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A note on manna feeding by ants (Hymenoptera: Formicidae)

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The production of manna is often associated with the feeding injuries of the coreid, *Amorbus obscuricornis* (Westwood) (Hemiptera: Coreidae). The manna produced as a result of the injuries caused by *A. obscuricornis* is extremely attractive to ants and it is often taken right from underneath feeding bugs. Observations of a number of Tasmanian ant species feeding upon eucalpyt manna, suggest that this substance is an important source of carbohydrate for the ants. The possible significance of manna secretion is considered.

KEYWORDS: Ants, Formicidae, Coreidae, Heteroptera, eucalypt manna, rapidly induced response, Tasmania.

Introduction

Manna is a saccharine secretion exuded from stems and leaves of certain trees that is produced following injury caused by insects. The exudate, which forms white nodules upon crystallizing, generally consists of 60% sugars (namely raffinose, melibiose, stachyose, sucrose, glucose and fructose), 16% water, 20% pectin and uronic acids (Basden, 1965). Manna has been recorded from a range of eucalypt and *Angophora* species, including *Eucalyptus punctata*, *E. viminalis*, *E. mannifera*, *E. maculata*, *E. citriodora*, *E. tereticornis*, *Angophora floribunda*, *A. costata* (Basden, 1965), *Eucalyptus obliqua* (Green, 1972), *E. nitens* (S. Candy, pers. comm.), *E. regnans*, *E. tenuiramis*, *E. amygdalina* × *E. risdonii* hybrids and *E. delegatensis* (pers. obs.).

Manna has been shown to be produced as a result of injuries inflicted by a number of insect species (Table 1), and according to Basden (1965) could not be artificially induced.

As manna is a rich source of carbohydrate it is a very attractive food for many animals. Birds, such as honeyeaters and silvereyes (Paton 1979, 1982; Recher *et al.*, 1985), and arboreal animals such as Leadbeaters Possum (Smith, 1984) often feed on manna. Similarly, the attractiveness of manna to ants has been noted previously (Smith, 1897; Green, 1972; Bashford, 1992). Although adult ants are liquid-feeders and most forage for carbohydrate-rich plant exudates (Andersen, 1991; Taylor, 1991), the importance of manna as a source of nourishment for foraging ants does not appear to have been studied in detail.

Results

Table 2 summarises observations made of ants feeding upon eucalypt manna

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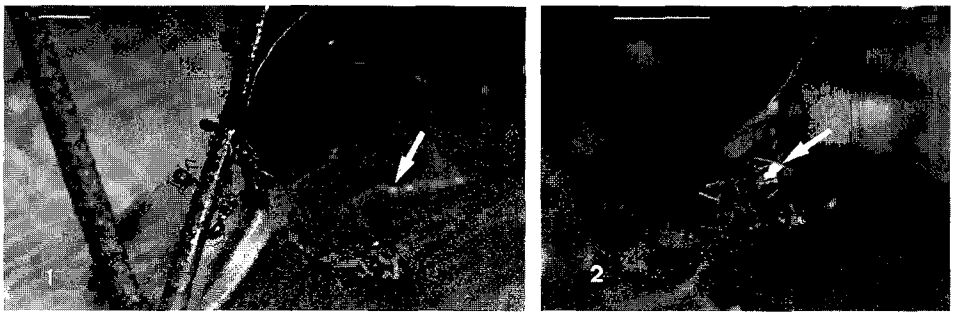
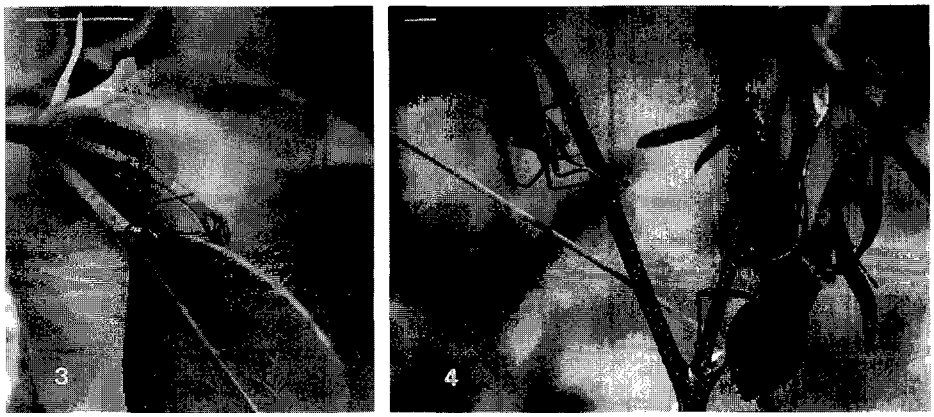
Table 1. List of insect species known to cause manna secretion and the eucalypt species concerned.

Insect species (Order: Family)	Eucalypt species	Reference
Hyalarcta huebneri (Westwood) (Lepidoptera: Psychidae)	not given	Basden, 1965
Phylacteophaga eucalypti (Frogg.) (Hymenoptera: Pergidae)	not given	Basden, 1965
Perga dorsalis (Leach) (Hymenoptera: Pergidae)	not given	Basden, 1965
beetle larva (unidentified species) (Coleoptera)	*E. punctata*	Basden, 1965
Chrysophtharta bimaculata (Olivier) (Coleoptera: Chrysomelidae)	*E. nitens*	S. Candy, pers. comm.
Eurymelid (unidentified species) (Hemiptera: Eurymelidae)	*E. nitens*	Pers. obs.
Psaltoda moerens (Germar) (Hemiptera: Cicadidae)	*E. viminalis*	Elliott and deLittle, 1985
Amorbus obscuricornis (Westwood) (Hemiptera: Coreidae)	*E. obliqua*; *E. viminalis*; not given	Green, 1972; Elliott and deLittle, 1985; Bashford, 1992 (respectively)

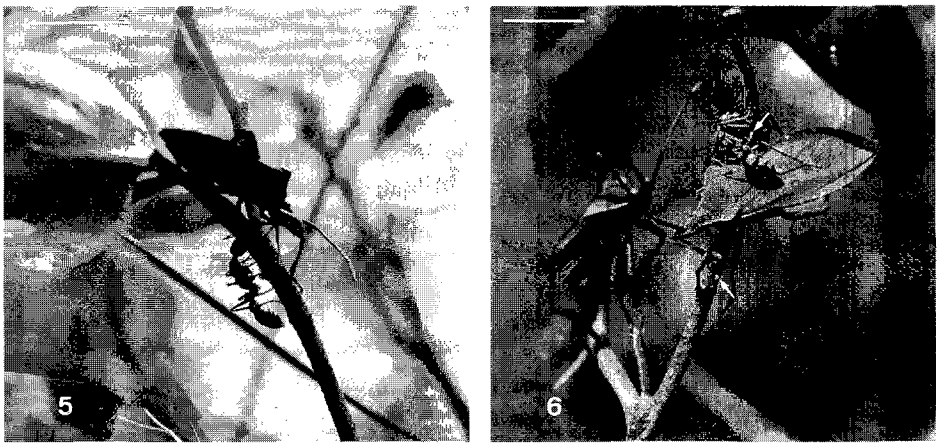


FIGS 1, 2. (1) Numerous ants of the *Iridomyrmex anceps* group feeding on liquid manna (arrowed) from *E. obliqua* at Ridgeway (scale line = approx. 3·5 mm). (2) An ant of the *Myrmecia gulosa* group feeding on crystallized *E. obliqua* manna (arrowed) after rain, Ridgeway (scale line = approx. 20·0 mm).

exuded as a result of the feeding damage caused by *A. obscuricornis*. Ants belonging to the *Iridomyrmex anceps* (Figs 1, 4), *Iridomyrmex* species, *Myrmecia gulosa* (Fig. 2), *Camponotus nigroaeneus* (Fig. 3) and *Myrmecia pilosula* (Figs 5, 6) groups were observed feeding upon liquid and crystallized manna exuded from the feeding injuries caused by *A. obscuricornis*. Because *A. obscuricornis* will feed on a given eucalypt tree for some days, possibly weeks, ants will keep returning to these trees in order to locate manna. For example, at the Forest Resources concession (Table 2) ants kept returning to trees infested with *Amorbus* for a period of some weeks. Often these ants come in close contact with the feeding bugs in order to ingest manna (Figs 4, 6). A number of ants were observed to take the manna exuding from around the bug's inserted labium (Fig. 5).



FIGS 3, 4. (3) An ant of the *Camponotus nigroaeneus* group feeding at an abandoned *Amorbus* wound on *E. obliqua* at the Forest Resources concession (scale line = approx. 8·5 mm). (4) An ant of the *Iridomyrmex anceps* group taking manna from the wound caused by a feeding *A. obscuricornis* adult ♂, Ridgeway (scale line = approx. 3·5 mm).



FIGS 5, 6. (5) An ant of the *M. pilosula* group taking liquid manna from near the inserted rostrum of an *A. obscuricornis* ♂ on *E. obliqua*, Forest Resources concession (scale line = approx. 11·0 mm). (6) An ant of the *M. pilosula* group taking dried manna (arrowed) whilst resting on the back of an *A. obscuricornis* ♀ on *E. obliqua*, Forest Resources concession (scale line = approx. 11·0 mm).

Although ants belonging to the genus *Myrmecia* are solitary predators (Gray, 1971) no incidences of predation of adult *A. obscuricornis* were observed. This is despite observations of individual *M. pilosula* carrying prey during the period when adult coreids are active. The bugs displayed little agitation in the presence of the ants which is evidenced by the fact that they did not withdraw their labia and try to leave. On one occasion an ant was seen to ingest *Amorbus* excreta found in the vicinity of a feeding adult. The records presented illustrate that ants were able to find manna throughout spring and summer at the sites visited. According to Basden (1965) the exudation of manna occurs throughout the year but is more common during spring and early summer.

Table 2. Observations of ants feeding upon manna exuding from eucalypt wounds caused by the feeding activities of *A. obscuricornis*.

Date	Location/Weather	Observations
1 Nov. 1994	– Ridgeway, Tas. (42°55′S 147°17′E) – overcast with light rain	– numerous ants of the *Iridomyrmex anceps* group feeding upon liquid manna exuding from injured *E. obliqua* shoots – two ants of the *Myrmecia pilosula* group and one ant of the *M. gulosa* group feeding upon dissolving manna encrustations on *E. obliqua* shoots – 8 adult ♂♂ and 6 adult ♀♀ of *A. obscuricornis* feeding upon this same tree
4 Nov. 1994	– Ridgeway, Tas. – sunny and warm	– numerous ants of the *Iridomyrmex anceps* group feeding upon liquid manna exuding from injured shoots near feeding bugs (same tree as 1 Nov. 1994 observation) – tree infested with numerous *A. obscuricornis* adults
11 Nov. 1994	– Forest Resources concession (42°43′S 147°45′E approx.) – windy but mild	– lone ant of the *Myrmecia pilosula* group feeding upon manna from an *E. obliqua* sapling (approx. 5 years old) infested with 2–3 *A. obscuricornis* adult ♂♂ and 1 adult ♀ – ant took manna from stem whilst perched on the back of the *A. obscuricornis* adult ♀ and from around the bug's labium – same ant observed ingesting excreta on a *Gahnia* spp. below an *A. obscuricornis* ♂
18 Nov. 1994	– Forest Resources concession – sunny and warm	– observed a lone ant of the *Myrmecia pilosula* group remain in close proximity to a feeding *A. obscuricornis* ♂ for approx. 30 mins. intermittently ingesting liquid manna from around bug's inserted rostrum and nearby encrustations (same tree as the 11 November 1994 observation) – bug apparently only occasionally agitated by ant's presence – ant showed no interest in ingesting bug excreta when released – an ant of the *Iridomyrmex* species group observed feeding upon liquid manna
6 Dec. 1994	– Forest Resources concession – sunny and hot	– two ants of the *Camponotus nigroaeneus* group observed feeding from around the inserted labium of an *A. obscuricornis* adult ♂ feeding upon an *E. obliqua* sapling (different tree to that of the 11 and 18 Nov. 1994) – bug seen to move to site where ants were aggregated to resume feeding – ants remained near bug for duration of observation (approx. 10 min) – tree infested with 2 *A. obscuricornis* adult ♂♂ and 2 adult ♀♀

Table 2. Continued.

Date	Location/Weather	Observations
14 Feb. 1995	– Forest Resources concession – overcast, mild and humid	– an ant of the *Camponotus nigroaeneus* group observed feeding from around the inserted labium of an *A. obscuricornis* adult ♀ feeding upon an *E. obliqua* sapling (same tree as the 6 Dec. 1994 observation) – 2 to 3 other ants of the *Camponotus nigroaeneus* group observed feeding at abandoned *Amorbus* wounds – tree infested with 2 *A. obscuricornis* adult ♂♂ and 1 adult ♀
17 Feb. 1995	– Darcy Link Rd. (43°21′S 146°49′E approx.) – intermittently cloudy with showers	– observed a number of ants of the *Iridomyrmex* species group foraging in a *E. obliqua*/*E. regnans* (approx. 4 years old) – one ant observed feeding at an abandoned *Amorbus* wound – tree infested with 4 fifth instar *A. obscuricornis* nymphs
28 Mar. 1995	– Forest Resources concession – sunny and warm	– observed two ants of the *Myrmecia pilosula* group feeding on manna exuding from a wound to *E. obliqua* caused by the feeding activity of a fourth instar *A. obscuricornis* nymph – on two occasions when the nymph came into contact with these ants it reared up on all legs and appeared very agitated by their presence, however, the ants did not harm the bug

Discussion

Manna appears to be a very attractive source of carbohydrate for a number of Tasmanian ant species. Given that eucalypt forests have few such rich carbohydrate resources other than nectar from flowers and/or extrafloral nectaries, and that the availability of these substances can be very seasonal (Paton 1979, 1982; Smith, 1984; Recher *et al.*, 1985) in the case of nectar from flowers it is hardly surprising that ants will take manna from any available site, even from close proximity to feeding herbivores such as *A. obscuricornis*. Basden (1965) suggested that manna secretion did not commence immediately following insect attack, meaning that the causal agent had usually left prior to its exudation. The findings presented herein differ from this suggestion and indicate that manna begins to exude very shortly after an insect has commenced feeding. In the case of wounds inflicted by *A. obscuricornis*, rapid inducement of manna secretion often causes the bugs to come into direct contact with foraging ant species attracted by the exudate. Given that the method by which the Coreidae feed differs notably from that of other sucking insects (Miles and Taylor, 1994) it is possible that this causes eucalypts to respond differently to attack by these insects compared to that of other phytophages.

Although Green (1972) reported observing a large *Myrmecia* species (probably of the *M. gulosa* group) carrying a second instar *A. obscuricornis* nymph between its mandibles, no predation of adult *Amorbus* by ants was observed, neither was it observed in the present study. Wheeler (1933) considered that *Myrmecia* species prey mainly upon soft-bodied insects which may explain this apparent stage-specific predation by ants. In addition, Gray (1971) noted that prey/nectar availability and colony composition influenced the predatory behaviour of ants. Although one ant was seen ingesting *Amorbus* excreta this material was not taken directly from the bug therefore it appears unlikely that *Amorbus* has a mutualistic relationship with these ants as has been observed in some other south-east asian Coreidae (Maschwitz and Klinger, 1974; Maschwitz *et al.*, 1987).

Plants which supply carbohydrate-rich secretions from extrafloral nectaries entice ants to forage on their surfaces (Bentley, 1977; Tilman, 1978; Buckley, 1982; Koptur, 1984; Beattie, 1985; Heads, 1986; Hölldobler and Wilson, 1990; Fiala *et al.*, 1994). Similarly, plants in flower are more attractive to foraging ants than those not in flower (Woinarski and Cullen, 1984). Both of these methods of attracting ants appear to be different phenomena to the secretion of manna which is released directly from the site of insect damage, not at some distant location, and is then only released in response to insect injuries. That sugary secretions other than those from extrafloral nectaries could be an important mechanism aiding plant protection by ants was first proposed by Scott (1980). The findings of Skinner and Whittaker (1981), Fowler and MacGarvin (1985), Grant and Moran (1986) and Mackay (1991) suggest that when plants do not provide external sources of nourishment for foraging ants then the reduction in herbivore numbers and/or herbivore damage through ant predation is minimal. This relationship appears to change markedly when external sources of carbohydrate are present on plant surfaces. For example, Floate and Whitham (1994) found that the availability of aphid honeydew resulted in a two-fold reduction in chrysomelid herbivory on hybrid beech trees which was the result of ant predation. Similarly, Fiala *et al.* (1994) found that ant-attended *Macaranga* trees suffered considerably increased rates of leaf damage following the exclusion of ant mutualists. However, the exudation of manna following attack by *A. obscuricornis* does not appear to result in ant predation of adult bugs. Fowler and MacGarvin (1985) suggest

that 'distasteful' species may be less vulnerable to ant predation which could explain why adult coreids were not attacked by ants given that these insects posses pungent defensive secretions (Steinbauer and Davies, 1995). The observations show that manna secretion by eucalypts is a rapidly induced response to injuries caused by feeding insects which attracts ants to sites of exudation. Whether it is possible that the secretion of manna by eucalypts could be a rapidly induced 'defence' which acts by attracting various predators (such as ants, birds and arboreal animals) which could then prey upon non-distasteful and/or soft-bodied insects remains an open question, however, the role of this substance would appear to provide an interesting area of further investigation.

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