

The impact of honeydew on the behaviour of sugar-feeding animals in regenerating forest, Auckland, New Zealand

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Abstract: New Zealand kanuka (Myrtaceae: *Kunzea ericoides*) is often heavily infested by the endemic honeydew-producing scale insect *Coelostomidia wairoensis* (Hemiptera: Coelostomidiidae). In summer, the honeydew standing crop can exceed the kanuka nectar standing crop and hence honeydew has the potential to disrupt the sugar economy operating in kanuka stands by providing an alternative food resource for nectar-feeding animals. In this study, animal visitation rates and feeding rates were recorded on infested and un-infested kanuka over the kanuka flowering period. It was predicted that honeydew would attract sugar consumers and that scale insect infestation would alter visitation patterns to kanuka flowers. These predictions were not supported by the study data. Despite the presence of abundant honeydew, fewer animals were observed feeding on honeydew than on nectar and social wasps were the only group that showed a strong response to the honeydew resource. Floral visitation patterns did not differ between infested and un-infested trees. Overall these results suggest that the presence of honeydew does not affect the kanuka sugar economy directly and it appears that few animal species utilise honeydew. Possible explanations for this low rate of utilisation are examined.

Key words: *Coelostomidia wairoensis*, kanuka, floral visitors, honeydew feeding, ants, *Vespula* spp.

Introduction

Plant sugars are typically a guarded resource: phloem sugars are defended (both mechanically and chemically) and plants generally only present sugar in flowers or extra-floral nectaries to secure beneficial interactions with sugar-feeding animals. However, honeydew-producing insects can make considerable quantities of plant-derived sugars available to consumers. As a result, honeydew-producing insects have the potential to alter existing sugar-based plant-animal interactions or to create new sets of interactions. To date most research in this area has focused on the effect of honeydew-producing hemipterans on associations between ants and extra-floral nectaries (EFNs).

Ants often feed on the nectar provided at EFNs and such ant attendance can reduce herbivory on the host plant (de la Fuente & Marquis, 1999; Styrsky & Eubanks, 2007). In some situations honeydew-producing hemipterans can function as ecological analogues of EFNs, attracting ants and conferring similar protection against herbivory (Messina, 1981; Styrsky & Eubanks, 2007). Nevertheless, ant-hemipteran mutualisms are not always beneficial to the host (Styrsky & Eubanks, 2007). Becerra & Venable (1989) proposed that in some situations EFNs may function as a defence against damaging ant-scale insect mutualisms by distracting ants away from honeydew-producing hemipterans, making the abandoned hemipteran colonies more vulnerable to predation and parasitism. However experimental studies to date indicate that, contrary to Becerra and Venable's predictions, ants often prefer honeydew to EFN nectar and will continue to utilise honeydew even when presented with new sugar sources (Buckley, 1983; Del-Claro & Oliveira, 1993; Katayama & Suzuki, 2003).

The effect of honeydew on plant-pollinator associations has received little attention, but a similar range of interactions are possible: honeydew could either decrease flower visitation

rates by distracting nectar-feeders, or increase flower visitation rates by attracting generalist sugar-feeders to infested plants. Murphy and Kelly (2001) investigated whether honeydew distraction was contributing to low pollination rates in mistletoe plants. They found that the main avian pollinator did feed on both honeydew and mistletoe nectar, but that there was no evidence of distraction. The authors concluded that reduced pollinator abundance was the most likely cause of the observed pollination failure. Further studies of consumer responses to diverse natural sugar sources are required to better understand the ecological role of honeydew-producing insects.

In New Zealand honeydew-producing scale insects occur in close proximity to flowers on kanuka trees (Myrtaceae: *Kunzea ericoides*). This pattern of infestation provides an opportunity to examine the effects of honeydew on the sugar economy of a flowering tree species. The specific aims of this study were to compare consumer responses to honeydew and floral sugar resources. Animal visitation rates and feeding rates were recorded on kanuka with and without scale insect infestations during the kanuka flowering period. It was predicted that honeydew would attract sugar consumers and that scale insect infestation would alter visitation patterns to kanuka flowers.

Materials and methods

The study was carried out in the Karamatura Valley in the Waitakere Ranges, a forested plateau of approximately 30,000ha lying 15 km to the west of Auckland City (Denyer *et al.*, 1993). The Auckland climate is relatively mild and moist with a mean summer temperature of 20°C and mean summer monthly rainfall of 77 mm (Mackintosh, 2001).

The study site contained grazed pasture and fenced areas of teatree scrub, a widespread secondary-succession vegetation type dominated by two Myrtaceae species, kanuka and manuka (*Leptospermum scoparium*) (Scott *et al.*, 2000). Kanuka is the main host of the honeydew-producing scale insect *Coelostomidia wairoensis* (Hemiptera: Coelostomidiidae) (Morales, 1991). The feeding stages of *C. wairoensis* settle preferentially on branch tips and excrete excess carbohydrates as honeydew droplets from a waxy anal filament (Morales, 1990). Densities of *C. wairoensis* on branch tips can reach 10,000 m⁻² or more over summer months and kanuka foliage is frequently blackened with sooty moulds growing on honeydew (Morales, 1990). Kanuka flowers are also produced from the branch tips from September to February (Allen, 1961). The flowers are open dish blossoms, 3-5 mm in diameter, and are typically clustered to form 2-5 flowered cymes (Allen, 1961; Newstrom & Robertson, 2005). Nectar is probably produced from nectiferous tissues in the floral cup, as in related taxa (Beardsell *et al.*, 1989; O'Brien & Calder, 1993). Hence, during the flowering season, honeydew droplets and kanuka flowers occur in close proximity on infested trees and both provide readily accessible sugar.

To compare consumer responses to honeydew and floral resources, protocols developed at Landcare Research (Pollination Biology Research Group) were adapted to record visitors to flowers and honeydew on kanuka trees. Twenty kanuka with accessible flowering branches were selected for the study, ten with heavy *C. wairoensis* infestation and ten with low infestation or no observable infestation (referred to as un-infested trees for remainder of paper). The trees were selected to ensure that spatial distribution, exposure to sun, and floral resource sizes were similar for infested and un-infested trees. The study trees were visited repeatedly over a 10-day period, from 13 to 22 December 2006. Each day a series

of near-instantaneous scans were conducted at 0900, 1100, 1300 and 1500 hours. Each scan had two parts. First the number of birds and butterflies in contact with flowers or honeydew was recorded from a distance of approximately 3 m. Then, from a distance of approximately 0.5 m, a portion of accessible flowering branch (c. 0.75 x 0.75 m surface area) was scanned for floral and honeydew visitors (i.e. animals in contact with flowers or scale insect anal tubes/honeydew droplets respectively) and for nectar and honeydew feeders (any animal with mouthparts in contact with floral cup or honeydew droplets respectively). No attempt was made to identify insects to species level in the field. Instead, insects were assigned to functional categories as per Landcare Research protocols and the number and functional category of each visitor and feeder was recorded. The categories used are given in Figure 2.

To estimate the relative size of the sugar resources present in the scanned areas nectar and honeydew samples were collected on 23 December 2006 between 9 am and 11 am. At each of the trees used in the study, twenty flowers were selected randomly and the floral cup of each flower was gently probed with the tip of a piece of pre-weighed filter paper to collect any liquid nectar present. At infested trees twenty honeydew droplets were also collected from the scan area on a separate piece of pre-weighed filter paper. The number of open flowers and honeydew droplets in the scan area on each tree was estimated by either direct counting, or by counting a subsection of and multiplying to give an estimate for the whole scan area. Filter papers were then dried and reweighed to determine the dry weight of sugar present as per Dungan *et al.* (2004).

As ants are major honeydew consumers in other ecosystems additional non-toxic baiting was used to determine a) what ants were present in the study area, b) whether ants present foraged in tree foliage or were restricted to the ground and c) whether ants present were attracted to sugar. Ten infested trees were randomly selected for this baiting study and three baits were used: water (cotton wool soaked in water), sugar (cotton wool soaked in a saturated sucrose solution) and protein (c.1 g canned tuna). All baits were placed in 5 ml clear plastic vials. Six vials of each of the baits were placed at each tree, three on the ground and three attached to branchlets with honeydew present. Vials were placed in the field between 11.45 am and 12.45 pm on 23 December 2006 and were checked after two hours. All ants present on baits were collected and identified in the laboratory.

Data from the ten day sampling period were treated as a cumulative measure of honeydew and flower visitation patterns. Data from each tree were pooled and paired t-tests were used to test for differences between floral visitor numbers and honeydew visitor numbers on infested kanuka. In addition, analysis of variance was used to test the hypothesis that infested and un-infested trees differed in floral visitor numbers and/or composition. Data were transformed to meet model assumptions and non-parametric tests used when necessary. Analyses were conducted using SPSS 15.0, PRIMER 6.1.6, and PERMANOVA (Anderson, 2005). Multivariate data were square root transformed to down-weight common species and the Bray-Curtis coefficient was used to construct similarity matrices used in multivariate analyses.

Results and discussion

Humid cloudy conditions prevailed for the first five days of the study, followed by several days of intermittent showers and then two days of cooler dry weather (Fig. 1, a). A total of 284 insects were observed in the scan areas on flowers or honeydew and visitor activity remained relatively constant over the study period (Fig. 1, b). On average, insect

activity was recorded in $35\% \pm 3\%$ (mean ± 1 SE) of all the scan areas each day and a total of 56 ± 8 insects were observed per day.

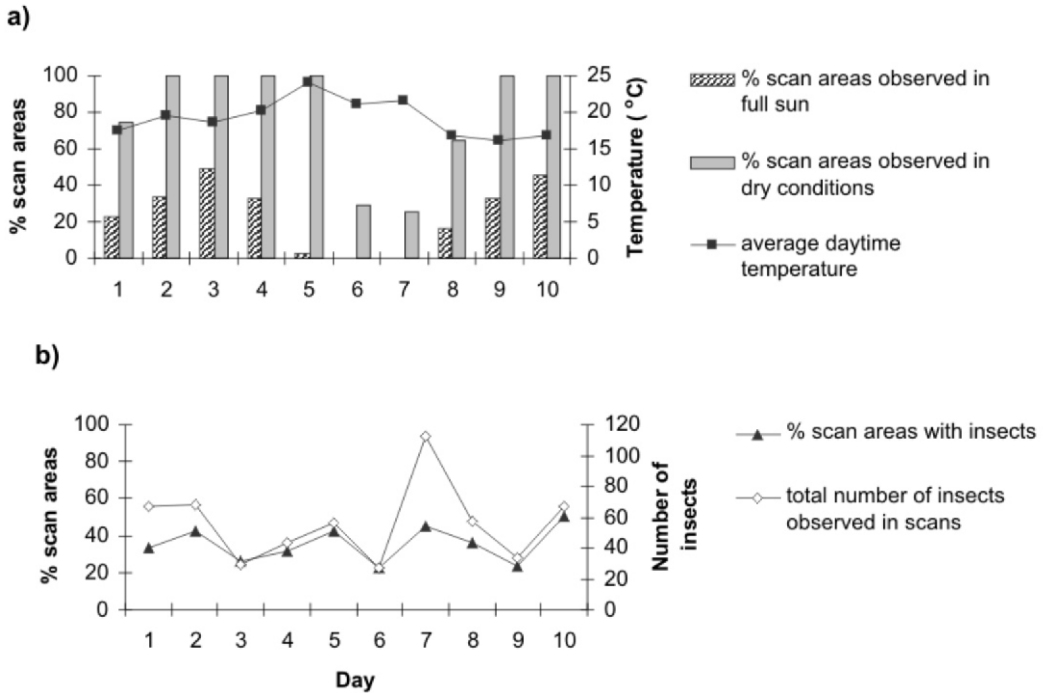


Figure 1. Summary of a) weather conditions and b) insect activity on flowering kanuka, Karamatura Valley, 13-22 December 2006.

The amount of sugar available from honeydew was approximately five times higher than the amount of sugar available in nectar on infested trees. The median dry weight of honeydew sugar per scan area was 96.65 mg whereas the median dry weight of liquid nectar sugar per scan area was significantly lower at 19.5 mg (paired t-test on $\log(n)$ transformed data: $t(9) = -3.79$, $p = 0.004$). In addition, the mean dry weight of sugar was higher per honeydew droplet ($0.22 \text{ mg/droplet} \pm 0.02$) than per individual flower ($0.06 \text{ mg/flower} \pm 0.01$) (paired t-test: $t(9) = -6.14$, $p < 0.001$).

Despite the amount of honeydew sugar available, flowers were visited more often than honeydew droplets and nectar feeding was observed more often than honeydew feeding in infested trees (Fig. 2). Differences in overall visitation frequency were pronounced, with a total of 269 insects observed on flowers but only 15 insects observed in contact with scale insect anal tubes or honeydew droplets ($\chi^2(1, N = 284) = 227.17$, $p < 0.001$). The mean number of visitors was significantly higher on flowers than on honeydew (Wilcoxon signed ranks test on paired data: $Z = -2.81$, $p = 0.005$). Overall feeding frequency also differed significantly between sugar sources with a total of 36 insects observed feeding on

nectar and 13 observed feeding on honeydew ($X^2_{(1,49)} = 10.8, p = 0.001$). However there was no significant difference in the mean number of insects feeding on honeydew and nectar (Wilcoxon signed ranks test on paired data: $Z = -1.75, p = 0.08$).

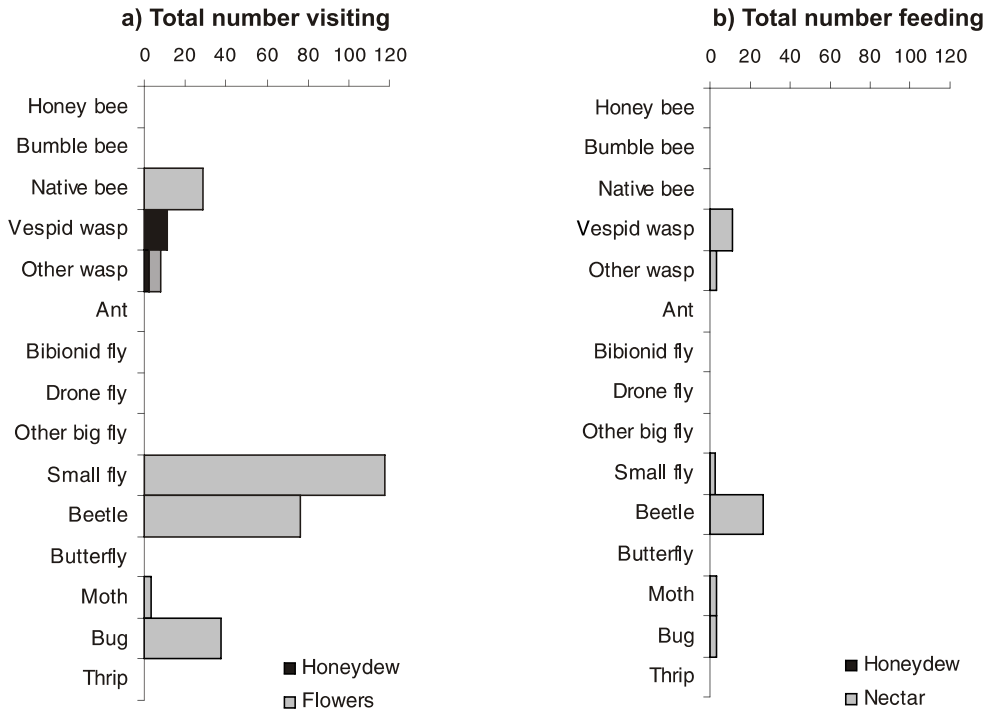


Figure 2. Total number of insects observed a) visiting honeydew and flowers and b) feeding on honeydew and nectar on scale-infested kanuka trees.

Social wasps (Vespidae) were the most common insect visiting and feeding on honeydew, accounting for 73% of all visitor observations and 85% of all feeding observations on honeydew. All specimens collected from honeydew were identified as *Vespula vulgaris*, but *V. germanica* was also present at the field site and it is probable that both wasp species were feeding on honeydew. In contrast to this, social wasps were not seen on flowers of any infested trees during the study period. Fisher's exact tests indicated that sugar source (honeydew/nectar) and insect group (social wasp/other insect) were significantly associated for both visitors ($p < 0.001$) and feeders ($p < 0.001$) on infested trees.

Birds were observed searching for and feeding on insects and perching amongst flowers in study trees, but were not observed feeding on either nectar or honeydew. No ants were observed on kanuka flowers or honeydew during the study period. However, baiting indicated that tree-climbing ants responsive to sugar baits were present in the study area (Fig. 3). Three species of ants were collected from the baits, two endemics (*Huberia striata* and *Monomorium antarcticum*) and one exotic species (*Technomyrmex albipes*). The endemic species were collected from ground baits only whereas *T. albipes* was collected from sugar and protein baits in foliage and on the ground.

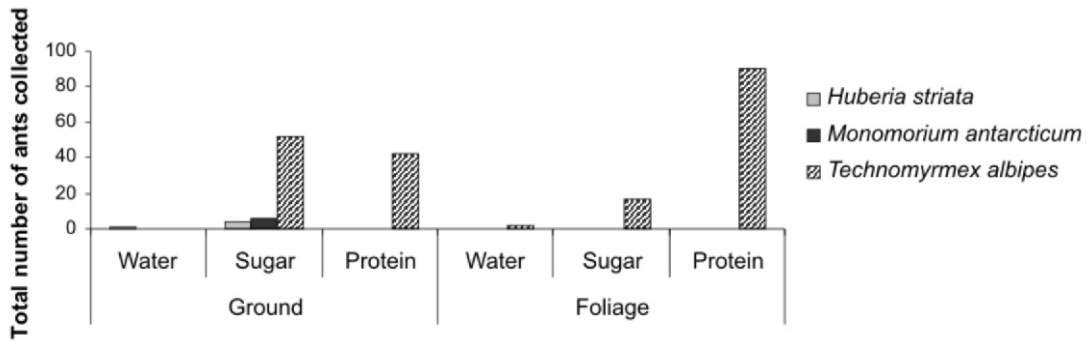


Figure 3. Ants responses to water, sugar and protein baits placed on ground beneath or in foliage of scale-infested kanuka trees, Karamatura Valley.

The presence of honeydew in close proximity to the kanuka flowers had no discernible effect on flower visitation patterns. Insects were the main floral visitors and there was no difference in the median number of insect visitors to flowers on infested and un-infested trees (t-test on $\log(n)$ transformed data: $t_{(18)} = -1.05$, $p = 0.31$). There was also no significant difference in the composition of insect floral visitors on infested and un-infested trees (PERMANOVA: $F_{(1,18)} = 1.52$, $p = 0.24$). Small flies were the most abundant floral visitors, detected on 60% of infested trees, 80% of un-infested trees and accounting for 47% of all flower visitor observations. The next most commonly observed visitors were beetles, detected on all trees and accounting for 28% of all flower visitor observations.

This study confirms that the endemic scale insect *Coelostomidia wairoensis* produces significant amounts of bio-available sugar, and that the honeydew resource can exceed the nectar resource on infested trees. However there is no evidence that honeydew has any direct impact on kanuka-pollinator interactions as the number and composition of floral visitors did not differ between infested and un-infested trees. There was no indication of any insects feeding on both nectar and honeydew or switching between the two sugar sources. Instead, the honeydew-feeding fauna and the nectar-feeding fauna appear to be discrete with little or no overlap between the two groups. The honeydew-feeding fauna also had limited membership (3-4 species) suggesting that few sugar-feeding animals utilise kanuka honeydew.

Laboratory studies indicate that honeydew may be sub-optimal as a food source compared to nectar, as honeydew-fed parasitoids have reduced longevity compared with nectar-fed parasitoids (Lee *et al.*, 2004; Winkler, Wackers *et al.*, 2005). However, field studies show that despite their laboratory preferences, wild parasitoids do readily feed on honeydew (Lee *et al.*, 2006; Wackers & Steppuhn 2003, cited in Wackers *et al.*, 2005) Indeed, Wackers and Steppuhn (2003) found that even in fields with abundant nectar sources between 55% and 68% of the parasitoids captured had fed recently on honeydew. Studies of native ecosystems also show honeydew is an important food resource for a wide range of animals (Paton, 1980; Towns, 2002).

In the present study, exotic social wasps (*V. vulgaris* and probably *V. germanica*) were the only animals observed feeding regularly on honeydew. Both these species are recent accidental introductions to New Zealand (Beggs & Rees, 1999). Native honeydew feeders were absent or sparse, as only two other insects (one fly and one solitary wasp, origins

unknown) were observed feeding on honeydew. It is possible that nocturnal native honeydew feeders (e.g. geckos: Towns, 2002) were present at the site but not detected. However, it is also possible that the limited number of daytime honeydew feeders is an indication that the native honeydew-feeding fauna is impoverished. Some honeydew-feeding taxa may be absent due to biogeographical processes as New Zealand is remote island archipelago with a disharmonic, depauperate native fauna (Daugherty *et al.*, 1993). For example, ants are frequent honeydew consumers in other ecosystems, but New Zealand has just 11 native ant species and none are strongly arboreal (Styrsky & Eubanks, 2007; Ward, 2005). This low level of taxonomic and functional diversity may account for the lack of native ant honeydew feeding in the present study.

Other absences may be more recent, caused by human disturbance and habitat modification. Approximately 40% of New Zealand land vertebrates have become extinct since human habitation began and surviving species typically have reduced and fragmented ranges and/or reduced population sizes (Atkinson & Cameron, 1993). Surviving native species also occupy highly modified landscapes and contend with an array of exotic competitors and predators (Atkinson & Cameron, 1993). All of these changes could reduce the native honeydew-feeding fauna at the study site. For example, it is possible that native honeydew-feeding insects have been negatively affected by the exotic *Vespula* wasps through either competition or predation. In New Zealand beech forests, exotic wasps can reduce the honeydew standing crop by more than 99% and exclude other species by resource exploitation (Moller *et al.*, 1991; 1996). Moreover, *Vespula* wasps are generalist predators, gaining their protein requirements through scavenging and by preying on live invertebrates (Harris, 1993). When abundant honeydew sources fuel high wasp numbers, the wasps can exert considerable predation pressure on the native invertebrate community (Beggs & Rees, 1999; Toft & Rees, 1998). It may be that, by supporting a generalist invasive predator, honeydew itself contributes to the impoverishment of the honeydew-feeding fauna in kanuka stands.

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