summary:** Honeydew, the sugary exudate of the scale insect *Ultracoelostoma brittini*, is an important food source in black beech (*Nothofagus solandri* var. *solandri*) forests in the South Island of New Zealand. Two of the most prominent foragers of honeydew are honey bees (*Apis mellifera*) and wasps (*Vespula germanica* and *V. vulgaris*). Observations in the field and using a captive bee hive were used to investigate competition between bees and wasps feeding on honeydew. In laboratory trials, interference competition was often strong, and many cases of aggression were noted. In the forest, there was invariably enough room on the trees for bees and wasps to feed while rarely encountering one another. Over the whole year, environmental variables (especially low temperatures and rain), were found to constrain honey bee foraging to a greater degree than competition with wasps. Because the competition that did occur was primarily exploitation competition, reciprocal effects were likely to be felt. At Coopers Creek, bees may be reducing wasp densities, compared with the situation in Nelson - Marlborough where commercial hives are scarce. It may be possible to reduce wasp densities locally by increasing the number of bee hives in an area.

**Keywords:** Honeydew; black beech; *Nothofagus solandri* var. *solandri*; sooty beech scale; *Ultracoelostoma brittini*; honey bees; *Apis mellifera*; wasps; *Vespula vulgaris*; *Vespula germanica*; competition; control.

### Introduction

The sooty beech scale insect, *Ultracoelostoma brittini* (Morales) (Hemiptera: Margarodidae), infests the trunk and branches of many New Zealand beech trees (*Nothofagus*<sup>1</sup> spp.). First instar *Ultracoelostoma* (crawlers) settle in *Nothofagus* bark, insert their stylets and feed on the sap. The residue is excreted out of a characteristic white waxy anal filament as honeydew (Morales, Hill and Walker, 1988).

Honeydew provides a major food source for many species living in beech forest. It nourishes bacteria and encourages microbial activity in the soil (Moller *et al.*, 1987). The black sooty mould (probably *Capnocybe novae-zealandiae* (Hughes) (Morales *et al.*, 1988) that cloaks many infested beech trees is maintained by the honeydew. The mould provides food for many arthropods (Morales *et al.*, 1988) and they, along with the mould and the honeydew itself are eaten by other forest insects and vertebrates (Moller *et al.*, 1987). Two of the most prominent and widespread consumers of honeydew are honey bees (*Apis mellifera* (L.)) and German

(*Vespula germanica* (F.)) and common (*V. vulgaris* (L.)) wasps.

*Ultracoelostoma* is native and has presumably been in New Zealand beech forest for millennia. Honey bees were only established in the early 1900s (Cook, 1978) and German wasps were introduced around 1945 (Donovan, 1984). Common wasps were first recorded around 1978 and by 1989 were widespread in honeydew beech forest in Canterbury and Nelson. Common wasps are now probably the more prevalent wasp in honeydew beech forest (Sandlant and Moller, 1989).

Moller and Tilley (1989) attempted to quantify the effects of wasps in mixed beech forest at Trass, near Nelson during 1986 and 1987. The number of honey bees feeding on beech trees at Trass declined as the number of wasps increased (Moller and Tilley, 1989). Honey bee foraging activity is affected by temperature, light, humidity, rain and the nature of the available food (Nelson and Jay, 1968; Gary, Witherel and Marston, 1972; Burrill and Dietz, 1981; Roubik and Buchmann, 1984). However, Moller and Tilley (1989) did not find that the decline in honey bee numbers was correlated with any of these factors. Competition with wasps was concluded to be the most likely reason for the drop in honey bee numbers.

<sup>1</sup> Nomenclature follows Allan (1961) and Edgar (1971).

The primary aims of our work were to investigate competition between wasps and honey bees feeding on beech honeydew, and to determine if similar patterns in both honey bee and wasp numbers and honeydew resource levels occur in honeydew beech forests other than at Trass. Our main focus was to establish the extent to which competition between bees and wasps affected foraging by bees, and compare this with the effects of other environmental variables.

Connell (1980) set out a series of experimental procedures that he considered necessary and sufficient to show if niche divergence due to competition had occurred. Individuals from a population allopatric with a potential competitor are moved into an area where populations of the same species live sympatrically and *vice versa*. Any changes in niche width are then measured. A protocol similar to that proposed by Connell would be useful in determining the influence of competition. However, experimental removal of wasps has not been successful in honeydew beech forest in New Zealand (Moller *et al.*, 1988; Thomas *et al.*, 1989). So we used statistical analysis to determine the important variables affecting honey bee foraging (c.f. Dhondt and Eyckerman, 1980; Minot, 1981). We supplemented our field work with observations in a laboratory situation.

To show how competition influenced honey bee foraging patterns, we determined the effects that wasps had on the honeydew available to bees, and how the behaviour of bees appeared to be altered by the presence of wasps. The relationship between other environmental variables and honey bee foraging was analyzed to determine the relative importance of these factors.

## Methods

### Study site

The study area was at the base of Mt. Oxford in the foothills of Canterbury. The work was carried out in a patch of forest (map reference NZMS 260 L34 364713) adjacent to Coopers Creek. The dominant vegetation was *Nothofagus solandri* var. *solandri* (black beech), up to 20 m tall, with *Leptospermum scoparium* (manuka) at the forest margins, and a sparse understorey of beech seedlings, *Cyathodes juniperina* and *Coprosma rhamnoides*. Occasional *Pseudopanax arboreus*, *Carpodetus serratus* and *Coprosma lucida* were also found (see Kelly *et al.*, 1992).

Four commercial apiaries are maintained in the nearby farmland. The site was chosen so that no

sample was taken more than 1 km from a honey bee hive. Wasp nests were present throughout the study area during the wasp season.

Eight trees were randomly selected within the forest stand at the site. This selection gave a range of trees in different situations (Table 1). Within this overall area there were two sub-sites. The first was a west facing river terrace of approximately 15° slope containing trees 1-4. The second sub-site was approximately 500 m upstream from the first. It was on a north-east facing slope of up to 45° and contained trees 5-8.

Aspect and slope of the hill where each tree grew and tree height were determined with an Abney level. Tree diameter was recorded at breast height (1.4 m), and the relative shading at each tree was estimated from the average light intensity in  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  at each tree over the year and an estimate of the surrounding vegetation cover.

### Quadrats

Quadrats 0.1 m by 1 m were marked on each tree (square quadrats would not fit on the visible surface of the trunk). Quadrats were marked with nails at each corner only, after preliminary observations showed that bees turned away at permanent string lines. Nails had no noticeable effect on the progression of insects. We placed the quadrats on the north face of each tree. Crozier (1978) found significantly more honeydew droplets on the north face of a black beech tree than on the south. Although this finding was not corroborated by Kelly (1990) or Kelly *et al.* (1992), it provided a standard, i.e., northerly, aspect for quadrats.

Table 1: Characteristics of each black beech tree studied at Coopers Creek in 1992. Site 1 is downstream of site 2. DBH is diameter at breast height (1.4 m). Aspect and slope are given for each tree. Shade ranks (8 the darkest and 1 the lightest) are based on average light intensity in  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  at each tree over the year, and on an estimate of the surrounding vegetation cover.

Site	Tree	Height (m)	OBH (m)	Aspect (°magnetic)	Slope (°)	Shade (rank)
1	1	9.24	0.315	320	04	1
1	2	8.99	0.175	305	33	2
1	3	5.20	0.140	260	22	3
1	4	9.21	0.175	245	17	4
2	5	13.6	0.215	045	31	5
2	6	21.87	0.318	114	10	6
2	7	18.2	0.331	080	27	7
2	8	9.35	0.159	080	25	8

### Timing of samples

Samples were taken at Coopers Creek throughout 1992. The dates of sampling and the number of samples each period are presented in Appendix 1. Two 15-minute samples were taken at each tree on each sampling day. The order in which each tree was sampled throughout the day was determined randomly. Sampling began approximately 1 hour after sunrise each morning and continued until late afternoon. Microclimate readings were taken every 30 seconds and the mean calculated every 15 minutes.

### Variables measured

#### *Microclimate*

At each tree, microclimate measurements were taken with a Campbell Scientific CR21X micrologger. In every sample, a vertically oriented LI-COR LI200s silicon pyranometer was placed on the ground at the base of the tree to record light intensity in  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . A CSI 207 temperature/relative humidity probe was used to record temperature ( $^{\circ}\text{C}$ ) and percentage relative humidity. The presence or absence of rain in each 15 minute sample was recorded.

#### *Insects*

During each sample, the time of arrival and departure of every honey bee and wasp to and from the quadrat was recorded. We were thus able to calculate the total number of bees and wasps visiting and the average length of their stay. Both wasp species may have been present, but rapid enough identification of the species present in a given sample was not possible. We therefore followed the methodology of Boyd (1987) and identified them as wasps, regardless of species.

#### *Honeydew*

At the end of each sample, the number of drops of honeydew in the quadrat was counted. This method discounted any drops removed during the sample, but was necessary to avoid disturbing insects already feeding at the start of sampling. Before each morning's sampling and again at the end of the day, a known number of honeydew drops was collected from each tree using micro-haematocrit capillary tubes. These have a uniform bore, with 1 mm of tube equal to 1  $\mu\text{l}$  of solution. Usually, two samples of 40 drops were collected from each tree, but on some occasions not enough drops were found and smaller samples were taken. The volume of honeydew in each sample was measured and the average size of the drops on each tree calculated.

### Laboratory data

#### *Quantitative data*

Experiments were carried out using a honey bee hive maintained on the University of Canterbury campus, in March, April and May 1992. There were large numbers of wasps present in the area, from wild nests situated around the campus. A feeding station (a plastic bowl) was set up on the ground 20 m from the bee hive. A solution of sucrose, glucose and fructose (Grant and Beggs (1989) found that these were the primary constituents of honeydew) was made up to a concentration of approximately 40 % in tap water. Paper towels were put in the bowl and soaked with the solution so that the insects could feed without drowning. A paper towel soaked in the sugar solution was placed on the "doorstep" of the hive to encourage bees to visit the feeding station.

Once the feeding bowl had been found, large numbers of bees and wasps were soon recorded feeding and a smaller arena was needed for quantitative studies. At the beginning of a sampling session, the bowl (with bees and wasps feeding) was removed from the study area and replaced with a Petri dish containing either 1 cm<sup>3</sup> or 5 cm<sup>3</sup> of sugar solution. Two small pieces of wood were placed in the dish so that bees could feed at the dish and keep their feet dry. The number of bees and wasps arriving at the dish and the number of aggressive interactions that resulted in an insect being deterred from feeding were recorded. Five-minute samples were taken until no sugar syrup remained in the Petri dish (approximately 1 hour). The winner of a fight was deemed to be the insect that continued feeding or the insect that was shifted the least distance from the dish by the altercation.

#### *Qualitative data*

As well as the Petri dish samples, observations of larger numbers of honey bees and wasps feeding at the bowl were made throughout 1992 and in January and February 1993. Observation of the behaviour of bees in the presence of wasps, and of the relationship between feeding patterns and the amount of food available, allowed analysis of elements of behaviour that was not possible with the smaller Petri dish samples. It also allowed comparison of bee and wasp behaviours when food was plentiful, in contrast to the Petri dish, where it was scarcer.

### Statistical analysis

The SAS, SHAZAM and STATISTIX statistical packages were used to analyze the data from each monthly sampling period and from the laboratory. Means are quoted  $\pm$  95% C.I.

## Results

### Coopers Creek

Wasps were not observed at Coopers Creek between June and September inclusive, and were only present in the May and October halves of these combined sampling periods. Wasps were only abundant in February and March (Table 2). Honey bees were noted in all sampling periods. The mean numbers of bees recorded in each sample were relatively constant through the warmer months (November to March), but declined in winter samples (April to October) (Table 2). When wasp numbers were at their peak, the number of bees was not significantly lower than in any of the summer sampling periods ( $F_{7,450} = 17.31, P > 0.05$ ). On average over the year, 99.0 wasps  $m^{-2} hr^{-1}$  and 96.1 bees  $m^{-2} hr^{-1}$  arrived at our trees. The mean length of stay in a quadrat by wasps was 10.4 seconds, and by bees, 45.5 seconds. Because of the differing

lengths of time spent by wasps and bees in the quadrats, on average over the year wasps were on trees for 17.2 minutes  $m^{-2} hr^{-1}$  and bees for 72.9 minutes  $m^{-2} hr^{-1}$ .

The amount of food available was a significant predictor of how many bees would be feeding. The trees (No. 5-8) at the upstream site all had significantly fewer bees feeding on them than the downstream (No. 1-4) trees ( $t_{[259,8]} = 10.51, P = 0.0001$ ; variances unequal:  $F_{[217,239]} = 25.22, P = 0.0001$ ) and had fewer drops of honeydew ( $t_{[357,2]} = 9.48, P = 0.0001$ ; variances unequal:  $F_{[217,239]} = 4.06, P = 0.0001$ ).

The amount of honeydew on the trees varied throughout the year (Table 3). During February and March the mean number of honeydew drops available ( $657 \pm 123 m^{-2}$ ) was significantly less than that available over the rest of the year ( $1128 \pm 109 m^{-2}$ ) ( $U$  test,  $Z_{[458]} \approx 4.87, P < 0.05$ ). The drops were also smaller (Table 3).

Table 2: The number of wasps and bees arriving in a  $0.1 m^2$  quadrat on a black beech tree in a 15-minute sample at Coopers Creek over 1992. All values are means of 42-64 samples  $\pm 95\%$  C.I. Means are not significantly different ( $\alpha = 0.05$ ) within homogenous groups.

Sampling period	Wasp number	Bee number	Wasp		Bee	
	X $\pm$ 95% C.I.	X $\pm$ 95% C.I.	homogenous groups		homogenous groups	
January	0.64 $\pm$ 0.24	3.15 $\pm$ 0.96	C		B	C
February	15.7 $\pm$ 2.91	5.04 $\pm$ 2.42	A		A	B
March	10.2 $\pm$ 3.56	4.61 $\pm$ 1.90	A		A	B
April	1.83 $\pm$ 0.74	1.41 $\pm$ 0.87	B			C D
May-June	0.13 $\pm$ 0.12	0.28 $\pm$ 0.26			D	D
Sep-Oct	0.04 $\pm$ 0.05	0.91 $\pm$ 0.68			D	D
November	0.05 $\pm$ 0.07	4.36 $\pm$ 0.26			D	A B
December	1.11 $\pm$ 0.69	6.80 $\pm$ 2.16	B	C	A	

Table 3: Honeydew drop number and volume at Coopers Creek throughout 1992. All values except maxima and minima are means of 42-64 samples  $\pm 95\%$  C.I., for each month over eight trees. Range is the minimum and maximum value for any tree sampled in that month.

Sampling period	Drops $m^{-2}$	Drops $m^{-2}$	Drop size ( $\mu l$ )	Productivity ( $\mu l m^{-2}$ )
	Mean	Range		
January	891 $\pm$ 14	50 - 2040	0.85 $\pm$ 0.30	757.3
February	353 $\pm$ 87	0 - 1360	0.04 $\pm$ 0.01	14.1
March	884 $\pm$ 19	90 - 4250	0.40 $\pm$ 0.05	353.6
April	1323 $\pm$ 29	50 - 5200	0.45 $\pm$ 0.07	595.4
May-June	1190 $\pm$ 26	30 - 3940	0.58 $\pm$ 0.10	690.2
Sep-Oct	1035 $\pm$ 20	10 - 3650	0.45 $\pm$ 0.07	465.8
November	2127 $\pm$ 46	70 - 5520	0.86 $\pm$ 0.08	1829
December	449 $\pm$ 85	10 - 1340	0.67 $\pm$ 0.08	300.8

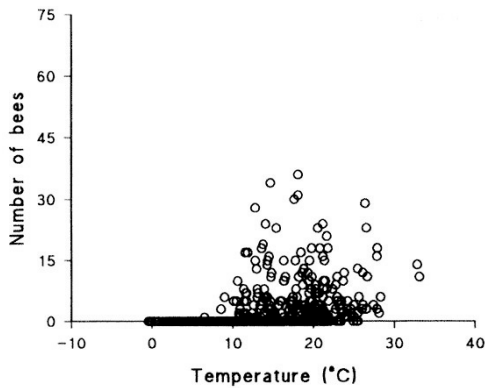


Figure 1. Number of honey bees feeding at different temperatures in  $0.1 \text{ m}^2$  quadrats on black beech trees at Coopers Creek throughout 1992.

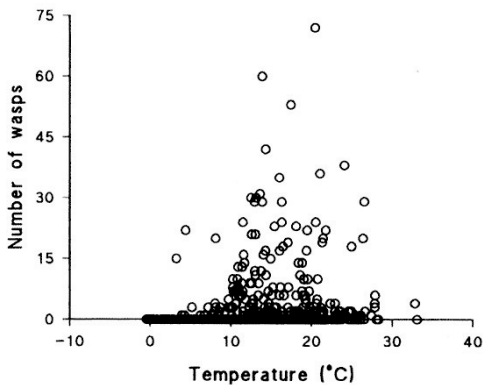


Figure 2. Number of wasps feeding at different temperatures in  $0.1 \text{ m}^2$  quadrats on black beech trees at Coopers Creek throughout 1992.

Both bees and wasps preferred to forage in light, sunny areas. Over the year, 87% of the bees recorded were on the four most well illuminated trees (trees 1, 2, 3 and 4, Table 1); an identical result was found in February and March. Similarly, 68 % of wasps were found on trees 1-4 over the year and 71 % in February and March.

Honey bees were only recorded flying when the temperature was over  $6.4 \text{ }^\circ\text{C}$  and 99% of bees were recorded in temperatures over  $10 \text{ }^\circ\text{C}$  (Fig 1).

The minimum temperature at which wasps were recorded was  $3.3 \text{ }^\circ\text{C}$  and 94% of wasps were recorded at temperatures over  $10 \text{ }^\circ\text{C}$  (Fig. 2). Seventy-two percent of samples were taken when the temperature was above  $10 \text{ }^\circ\text{C}$ .

Rain was a significant predictor of the number of bees feeding (regression,  $t = -2.255$ ,  $P < 0.05$ ). Over the whole year, 46 of the 450 samples were taken when it was raining. On only one occasion when rain was recorded in a sample, were honey bees also found feeding. Wasps were recorded in 8 wet samples, all during March (total number of wasps involved = 62, mean per sample =  $7.75 \pm 1.65$ ).

Aggressive interactions between honey bees and wasps feeding on honeydew in the field were witnessed on a number of occasions. Often, bees were eating honeydew when a wasp attempted to land in the same position. In most instances, both insects "bounced" off and then flew around in front of the tree for approximately 5-10 seconds. Both insects would then return to the tree, or another adjacent one and resume feeding.

More prolonged fights were occasionally seen, and in one instance a fight to the death between a bee and a wasp was noted. The wasp was the eventual victor, defeating the bee by biting its wings off. The wingless bee was left on the forest floor and was not harvested by the wasp for food.

### Laboratory

Honey bees and wasps fed side by side in the Petri dish, without any obvious aggression for on average 3.08 minutes. While there was space for honey bees to land, both species would feed without conflict. When food began to run out, aggression between bees and wasps began to occur. As fighting between the two species increased, the number of bees that actually reached the Petri dish declined and the number of fights also declined. Figure 3 shows an example from one sample period.

Fights were almost invariably initiated by wasps. A bee attempting to land or already feeding, would encounter a wasp, either in the air or the feeding area. The wasp would physically attack the bee, often quite violently. The two would couple, and spin around violently with much buzzing. Eventually one combatant was deterred from the feeding arena. This was usually the bee, but bees won 18 of 360 fights. In some cases the loser would return and attempt to feed again. Some intraspecific aggression was observed, but no data were collected.

Wasps did not appear to seek out honey bees to attack. If a wasp and a bee came into direct contact the bee was driven away, but a wasp could walk or fly

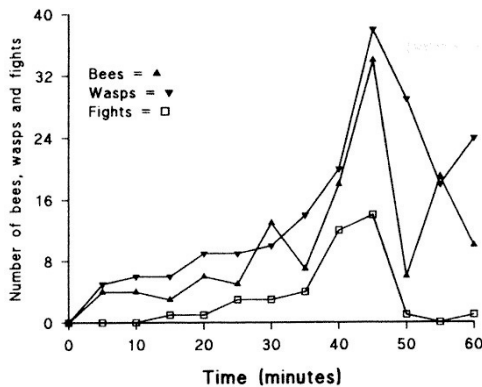


Figure 3. The number of bees and wasps feeding at a Petri dish containing 5 cm<sup>3</sup> of a sucrose, fructose and glucose solution during 12 five-minute samples on 31 March 1992. Fights are the number of acts of aggression between individuals of the two species in each sample. All fights in this experiment were won by wasps.

within 1 cm of a bee, yet not come into direct contact and no obvious aggression would occur.

When large numbers of wasps were feeding at the bowl, a bee would often circle around, and land only if a suitable area clear of wasps was found. If she subsequently met a wasp and was ejected from the bowl she would attempt to return to the bowl and resume feeding. This finding was also noted in the field. If the number of wasps present in the bowl was so high that acceptable landing spaces could not be found, bees would cease feeding there. As the density of insects increased, so did the number of encounters between individual insects and the number of acts of aggression between the two species.

The occurrences of interspecific aggression between bees and wasps were not directly related to the amount of food available at the Petri dish. There was no significant difference between the number of fights when 10 cm<sup>3</sup> or 5 cm<sup>3</sup> of food was provided to the insects feeding in the Petri dish ( $F_{[1,11]} = 3.15, P = 0.104$ ; variances equal:  $X^2_{[1]} = 0.11, P = 0.740$ ). The number of wasps in each sample did not differ significantly between samples with 10 cm<sup>3</sup> and those with 5 cm<sup>3</sup> ( $t_{[124]} = -0.82, P = 0.413$ ; variances equal:  $F_{[75,491]} = 1.20, P = 0.249$ ). There were however fewer bees when 5 cm<sup>3</sup> of syrup was provided than 10 cm<sup>3</sup> ( $t_{[124]} = 2.43, P = 0.0165$ ; variances equal:  $F_{[75,49]} = 1.39, P = 0.107$ ).

## Discussion

### Insect densities

Over February, March and April at Coopers Creek, we recorded a mean of 345.2 wasps m<sup>-2</sup> hr<sup>-1</sup> and 142.8 bees m<sup>-2</sup> hr<sup>-1</sup>. At Trass over February, March and April in 1986 to 1991 mean densities of 20.5 wasps m<sup>-2</sup> and 0.44 bees m<sup>-2</sup> were recorded (Boyd, 1987; Moller and Tilley, 1989; Moller *et al.*, 1988; Harris, 1992). To compare these values with ours, we assume that each sample at Trass took 30 seconds. The approximate equivalents from our data are 2.88 wasps m<sup>-2</sup> and 1.19 bees m<sup>-2</sup> at Coopers Creek. Hence, there were more bees and fewer wasps at Coopers Creek than at Trass.

In all months apart from February and March, wasp densities at Coopers Creek were such that they were not likely to have an impact on the number of bees feeding or their foraging patterns. During winter there was no potential for significant competition between bees and wasps.

### Effects on honey bees of competition with wasps

Interference competition has been viewed as a constant force operating regardless of the scarcity of resources (e.g., MacIsaac and Gilbert, 1991). This did not appear to be the case in competition between bees and wasps at Coopers Creek, where direct encounters between them occurred infrequently. As was shown in our laboratory trials, aggression only occurred when limited resources forced encounters between individuals. It is possible that densities as high as in the laboratory trials are reached at times in honeydew beech forest. Moller *et al.* (1987) reported point samples of 360 wasps m<sup>-2</sup> of tree trunk, but densities this high are likely to be rare, and not widespread.

Exploitation competition is more difficult to measure than interference, but its presence can be safely postulated from the available data. In February, when the greatest number of wasps was present on the trees, there was significantly less food available to bees than in other months.

Our findings of high wasp numbers and a reduced honeydew supply in February mirror those of other workers. Gaze and Clout (1983) investigated honeydew standing crop between August 1979 and July 1980, and found that the number of drops was lowest over February and March. Wasps were not numerous in beech forest at that time (Donovan, 1984), and they suggested that the stage of the scale insect's life cycle was responsible. Boyd (1987), Moller and Tilley (1989) and Harris (1992) all found a drop in honeydew density in February and attributed this to the

presence of wasps. Beggs and Wilson (1991) and Moller *et al.* (1991) showed that there was significantly more honeydew inside wasp enclosures than outside. Although there may have been a natural decline in the amount of honeydew over February, it seems likely that a significant proportion of the standing crop at Coopers Creek at this time was consumed by wasps.

Our results show that the amount of food available at a site is a significant determinant of the number of bees that will be foraging there. As there was less food available on trees in February, this would have had an effect on honey bee foraging. Hence, wasps probably cause some resource competition at Coopers Creek in February.

Wasp numbers did not appear to be influenced by the amount of food. Regardless of the amount of carbohydrate available, wasps continued to feed. However, Harris (1992) found a positive relationship between the number of drops harvested per minute and drop availability. When drop numbers were low, foragers spent more time crawling on trees than harvesting honeydew while flying. It is possible that insects were spending more time on each tree when resource levels were low, but were not spending any longer in our quadrats.

#### **Effects of environmental variables**

Although the amount of food available was a key determinant of where honey bees fed, it was not the only factor. Light intensity also influences honey bee foraging patterns (Burrill and Dietz, 1981). This was demonstrated by the differences in honey bee numbers in our samples on trees with differing levels of shade. As competition becomes more intense, honey bees may change their feeding site (Gary *et al.*, 1972). Competition by wasps did not, however, force more bees onto our shaded trees in February and March. Honey bees were not physiologically constrained from feeding on the shaded trees because 13% of the bees were still recorded on them.

Regardless of the number of wasps in the area, few honey bees flew at low temperatures (Fig. 1). Our sampling regime was biased away from the colder months (Appendix 1), but in the May - June sampling period, approximately 70% of the samples were taken at temperatures below 6.5°C. If this was typical of winter conditions over the whole year it was too cold for bees to fly 40% of the time, regardless of other variables.

Very few bees were recorded on honeydew trees if rain was heavier than a light drizzle, and rain restricted foraging for about 10% of the time.

As 75% of the wet samples also occurred when the temperature was below 10°C, the effects were not additive. In total, rain and low temperatures prevented foraging for about 43% of daylight hours. In contrast, wasps did forage in the rain (see also Kalmus, 1954; Spradbery, 1973) and in low temperatures. In these periods, direct competition would not occur.

#### **The effects of wasps compared to the effects of environmental variables**

Having shown that competition can occur between individuals of two species, one must then determine if this is important to the organisms, compared to the influences of other factors of the environment (Welden and Slauson, 1986). The number of bees in each sample did not change significantly throughout the spring, summer and autumn samples but significantly fewer bees were recorded in winter (Appendix 1; Table 2).

For ten months of the year, wasps were not present on honeydew trees in significant numbers. During this time, neither exploitation nor interference competition could occur and honey bee foraging was mainly restricted by temperature, rain and the amount of honeydew produced. Even when wasp numbers were at their highest, there were always other places to feed and some food available, whereas the influences of low temperature, rain and low light conditions were present all year round.

Because direct contact between individuals is not necessary for resource competition, there was still potential for this to occur in this study. There was an 80% reduction in the amount of honeydew available on trees in February. Even though the mean number of bees per sample was unchanged, the amount of food that each could collect per unit time was reduced. Because of this, bees would not be able to make as much honey, and the hive may have been affected. Clapperton *et al.* (1989) and Moller and Tilley (1989) suggest that the loss of production caused by wasp competition is a potentially serious problem for the honeydew honey industry, even though it seemed to be limited to a relatively short part of the year in this study.

Although honeydew was in short supply during February, for most of the year it was not. Honeydew not eaten by wasps was not necessarily extra food collected by honey bees. For much of the year, honeydew probably fell to the ground or was used by the sooty mould.

In February, when low food levels may reduce the fitness of honey bee colonies, there will also be an impact on the wasp population. Wasp foraging patterns are also affected by the amount of food available (Harris, 1992; Thomson, 1989). In

February, honeydew eaten by a bee, was unavailable to wasps, so removal of bees could lead to an increase in the number of wasps. Honey bees were present at Coopers Creek all year round, while wasps were only recorded from December to May. Therefore, each honey bee unit required food for twice as long as a wasp unit: 1 wasp  $\text{min}^{-1}$  bee. The food consumed during 17.2 wasp  $\text{min}^{-1} \text{m}^{-2} \text{hr}^{-1}$  might support a feeding rate of 8.6 bee  $\text{min}^{-1} \text{m}^{-2} \text{hr}^{-1}$ . If wasps were not foraging, a yearly mean of 81.5 bee  $\text{min}^{-1} \text{m}^{-2} \text{hr}^{-1}$  could be supported at Coopers Creek, an increase of 12%. In contrast, if all bees were removed from the area the population of wasps that could be supported could increase nine-fold, to 163 wasp  $\text{min}^{-1} \text{m}^{-2} \text{hr}^{-1}$ .

The bees at Coopers Creek were all introduced by humans, whereas at Trass they were not. It is possible that if bees were introduced to wasp-infested sites, wasp numbers could be restricted by exploitation competition (although at high densities interference competition may increase). These possibilities could be tested by manipulating bee densities, e.g., by adding hives to an area near Nelson and removing them from a small area in Canterbury. Because bees feed all year, this would have an effect on honeydew stocks and so affect birds, insects and fungi that feed on honeydew. However a reduction in wasps may benefit insects that are protein sources for wasps. While bee-mediated wasp reduction by subsidised hives may not affect the ecology of large forest tracts, it may be an effective palliative near picnic areas and other sites of interest to humans.

## Acknowledgements

We thank the Burrells and the St. Joseph's Scout Troop for access to Payton Lodge, Bruce Lingard for care and feeding of the captive bee hive, and Graeme Young for care and feeding of the data-logger. This paper benefitted greatly from the helpful and thorough comments of K. Clapperton, R. Fordham and K. Dickinson, and from detailed and patient editing by Dr J. Dowding.

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Appendix 1: Dates in 1992 during which samples at Coopers Creek were recorded. The number of samples and the mean temperature, over all samples at all eight sample trees ( $\pm 95\%$  C.I.) for each sample period is also given. Within homogenous groups, mean temperatures are not significantly different ( $\alpha = 0.05$ ).

Sampling period	Dates sampled	n	Mean temp. ( $^{\circ}\text{C} \pm 95\%$ C.I.)	Homogenous groups
January	13-17 January	64	20.4 $\pm$ 1.1	A
February	12-13 February	48	17.4 $\pm$ 1.1	B
March	10-11, 24-25 March	64	14.9 $\pm$ 1.5	C
April	7-8 and 28 April, 2 May	64	13.1 $\pm$ 1.3	C
May-June	26-27 May, 23-24 June	56	5.0 $\pm$ 0.9	E
Sep-Oct	15-16 September, 23, 28 October	56	9.5 $\pm$ 0.9	D
November	11-12, 29 November	42	19.7 $\pm$ 0.7	A
December	10-11 and 21-22 December	56	16.6 $\pm$ 1.1	B