[The Great Lakes Entomologist](https://scholar.valpo.edu/tgle)

Volume 32
Numbers 1 & 2 - Spring/Summer 1999 *Numbers 1 & 2 - Spring/Summer 1999*

Article 3

April 1999

Seasonal Response of Workers of the Allegheny Mound Ant, *Formica Exsectoides* (Hymenoptera: Formicidae) to Artificial Honeydews of Varying Nutritional Content

C. M. Bristow
Michigan State University

E. Yanity
Michigan State University

SEASONAL RESPONSE OF WORKERS OF THE ALLEGHENY MOUND ANT, *FORMICA EXSECTOIDES* (HYMENOPTERA: FORMICIDAE) TO ARTIFICIAL HONEYDEWS OF VARYING NUTRITIONAL CONTENT

C. M. Bristow[1] and E. Yanity[1,2]

ABSTRACT

Field colonies of Allegheny mound ants, *Formica exsectoides*, were tested at monthly intervals throughout the summer to assess their preference for artificial honeydews containing varying compositions of sugars and amino acids. In choice tests, foragers significantly preferred high sugar honeydews early in the season, but shifted in mid-season to a strong preference for high amino acid honeydews. Late-season foragers slightly preferred sugars. When offered in equal concentrations, the honeydew sugar, melezitose, was consistently less attractive to foragers than sucrose. However both sugars were readily fed upon, and appeared to attract ants in an additive fashion. No single amino acid was significantly preferred; however the combination of asparagine, glutamine and serine was highly attractive during the mid-season sampling period. The seasonal switch in forager preference between sugars and amino acids coincides with an increase in the amount of actively growing brood.

Most ant species, including some thought to be primarily predaceous, actually employ a mixed foraging strategy by supplementing arthropod prey with the sugary secretions of plants, Homoptera, or lycaenid butterfly larvae (Evans and Leston 1971, Wellenstein 1952, Wilson 1962). These secretions can contain complex blends of nutrients chief among which are sugars including oligosaccharides (Baker and Baker 1983, Klingauf 1987). Nectars and honeydews have generally been thought to contribute primarily carbohydrate used by workers to augment activity (Carroll and Jansen 1973). Some researchers have suggested that ants may specifically be attracted to certain sugars such as the Homopteran-synthesized trisaccharide, melezitose, thus promoting formation of mutualistic associations (Duckett 1974, Kiss 1981). In addition to sugars, however, virtually all honeydews and nectars also contain a measurable amount of nitrogen (Auclair 1963, Baker and Baker 1973, Pierce 1985, DeVries and Baker 1989). Recent work (Lanza and Krauss 1984, Lanza 1988, 1991) using several tropical and subtropical ant species, has suggested that foragers may discriminate and prefer solutions with high amino acid concentrations. Many tropical species are thought to be more highly specialized in diet choice than their temperate counterparts. Thus these results could reflect a degree of discrimination not found in species

[1]Department of Entomology, Michigan State University, East Lansing, MI 48824-1115.

[2]Current address: San Antonio Zoological Gardens and Aquarium, 3903 North Saint Mary's Street, San Antonio, TX 78212-3199.

that obtain their proteins from predation or scavenging. We address the question—is the ability to discriminate different nutrients in nectar or honeydew also developed in temperate ant species?

Among temperate ant species, the habit of feeding on exogenous carbohydrate secretions is particularly well-developed in members of the genera *Formica* and *Camponotus* feeding in boreal and deciduous forests (Carroll and Jansen 1973, Hölldobler and Wilson 1990) or desert steppe habitats (McIver and Yandell 1998). In these seasonal ecosystems, the primary sources of sugars are the honeydews of homopterans rather than floral and extrafloral nectars. Nutritionally, honeydews resemble nectars, with the primary rewards being sugars (0.5% to 10% of the weight of the solutions). Over 20 amino acids have also been recorded from honeydews, and make up from less than 0.01% to over 5% of the honeydew (Auclair 1963).

A range of studies on honeydew-feeding by predaceous forest ants indicates that honeydew may comprise a major food source for these species (Horstmann 1974, 1982; Zoebelein 1956, Skinner 1980, Degan et al. 1986). Researchers conclude that both sugars (Way 1954) and amino acids (Gosswald 1954, Kloft 1953) may contribute substantially to colony nutrition, and that protein-rich foods are needed when larvae are developing in the nest, while sugar-rich foods are collected to provide energy for worker activity (Edwards 1951, Wilson and Eisner 1957, and Driessen et al. 1984). The European wood-ant *Formica lugubris* Zett. exhibited a shifting threshold to sucrose baits across the season (Sudd and Sudd 1985), accepting low-quality baits early in the season, but rejecting them later as Homopterans became more abundant. These trials were limited to sucrose, however, and did not assess whether ants could discriminate amino acids in honeydews. Other field data on diet preference are also inconclusive. Wellenstein (1952) reported that *Formica rufa* L. workers foraged on honeydew early in the season when insect prey were scarce but switched to insect food as soon as it became available. Ayre (1958, 1959), in a study with a closely related species, *F. subnitens* Creighton, found the opposite—that ants foraged on insect prey early in the season and switched to honeydew as it became more available. Skinner (1980) found that although more honeydew was brought back early in the season, it continued to provide a major portion of the calories obtained by the colony throughout the foraging cycle. Thus there is no common agreement regarding the extent to which ants discriminate among different nutrients, nor how shifting colony needs may influence forager preference.

This study was conducted using experimentally manipulated food sources to determine whether a predaceous temperate-zone ant discriminates between different nutrients found commonly in Homopteran honeydews, and if so, whether there is any seasonal component to preference. Specifically we wished to determine the seasonal responses of workers to various honeydew nutrients coinciding with periods of early brood initiation, peak larval production and the post-reproductive phase of the active colony cycle. We predict that foragers should prefer sugars when the demands of nourishing growing brood are low (early and late-season), but should prefer amino acids in periods of high brood growth (mid-season). We additionally tested whether ants preferred melezitose compared to sucrose, and whether they preferred individual amino acids.

METHODS AND MATERIALS

Field site and species studied. The study was conducted in the summer of 1991 in a jack pine (*Pinus bansksiana* Lambert) forest stand near

Hunter Lake in the Huron-Manistee National Forest in Crawford County, Michigan. The stand (Compartment 79, Stand 3, planted in 1946) is mature open canopy jack pine with an understory of northern pin oak (*Quercus ellipsoidalis*) saplings. Ground cover is primarily lichen, low bush blueberry (*Vaccinium angustifolium*) and sweet fern (*Comptonia peregrina*) with mixed grasses in the more open areas. Jack pine forests in this area are maintained by clear-cut and restocking as wildlife habitat for kirtland warblers (*Dendroica kirtlandii* (Baird)), an endangered groundnesting species whose breeding grounds are restricted to new growth jack pine forests in the northern lower peninsula of Michigan (Mayfield 1992).

The area contains numerous well-established populations of the Allegheny mound ant, *Formica exsectoides* Forel, a common mound-building ant in North America (Wheeler 1910). In areas where populations have become established, the large thatched mounds form a conspicuous feature of the landscape. Colony densities of more than 100 mounds per ha have been described in Pennsylvania (McCook 1877) and Maryland (Andrews 1925a, b). Colony densities at the study site were approximately 70 mounds per ha (Bristow et al. 1992).

Individual mounds may contain up to a quarter of a million workers whose predatory activities can have a significant impact on arthropods in the surrounding area (Cory and Haviland 1938, Campbell 1990). The colony cycle of *F. exsectoides* in mid-Michigan was determined by excavations of several dozen mounds over the active season (Bristow et al. 1992). The first brood, initiated in June, produces the alate reproductives which swarm in the latter half of July and early August. Worker brood is produced after the sexual brood. The greatest number of larvae, the active feeding stages, are present in mid- to late-July. By mid-August, most larvae have entered or completed pupation, and there are few actively growing stages in the nest. Within a given area, nests are highly synchronized.

In addition to their predatory activities, *F. exsectoides* workers readily collect honeydew from a variety of homopterans on both pines and oaks (McCook 1877, Andrews 1929). At the study site, a number of homopteran species were found regularly associated with attendant ants on both oaks and pines. Two species were common on jack pine: the pine tortoise scale, *Toumeyella parvicornis* (Cockrell), and the jack pine aphid,*Cinara banksiana* Pepper and Tissot. On oaks, three types of homopterans were commonly tended by ants: the European fruit lecanium, *Parthenolecanium corni* (Bouché), an unidentified aphid species, and several species of treehoppers including *Glossonotus univittatus* (Harris), *Ophiderma flavicephala* Goding, and *Cyrtolobus* sp. near *clarus* Woodruff.

General protocol for bait experiments. A series of choice experiments were conducted to assess ant discrimination among three sets of nutrients: 1. sugars vs. amino acids, 2. sucrose vs. melezitose, and 3. different amino acids. To identify seasonal changes in ant response, the three experiments were repeated at monthly intervals coinciding with colony stages of brood initiation (early season), peak larval production (mid-season) and post-reproductive activity (late-season). The dates, experimental order and ambient temperature at the time of the specific experiments (0900 hr) are outlined in Table 1.

The general protocol was similar for all experiments. In late June, eight active colonies of *F. exsectoides* were randomly selected from a mapped population of approximately 50 nests. Around each mound, 18 bait stations were set out in a circular array 1 m out from the base of each mound. Eighteen stations permitted each position to be separated from adjacent stations by at least half a meter, while allowing for two or three replicates of each solution,

Table 1. Date order of presentations and environmental conditions for discrimination experiments.

Date	Sugar-Amino Acid	Melezitose Single	Single Amino Acid
Early season	June 25, 1991 19° C	June 26, 1991 21° C	
Mid-season	August 1, 1991 19° C	July 30, 1991 20° C	July 31, 1991 22.5° C
Late-season	August 27, 1991 23° C	August 29, 1991 18° C	August 28, 1991 18° C

depending on the specific experiment. Each bait station consisted of a base, left in place for the duration of the season, and a removable cup. Both base and cup were constructed by cutting a small Styrofoam coffee cup in half horizontally. The upper portion, when inverted, made the base, while the lower portion made a bait cup that could rest securely in the base. Each cup received an aliquot of 15 ml of test solution.

All experiments were started at 0900 hr, and terminated one hour later. The number of ants present on the rim or inner surface of the bait cup was recorded at the end point. The one-hour time was chosen based on results of a pilot study conducted the previous year. *F. exsectoides* is a group-recruiting species in the sense of Hölldobler (1971). Placing bait stations close to the nest ensured that all baits were located by foragers within a few minutes, and recruitment was observed to level off within an hour. Recruitment over longer times was confounded by bait depletion, changes in concentration due to evaporation, and actual drowning of ants in crowded baits. The one-hour recruitment period thus minimized confounding effects of bait location and changes in quality (Peterson and Renaud 1989). The position of the treatments was randomized for each nest, experiment and date.

Due to transportation problems, the experiment discriminating individual amino acids was not conducted in June. Data were tested for and log-transformed to conform with the assumptions of analysis of variance. Analysis was performed using a repeated measure analysis of variance (Sokal and Rholf 1981) .

Experiment 1. Discrimination of sugar vs. amino acid. Ants were offered a choice test of combinations of sugar mixed with amino acids in concentrations approximating the high and low ends of natural honeydews. The sugar used was sucrose, offered at three levels—high (20.0% w/v), low (5.0%) or none. A mixture of three amino acids (asparagine, glutamine and serine) in a ratio of 10:5:1 was used to assess response to honeydew amino acids. The three amino acids selected occurred in almost all of the 17 homopteran honeydews whose composition was summarized by Auclair (1963), and collectively the three comprised more than 50% of the amino nitrogen in most honeydews. The ratio of asparagine to glutamine to serine of 10:5:1 was based on the relative abundance of the three amino acids in the honeydew of *Aulacorthum (Neomyzus) circumflexum (Buckton)* This species was selected because the data available on it were the most complete, and the range of concentrations of amino acids appeared typical of most other honeydews. The combined amino acids were also offered at three concentration levels: high (4%), low (1%) or none. This provided nine distinct combinations (high sugar, high amino acid, etc.) Two replicates of each bait were offered to each of the eight nests on the three dates.

Experiment 2. Discrimination of melezitose vs. sucrose. The response of foragers to the honeydew sugar melezitose was tested by offering foragers high levels of melezitose (10% w/v), low levels of melezitose (1%) or no (0%) melezitose in combination with sucrose (10% w/v) or no (0%) sucrose. Three replicates of each of the six treatments were offered to each of the eight nests on the three dates.

Experiment 3. Discrimination of individual amino acids. The eight most common amino acids in honeydews were offered individually to foragers in 1.0% (w/v) solutions. Based on Auclair's (1963) review, these (with their average contribution by percent of total amino acids shown in parentheses) were: asparagine (23.90%), glutamine (16.23%), serine (13.11%), leucine (11.53%), valine (6.00%), lysine (5.99%), methionine (4.24%) and thrionine (3.68%)—collectively accounting for almost 85% of the amino acids in the average honeydew. Pilot laboratory tests suggested that foragers would not feed at amino acid solutions in the absence of sugars, so each amino acid was offered in a 10.0% sucrose solution. A control (10.0% sucrose, no amino acids) was also offered, making nine possible treatments. Two replicates of each of the nine treatments were offered to each of the eight nests on the last two dates.

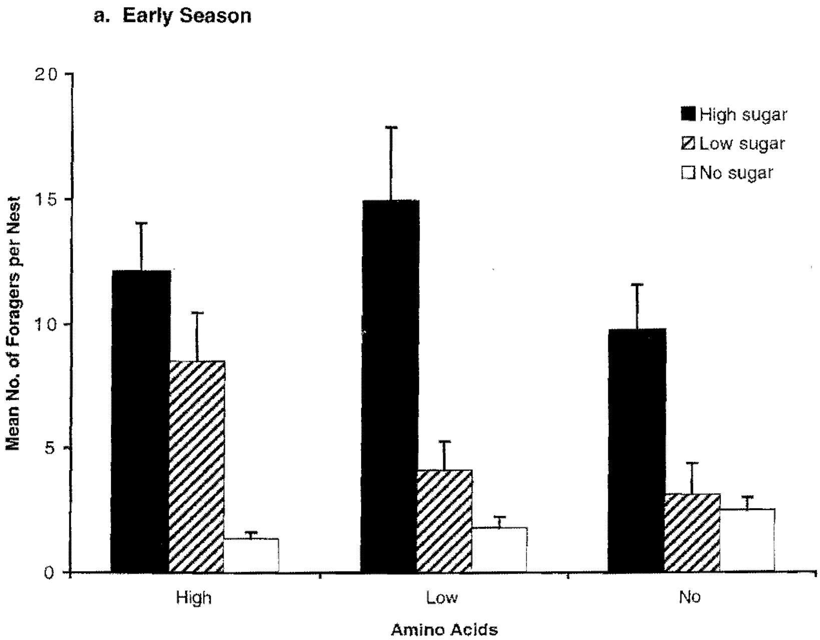
RESULTS

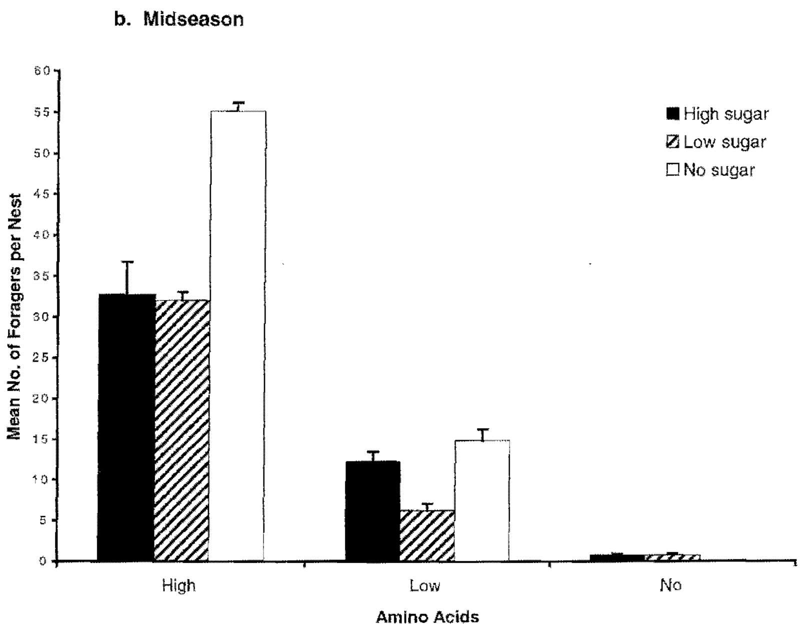
Preference for sugars vs. amino acids. Ant preference for combinations of sugar and amino acids shifted over the course of the season (Fig. 1). The most attractive baits early in the season were those with higher sugar concentrations; amino acid concentrations had no effect. Mid-season foragers, by comparison, were strongly influenced by amino acid concentration, but not by sugar concentration. Late-season foragers were slightly more attracted to sugars than to amino acids. The variables and interaction terms exhibiting significant differences between treatments according to 4-way repeated measure Analysis of Variance are summarized in Table 2a. All the main effects (nest, sugar concentration, amino acid concentration and season) were significant, as well as several of the interaction effects. However, the strongest effect was the seasonal shift in response to amino acids.

Preference for sucrose vs. melezitose. Ants also showed a seasonal shift in response to changing concentrations of sugar mixes (Table 2b). A comparison of ant recruitment to equivalent concentrations (10%) of sucrose vs. melezitose taken from the data collected in Experiment 2, showed a slight but significant preference for sucrose (Fig. 2).

The numerical response of ants to the changes in absolute sugar concentration over the season is also addressed in Experiment 2 and summarized in Fig. 3. Increasing sugar concentration increased bait attractiveness of the artificial honeydew in an additive fashion throughout the season. The strongest response to sugars, evidenced both by the absolute number of workers recruited and the slope of response to concentration, was seen early in the season. This pattern is consistent with the seasonal shifts in sugar response recorded in Experiment 1.

Preference among amino acids. The recruitment of ants to baits containing 1% solutions of single amino acids is shown in Fig. 4, with significant main effects and interaction terms summarized in Table 2c. There was no significant preference for any single amino acid in either mid- or late-season; however, recruitment was significantly stronger to all baits in the mid-season sampling period compared with the late period.


a. Early Season
20
15
10
5
0
Mean No. of Foragers per Nest
High sugar
Low sugar
No sugar
High
Low
No
Amino Acids


b. Midseason
60
55
50
45
40
35
30
25
20
15
10
5
0
Mean No. of Foragers per Nest
High sugar
Low sugar
No sugar
High
Low
No
Amino Acids

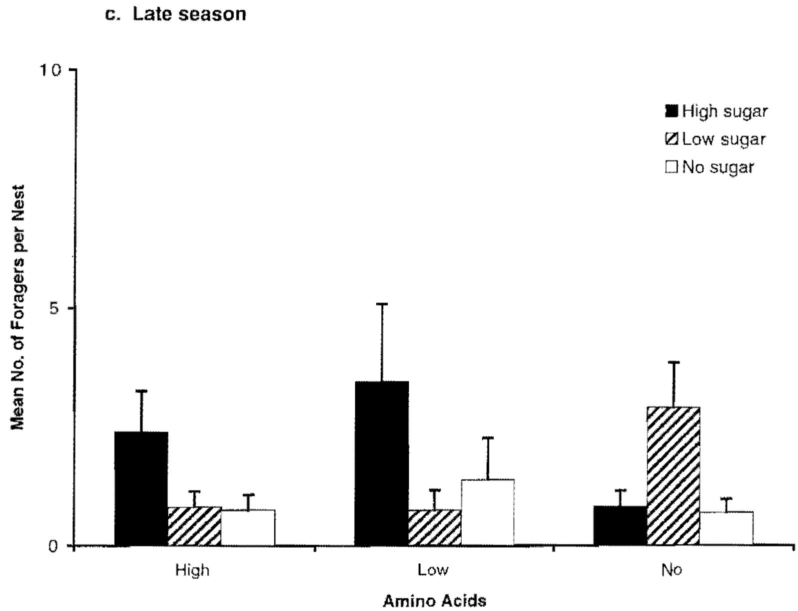


FIG. 1. *Formica exsectoides* forager recruitment response to varying concentrations of sugars and amino acids in artificial honeydew. Mean number of ants per nest (± 1 SE) recruited to baits, based on repeated measure of eight nests (a) early in the season, June 25; (b) mid-season, August 1; and (c) late-season, August 27. Baits were offered as combinations of sugars and amino acids. Sugar levels include 20% and 5% sucrose. Amino acid levels include 4% and 1% mixes of asparagine, glutamine, and serine.

DISCUSSION

Allegheny mound ants show a clear ability to discriminate between sugars and amino acids presented in artificial honeydews in a manner similar to that previously described for tropical species feeding on artificial nectars (Lanza and Krauss 1984, Lanza 1988, 1991). Although nectars and honeydews have traditionally been viewed as sources of carbohydrate, their role as a nitrogen resource may be equally widespread.

In addition to discriminating nutrients, we documented a strong seasonal shift in preference between sugars and amino acids in foraging *F. exsectoides* workers. Sugars were the preferred nutrient early in the season, while amino acids were preferred in mid-season. Very little active foraging occurred in the latter part of August. In the sucrose-melezitose discrimination trials, the degree of recruitment paralleled that seen in sugar-only treatments of the choice tests discussed above. The highest recruitment, 9.8 ants per nest, was seen to a 20% sugar solution (combined sucrose plus melezitose) early season, and the lowest, 0.3 ants per nest, was seen at the low melezitose, no sucrose treatment mid-season. These compare closely with the recruitment re-

Table 2. Variables and interactions exhibiting significant differences between treatments according to four-way repeated-measure analysis of variance on log transformed data.

Main effects & interactions	F (df)	Probability
a. Sugar-amino acid discrimination		
Main effects		
Nest	21.79 (7)	<0.001
Sugar concentration	8.36 (2)	<0.001
Amino acid concentration	58.82 (2)	<0.001
Season	50.72 (2)	<0.001
Interactions		
Nest * Sugar	2.08 (14)	<0.05
Nest * Amino Acid	2.32 (14)	<0.05
Nest * Season	6.03 (14)	<0.001
Sugar * Season	5.72 (4)	<0.001
Amino Acid * Season	33.52 (4)	<0.001
Sugar * Amino Acid * Season	2.51 (8)	<0.05
b. Sucrose-melezitose discrimination		
Main effects		
Nest	8.237 (7)	<0.001
Sucrose present	81.115 (1)	<0.001
Melezitose concentration	12.082 (2)	<0.001
Season	65.412 (2)	<0.001
Interactions		
Nest * sucrose	2.831 (7)	p = 0.01
Season * nest	4.027 (14)	<0.001
Season * sucrose	25.66 (2)	<0.001
Season * melezitose	5.62 (4)	<0.001
Season * nest * sucrose	2.406 (14)	<0.01
c. Individual amino acid discrimination		
Main effect		
Nest	2.34 (7)	<0.05
Season	18.38 (1)	<0.001
Interactions		
Nest * Season	3.40 (7)	<0.01

sponse of ants to the sugar-only components in the first experiment where the highest response was also to the high sugar-early season baits (20% sucrose) (9.8 ants per nest) and the lowest response was to no sugars—mid-season baits (0.6 ants per nest).

Foraging ants showed no preference for any single amino acid when presented with an array of the eight most common honeydew amino acids. They did however show a seasonal pattern of higher activity at single amino acids as well as a stronger preference for amino acid mixtures in the mid season period compared to their response in the late-season experiments.

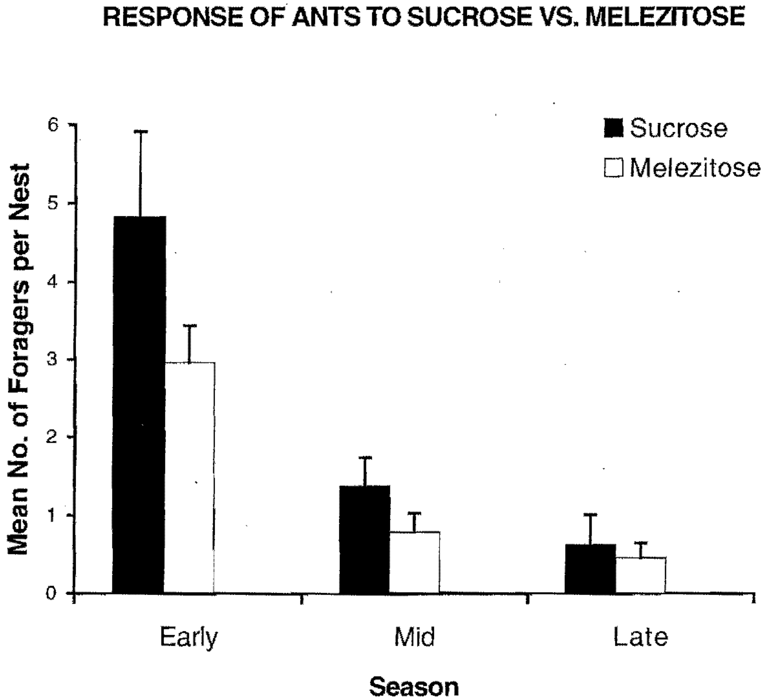


FIG. 2. *Formica exsectoides* forager recruitment response to 10% concentrations of two sugars, sucrose and melezitose. Mean number of ants recruited per bait (± 1 SE), based on repeated measure of eight nests early in the season, June 26; mid-season, July 30; and late-season, August 29. Repeated measure analysis of variance indicated that all main effects were significant. (Nest: $F=4.603$, $df = 7$, $p = 0.001$; sugar type, $F = 6.412$; $df = 1$, $p = 0.01$; Season: $F = 24.033$, $df = 2$, $p < 0.001$) No interaction terms were significant.

The results reported here suggest that the phenomenon of nutrient discrimination by ants feeding on liquid diet items such as nectars and honeydews may be both more widespread and more fine tuned than has previously been recorded. Additionally, the effects of seasonality may play an important role in shifting responses. The pattern demonstrated by *F. exsectoides* foragers is consistent with shifting nutrient demands within the colony. Further work is needed, however, to determine how these shifts relate to patterns of nutrients from natural environmental sources (honeydew and arthropod prey). The marked plasticity of *F. exsectoides* foragers to adjust their efforts, both in terms of individual and colony level responses, to take advantage of shifting patterns of resource availability may be a major factor contributing to the success of this group of arthropods.

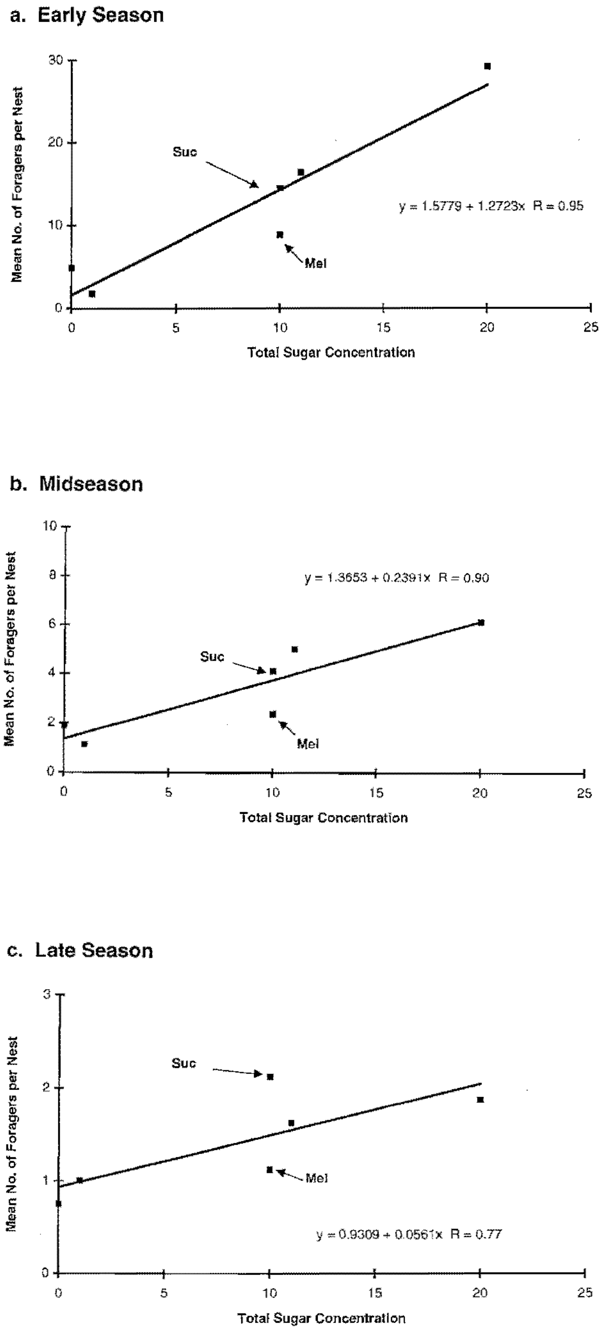


FIG. 3. *Formica exsectoides* forager recruitment response to varying concentrations of two sugars, sucrose and melezitose. Based on repeated measure of workers recruited to baits for eight nests. Sugar combinations, detailed in text, included 10% sucrose, 1% or 10% melezitose. Recruitment responses to equivalent concentrations (10%) of sucrose and melezitose are indicated with arrows. (a) early in the season, June 26; (b) mid-season, July 30; and (c) late-season, August 29.

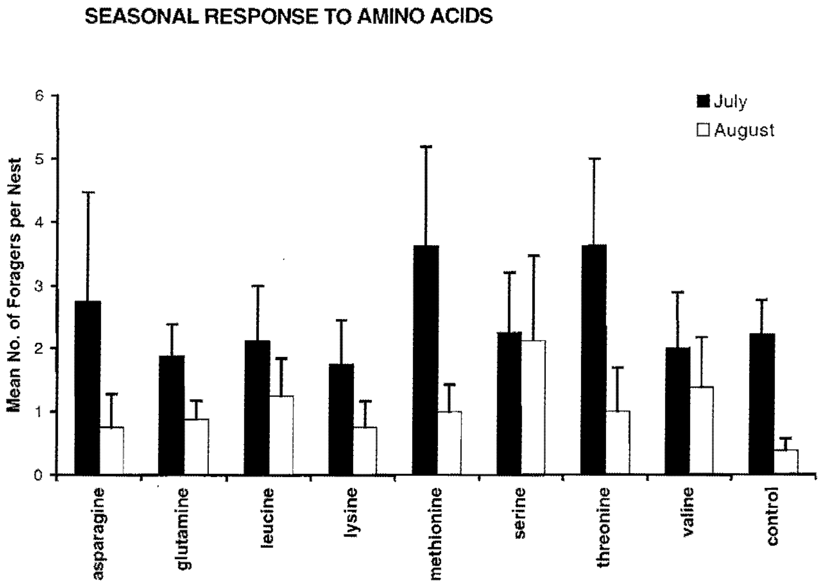


FIG 4. *Formica exsectoides* forager recruitment response to individual amino acids offered at 1% concentration in 10% sucrose solutions, with sucrose control. The mean number of ants (± 1 SE) recruited per nest, based on a repeated measure for 8 nests, is shown for mid-season (July 31) and late-season (August 28).

ACKNOWLEDGMENTS

We thank the USDA Forest Service for permission to work in the Huron-Manistee National Forest. André Francoeur provided identification of the ants, and Chris Dietrich identified the membracids. Helpful comments on an earlier draft of this manuscript were provided by Fred Dyer, Janet Lanza and Jim Miller. This work was supported by USDA Grant # 91-37302-6190 (to C. Bristow).

LITERATURE CITED

Andrews, E. A. 1925a. Growth of ant mounds. Psyche 32:75–87.

Andrews, E. A. 1925b. McCook's ant mounds in Pennsylvania, revisited (Hymen: Formicidae). Entomol. News 36:173–179.

Andrews, E. A. 1929. The mound-building ant, *Formica exsectoides* F., associated with tree-hoppers. Ann. Entomol. Soc. Am. 22: 369–391.

Auclair, J. L. 1963. Aphid feeding and nutrition. Ann. Rev. Entomol. 8: 439–490.

Ayre, G. L. 1958. Notes on insects found in or near nests of *Formica subnitens* Creighton (Hymenoptera: Formicidae) in British Columbia. Ins. Soc. 5:1–7.

Ayre, G. L. 1959. Food habits of *Formica subnitens* Creighton (Hymenoptera: Formicidae) at Westbank, British Columbia. Ins. Soc. 6: 105–114.

Baker, H. G. and I. Baker. 1973. Amino acids in nectar and their evolutionary significance. Nature 241: 543–545.

Baker, H. G. and I. Baker. 1983. A brief historical review of the chemistry of floral nectar, pp. 126–152. *In*: B. Bentley and T. Elias (eds.), The Biology of Nectaries. Columbia University Press, New York. 259 pp.

Bristow, C. M., D. Cappaert, N. J. Campbell and A. Heise. 1992. Nest structure and colony cycle of the Allegheny Mound ant, *Formica exsectoides* Forel (Hymenoptera: Formicidae). Ins. Soc. 39: 385–402.

Campbell, N.J. 1990. An evaluation of *Formica exsectoides* Forel as a potential biological control agent of insect pests of pines. Ph.D. Dissertation, Michigan State University, East Lansing.

Carroll, C. R. and D. H. Jansen. 1973 Ecology of foraging by ants. Ann. Rev. Ecol. Syst. 4:231–247.

Cory, E. N. and E. E. Haviland. 1938. Population studies of *Formica exsectoides* Forel. Ann. Entomol. Soc. Am. 31: 50–57.

DeVries, P. J. and I. Baker. 1989. Butterfly exploitation of an ant-plant mutualism: adding insult to herbivory. Jour. N. Y. Entomol. Soc. 97: 332–340.

Degan, A.A., M. Gersani, Y. Avivi and N. Weisbrot. 1986. Honeydew intake of the weaver ant *Polyrhachis simplex* (Hymenoptera: Formicidae) attending the aphid *Chaitophorous populialbae* (Homoptera: Aphididae). Ins. Soc. 33: 211–215.

Driessen, G. J. J., A. T. van Raalt and G. J. de Bruyn. 1984. Cannibalism in the red wood ant, *Formica polyctena*. Oecologia 63: 13–22.

Duckett, D. P. 1974. Further studies in the ant-aphis relation. Ph.D. Thesis, University of London, London.

Edwards, R. L. 1951. Change in foraging behavior of the garden ant *Lasius niger* L. Entomol. Month. Mag. (London) 87: 280.

Evans, H. C. and D. Leston. 1971. A ponerine ant (Hymenoptera: Formicidae) associated with Homoptera on cocoa in Ghana. Bull. Entomol. Res. 61: 357–362.

Gösswald, K. 1954. On the efficiency of group activity in red woodants. Z. Angew. Zool. 41: 145–185 (in German).

Hölldobler, B. 1971. Recruitment behavior in *Camponotus socius* (Hym. Formicidae). Z. Vergleichen. Physiol. 75: 123–142.

Hölldobler, B. and E. O. Wilson. 1990. The Ants. The Belknap Press of Harvard University Press. Cambridge, MA. 732 pp.

Horstmann, K. 1974. Investigations on food acquisition in woodants (*Formica polyctena* Foerstner) in oak forests, III. Annual balance. Oecologia 15: 187–204 (in German).

Horstmann, K. 1982. The energy balance of woodants (*Formica polyctena* Foerster) in oak forests. Ins. Soc. 29: 402–421 (in German).

Kiss, A. 1981. Melezitose, aphids, and ants. Oikos 37: 382.

Klingauf, F.A. 1987. Feeding, adaptation, and excretion, pp. 225–253. *In*: A. K. Minks and P. Harrewijn (eds.), Aphids: their Biology, Natural Enemies, and Control, vol. A. Elsevier, Amsterdam. 450 pp.

Kloft, W.J. 1953. The importance of some aphids in the ecology of forests. Mitteilung Biol Zentralan Land- und Forstwirtschaft Berlin-Dahlem. 75: 136–140 (in German).

Lanza, J. 1988. Ant preferences for *Passiflora* nectar mimics that contain amino acids. Biotropica 20: 341–344.

Lanza, J. 1991. Response of fire ants (Formicidae, *Solenopsis invicta* and *S geminata*) to artificial nectars with amino acids. Ecol. Entomol. 16: 203–210.

Lanza, J and B. R. Krauss. 1984. Detection of amino acids in artificial nectars by two tropical ants, *Leptothorax* and *Monomorium*. Oecologia 63: 423–425.

Mayfield, H.F. 1992. Kirtland_s Warbler *(Dendroica kirtlandi)*. Birds of North America 19: 1–16.

McCook, H. C. 1877. Mound-making ants of the Alleghenies, their architecture and habits. Trans. Entomol .Soc. Am. 6: 253–296 + plates 1–6.

McIver, J.D. and K.Yandell. 1998. Honeydew harvest in the western thatching ant (Hymenoptera: Formicidae). Amer. Entomol. 44 (1):31–35.

Peterson, C.H. and P. E. Renaud. 1989. Analysis of feeding preference experiments. Oecologia. 80: 82–86.

Pierce, N. 1985. Lycaenid butterflies and ants: selection for nitrogen-fixing and other protein-rich food plants. Am. Nat. 125: 888–895.

Skinner, G.J. 1980. The feeding habits of the wood-ant, *Formica rufa* (Hymenoptera: Formicidae) in limestone woodland in north-west England. Jour. Anim. Ecol. 49: 417–433.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry, 2nd ed. W. H. Freeman, San Francisco. 776 pp.

Sudd, J. H. and M. E. Sudd. 1985. Seasonal changes in the response of wood-ants to sucrose baits. Ecol. Entomol. 10: 89–97.

Way, M.J. 1954. Studies on the association of the ant *Oecophylla longinoda* (Latr.) (Formicidae) with the scale insect *Saissetia zanzibarensis* Williams (Coccidae). Bull. Entomol. Res. 45: 113–134.

Wellenstein, G. 1952. On the nutritional biology of red woodants (*Formica rufa* L.). Z. Pflanzenkrankheit Pflanzenschu.59: 430–451 (in German).

Wheeler, W. M. 1910 Ants: their structure, development and behavior. Columbia University Press, New York. 663 pp.

Wilson, E.O. 1962. Behavior of *Daciton armigerum* (Latreille), with a classification of self-grooming movements in ants. Bull. Mus. Comp. Zool. 127: 401–422.

Wilson, E. O. and T. Eisner. 1957. Quantitative studies of liquid food transmission in ants. Ins. Soc. 4: 157–166.

Zoebelein, G. 1956. Honeydew as food for insects, Part II. Z. Angew. Entomol. 39: 129–167 (in German).