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Nourishment affects colony demographics in the paper wasp *Polistes metricus*

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Abstract. 1. Colony survivorship and numbers of nest cells, pupae, and adult females were monitored throughout the nesting season for a cohort of 78 colonies of the paper wasp *Polistes metricus* Say. Thirty-nine colonies received a twice-weekly nourishment supplement of honey during pre-emergence and early emergence phases of the colony cycle; 39 colonies were unsupplemented controls.

2. Colony survivorship was unaffected by the supplemental nourishment. Loss of colonies to predation differed among three sites but was unaffected by supplementation.

3. Honey-supplemented colonies constructed more nest cells than did control colonies but this effect was not expressed until after supplementation had ceased.

4. Honey-supplemented colonies produced more pupae than did control colonies but the number of adult females at nests did not differ between supplemented and control colonies. Because honey-supplemented colonies had more offspring but fewer of them remained as workers at the nest, honey supplementation led to a lower frequency of workers and corresponding higher frequency of reproductives than in control colonies.

5. In a second year of study, colony survivorship and numbers of nest cells, pupae, and adult females were monitored from late pre-emergence until the end of the nesting season for a cohort of 32 colonies of *Polistes metricus*. In 16 colonies, trophallactic saliva was taken from final-instar larvae on nine dates in the late pre-emergence and early emergence periods; 16 colonies served as controls.

6. Saliva-diminished colonies had lower survivorship, fewer nest cells, fewer pupae, and fewer adult females at the nest than did control colonies.

7. These results show that variation in nourishment in the early to mid phases of the colony cycle can have significant effects on the subsequent colony demographics of *Polistes metricus* paper wasps.

Key words. Caste, demography, nutrition, *Polistes metricus*, social wasp, worker behaviour.

Introduction

Many traits of ecology and life history have been proposed to play roles in the evolution of social wasps (e.g. Evans, 1977; Andersson, 1984; Brockmann, 1984; Strassmann & Queller, 1989; Hunt, 1991, 1994). Hunt (1999) used cladograms of the order Hymenoptera and wasp family Vespidae to sequence first appearances of such traits. Proximity of a trait's appearance to the threshold of vespid eusociality was taken to be one measure of that trait's salience to eusociality. The ordination ascribed high salience to traits such as provision malaxation, inter-adult trophallaxis, and larva–adult trophallaxis that assure proteinaceous nourishment to colony foundresses and engender nutritional inequities among cofoundresses and/or between foundress(es) and first female offspring. For more than a century, these same factors have been argued to be central to vespid social evolution based on inferences from natural history observations (Marchal, 1897; Roubaud, 1916; Hunt, 1991, 1994). The threshold of vespid eusociality is crossed when female offspring differentiate into worker and reproductive castes

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(Hunt, 1991, 1999). O'Donnell (1998) reviewed relevant literature and argued in favour of the proposition that such caste differentiation among offspring is affected by differences in nourishment during larval development (e.g. West-Eberhard, 1987, 1988, 1996). Although high salience can be ascribed to traits involving nourishment in both the evolution of eusocial Vespidae and the ontogeny of eusocial vespid workers, few studies have investigated the roles and consequences of variation in nourishment in the ecology of paper wasps.

In a laboratory study, Mead *et al.* (1994) raised caged colonies of *Polistes dominulus* Christ at restricted and *ad libitum* levels of caterpillar feeding. Colonies receiving *ad libitum* caterpillars had less oophagy, shorter larval development times, lower larval mortality, more pupae, more offspring, and larger final nest size. Miyano (1998) reared single-foundress pre-emergence *Polistes chinensis antennalis* Pérez colonies in laboratory cages at three levels of caterpillar provisioning and found that foundresses with *ad libitum* access to caterpillars laid more eggs, constructed more new nest cells, and aborted fewer brood than did foundresses with restricted access to caterpillars. First-brood offspring of foundresses with *ad libitum* access to caterpillars had larger body sizes and shorter development times. Karsai and Hunt (2002) performed a laboratory study in which solitary foundresses of *Polistes metricus* Say were maintained on three levels of caterpillar nourishment: restricted, *ad libitum*, and *ad libitum* plus daily hand feeding of fourth- and fifth-instar larvae. Female offspring of the restricted treatment were smaller and had longer development times than the other treatments. Female offspring of the *ad libitum* plus daily hand feeding treatment had larger and heavier gasters than the *ad libitum* (control) treatment, and survived a cold test for significantly longer. Karsai and Hunt (2002) found no support for the parental manipulation hypothesis (Alexander, 1974) that foundresses restrict nourishment in order to produce first-brood workers or that they direct limited resources preferentially to one or a few larvae in order to produce workers quickly. Karsai and Hunt (2002) interpreted their results as evidence that higher caterpillar nourishment leads to a higher frequency of gyne (potential queen) production.

In one of few field studies in this area, Klahn (1981) used at-nest feeders to provide a liquid dietary supplement to adult *Polistes fuscatus* L. in nest boxes. Responses to supplementation included greater numbers of nest cells and offspring, higher larval survivorship, shorter larval development time, and larger body size among mid- to late-season offspring. Klahn (1981) suggested that naturally occurring variation in colony success among years and sites indicates that food availability may limit colony growth. Rossi and Hunt (1988) manipulated nourishment of single-foundress colonies of *Polistes metricus* in a field experiment by placing small droplets of slightly dilute honeybee honey twice weekly into nest cells of treatment colonies during the pre-emergence and early emergence phases of the colony cycle. Compared with controls, there was no difference in nest size at the early emergence collection date, but nests receiving the honey supplementation produced first offspring earlier than did controls. Offspring of supplemented and control colonies did not differ in size, as measured by wing length, but offspring of supplemented colonies had significantly higher fat content than either control offspring or any of the foundresses. Rossi and Hunt (1988) interpreted their results as evidence that colonies are normally food limited during the pre-emergence phase of the colony cycle and proposed that the behaviours and potential reproductive activities of offspring from honey-supplemented colonies would probably have differed from those of unsupplemented colonies.

Given the results of Klahn (1981), Rossi and Hunt (1988), Mead *et al.* (1994), Miyano (1998), and Karsai and Hunt (2002), it can be assumed that offspring of nourishment-manipulated colonies will develop differently in response to nourishment manipulations, and demographic variables will reflect colony-level consequences that follow from those developmental differences. The work reported here was designed to expand the understanding of the role of nourishment in paper wasp ecology by performing nutritional manipulations in the field during early and mid phases of the colony cycle and assessing colony-level consequences in a species for which individual-level consequences of nourishment manipulations are known, thus bridging the gap from individual to colony levels. Year one of the study was a replication of the honey supplementation protocol of Rossi and Hunt (1988), but with monitoring of colony demographic variables rather than individual development variables. In the second year of the study, a novel experiment was performed to diminish nourishment by removing trophallactic saliva from fifth-instar larvae and monitoring colony demographic reponse.

Materials and methods

Taxon and study site

Polistes metricus Say, the most common paper wasp in the St Louis, Missouri, area of the U.S.A., is typically a single-foundress (haplometrotic) paper wasp, and all colonies in this study had a single foundress/queen. The study was carried out at the Missouri Botanical Garden's Shaw Nature Reserve, $\approx$60 km SW of St Louis, 38°29′23′N, 90°49′00′W. The Reserve of $\approx$1000 ha includes restored tallgrass prairie, deciduous forests, and wetland areas. Second-growth deciduous woodlands, pastures, and low-density residential areas surround the site.

Data collection

Nest boxes, used to house the wasps studied in the experiment, were put in place during mid-March 1994 (year 1) and 1995 (year 2). Each box had a 13 × 13 cm plywood top and four 13 × 15 cm fibreboard sides; bottoms were open. A box was mounted with wire atop a 2 m piece of concrete-

reinforcing bar driven ≈0.3 m into the ground. Boxes were arrayed at 10-m intervals in three open fields containing mixed grasses and forbs and bounded by woodlands. The sites differed in maintenance: one site was burned in late winter and not mowed subsequently; the two other sites were not burned but were mowed occasionally during the spring and summer. Consequently, during mid and late summer, vegetation was considerably taller and more dense at the burned, unmowed site.

Polistes metricus will utilise boxes as nesting sites with no experimenter involvement. Several foundresses were already present when boxes were first checked on 19 April of year 1. One of two treatment categories was assigned haphazardly to nests at each site, with care taken to assure that treatments were not clumped spatially and that equal numbers of the two treatments were present at each site. Late-founding foundresses were added to the sample until the last founding on 27 April. In year 2, treatment was assigned to colonies in early June in the same manner as in year 1.

In year 1, treatment nests were supplemented with honeybee honey using the protocol of Rossi and Hunt (1988). Supplementation began on 3 May and was performed twice weekly for 8 weeks until 1 July. The honey was diluted with water 3:1 v:v so that it would flow through a 25 µl syringe, and drops of the honey solution were applied to the inner walls of nest cells. The points of the syringes were rounded in order not to damage the nest or its occupants; control colonies were probed with an empty, clean syringe to control for disturbance effects. Each nest received one 5 µl drop per two cells; i.e. a nest with 20 cells would receive 10 drops, each 5 µl in size. The size, number, and placement of added honey droplets were similar to naturally occurring honey droplets that are commonly stored in nests by pre-emergence foundresses (Hunt *et al.*, 1998). Honey on nest cell walls can be consumed by adults but not by the developing larvae (Hunt *et al.*, 1998). The maximum total amount of experimental supplementation was modest, being only ≈0.5 ml per nest over the 8-week treatment period.

In year 2, nourishment was diminished by taking trophallactic saliva from each fifth-instar larva beginning on 6 June, the earliest date that all colonies contained fifth-instar larvae. Treatments were administered twice a week for 3 weeks and once a week for 3 further weeks before cessation on 11 July. Saliva was collected by using a 50 µl micropipette to touch a larva's mouthparts; saliva is commonly released by social wasp larvae in response to such touching (Hunt *et al.*, 1982, 1987). The touching was continued until a larva ceased to give saliva. Amounts of saliva collected per larva were from < 5 µl to 20 µl. Control colonies were disturbed similarly to treatment colonies except that larvae of control colonies were not touched with a micropipette.

On each visit to every colony, the numbers of nest cells, pupal cocoons, and adult females, including the queen, present at the nest were recorded. Boxes were removed briefly from poles, if necessary, to ensure accurate recording of nest contents in year 1, and boxes were always removed for treatment and data recording in year 2. In both years, foundresses were marked with paint dots on the mesonotum before the experiment began. Foundresses were sometimes allowed to remain on the nest during pre-emergence treatment procedures and data recording, but once offspring were present all wasps were removed prior to treatment and data recording, by rapping sharply on top of the nest box and dislodging the wasps into an insect net below. In year 1, all female offspring were marked with paint dots on the mesonotum for individual recognition, using various colours and a colour-number code. Offspring in year 2 were not marked.

Statistical analysis

Colony survivorship values were calculated for treatment and control colonies, and survivorship differences for year 1 were then tested using the Lifereg Procedure (SAS, 1990) and differences for year 2 were tested using JMP (SAS Institute, Inc., Cary, North Carolina). These analyses yield the probability of obtaining, by chance alone, a χ^2 value greater than the computed value if there is no difference in survival between groups (Pyke & Thompson, 1986). For analysis of year 1 numbers of nest cells, pupal cocoons, and adult females, data were first arranged so that the ordinate showed the number of nest cells at the time that treatments were assigned in April and all values for the response variable were on the abscissa, and both treatment and control data were then fitted with linear regressions. Insignificant difference between slopes of the regressions for the two groups necessitated ANCOVA, with initial nest size as the covariate. In cases of significant difference between slopes of the regressions, repeated measures ANOVA was used, in which treatment and site were fixed effects and time was a continuous effect. Repeated measures methods were appropriate because each sample was not independent of samples obtained on previous sampling dates and because the analysis would reveal any treatment and site effects over time. Year 2 data had insufficient residual degrees of freedom for repeated measures tests. Data for colony response variables were square-root transformed. Statistical tests of colony response data for year 1 were performed using SAS (1990); tests for year 2 were performed using SPSS version 10.0 for Windows (SPSS Inc., Chicago, Illinois).

Results

Survivorship

The number of colonies surviving over time in year 1 is shown in Fig. 1. There was no difference in colony survivorship as a consequence of honey supplementation [$\chi^2 = 1.03$, 1 d.f. $(P > \chi^2) = 0.24$]. Survivorship differed among the three sites [$\chi^2 = 67.48$, 2 d.f. $(P > \chi^2) = 0.0001$] but this was independent of treatment: colonies at the unmowed site had lower survivorship than those at the two mowed sites. Although over 600 offspring were marked individually

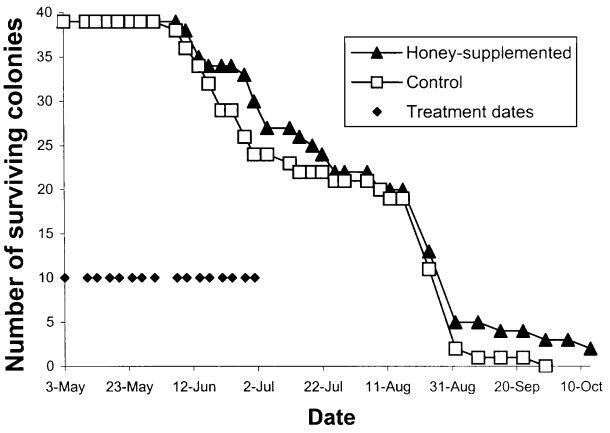

Fig. 1. Number of surviving colonies over time for a cohort that began with 39 saliva-diminished and 39 control colonies of *Polistes metricus* in 1994. Treatment colonies received honey droplets as food supplementation twice weekly from 3 May to 1 July on dates shown by the symbols at Y = 10.

in year 1, only two marked wasps were recovered in year 2, both of which had lost portions of their marks and were unidentifiable.

The number of colonies surviving over time in year 2 is shown in Fig. 2. Saliva-diminished colonies had lower survivorship than did control colonies [$\chi^2 = 4.079$, 1 d.f. ($P > \chi^2$) = 0.043] due primarily to abandonment by the foundress during the first 2 weeks of the treatment period. Only two saliva-diminished colonies (vs. six control colonies) survived into August, and one saliva-diminished colony (vs. five control colonies) survived into September. By the start date of the experiment, too few colonies remained at the unmowed site to be included in the experiment, so only colonies at the two mowed sites were used. Between-site differences in colony survival due to predation and unrelated to treatment were thus apparent without analysis.

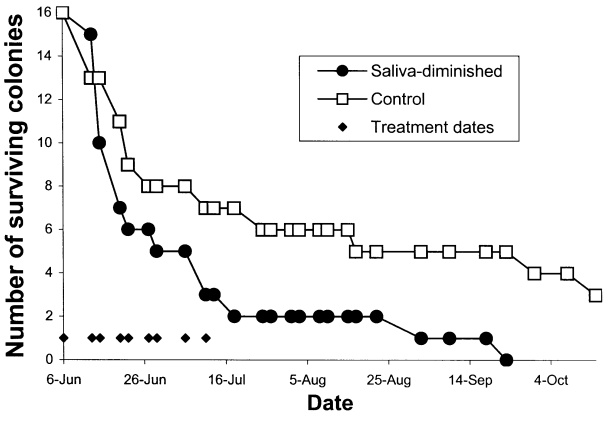

Fig. 2. Number of surviving colonies over time for a cohort that began with 16 saliva-diminished and 16 control colonies of *Polistes metricus* in 1995. Treatment colonies had trophallactic saliva taken from fifth-instar larvae on dates from 6 June to 11 July shown by the symbols at Y = 1.

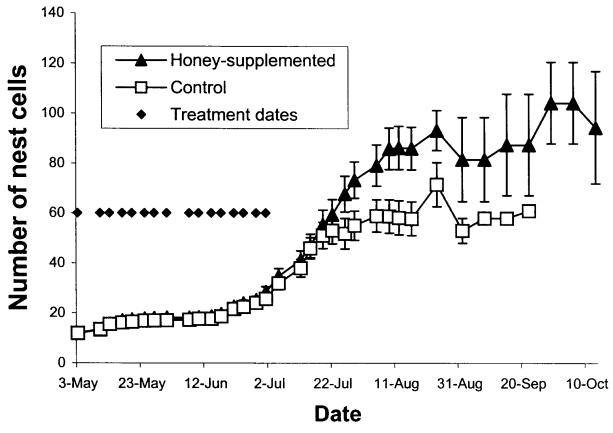

Fig. 3. Mean ± SE of the number of cells per nest in honey-supplemented and control colonies of *Polistes metricus* in 1994. Sample sizes at each data point are the values of Fig. 1. Decreases in mean number of cells reflect the termination of nests with high numbers of cells as the sample size diminished sharply in mid August (Fig. 1). Treatment colonies received honey droplets as food supplementation twice weekly from 3 May until 1 July on dates shown by the symbols at Y = 60.

Nest size

In year 1, colonies receiving honey supplementation achieved a greater number of cells per nest than did control colonies (ANOVA $F = 4.14$, 1 d.f., $P < 0.05$; Fig. 3). There was no size difference at the end of supplementation on 1 July (Fig. 3); instead, colonies diverged in size after the honey supplementation ended. Time was a significant factor in the repeated measures test ($F = 91.10$, 25 d.f., $P < 0.001$),

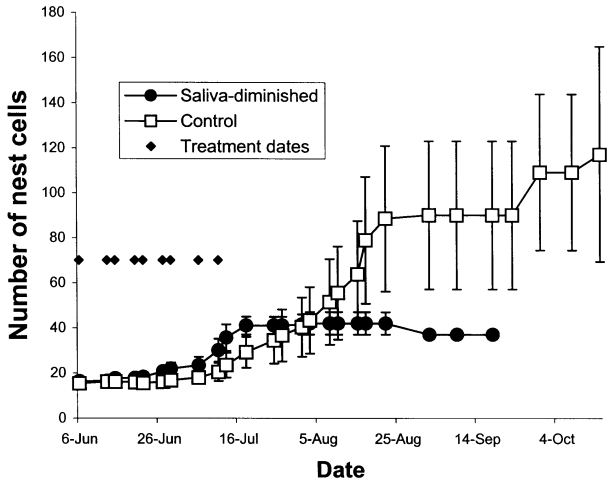

Fig. 4. Mean ± SE of the number of cells per nest in saliva-diminished and control colonies of *Polistes metricus* in 1995. Sample sizes at each data point are the values of Fig. 2. The decrease in mean number of cells for saliva-diminished colonies reflects the sample size decrease in mid August (Fig. 1). Treatment colonies had trophallactic saliva taken from fifth-instar larvae on dates from 6 June to 11 July shown by the symbols at Y = 70.

which confirms only that nests became larger as the season progressed. There were no significant interaction effects of time × treatment, time × location, or time × treatment × location.

In year 2, saliva-diminished nests reached smaller sizes than controls (ANOVA $F = 23.057$, 1 d.f., $P < 0.05$; Fig. 4). In fact, 14 of 16 saliva-diminished colonies did not increase in size after treatment was initiated, and the two nests that did increase in cell number reached only modest size.

Pupal cocoons

Analysis of pupal cocoon numbers in year 1 revealed no treatment difference between honey-supplemented and control colonies (ANCOVA $F = 0.37$, 1 d.f., $P =$ NS; Fig. 5). Because honey supplementation has been shown to affect the development of offspring (Rossi & Hunt, 1988), differences in offspring between treatments might promote demographic consequences that could not occur before offspring emergence. Therefore, a second analysis was performed using a data set truncated to begin on 14 June, which was the first sampling date on which an offspring appeared. The between-treatment difference for the truncated data set was not significant (ANCOVA $F = 3.80$, 1 d.f., $P = 0.059$), although the clearly greater numbers of pupae in honey-supplemented nests in late July and early August (Fig. 5) are evidence of a biologically meaningful treatment effect. Honey-supplemented colonies produced more pupae in late July and early August. Between-subjects repeated measures ANOVA for the full data set revealed significant effects of time ($F = 33.05$, 27 d.f., $P < 0.001$) and time × location ($F = 3.14$, 54 d.f., $P < 0.05$).

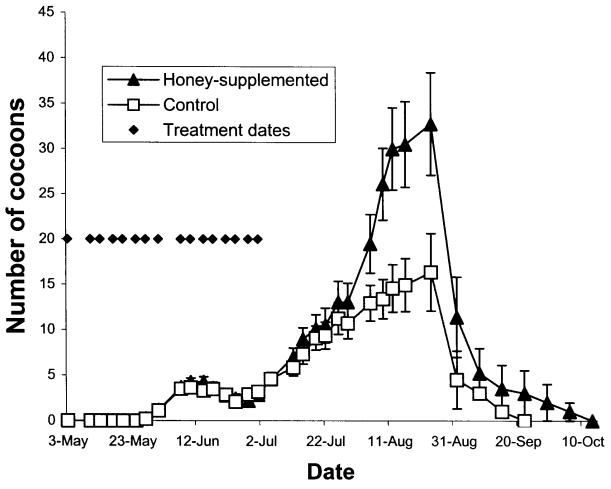

Fig. 5. Mean ± SE of the number of pupae per colony in honey-supplemented and control colonies of *Polistes metricus* in 1994. Sample sizes at each data point are the values of Fig. 1. Treatment colonies received honey droplets as food supplementation twice weekly from 3 May until 1 July on dates shown by the symbols at Y = 20.

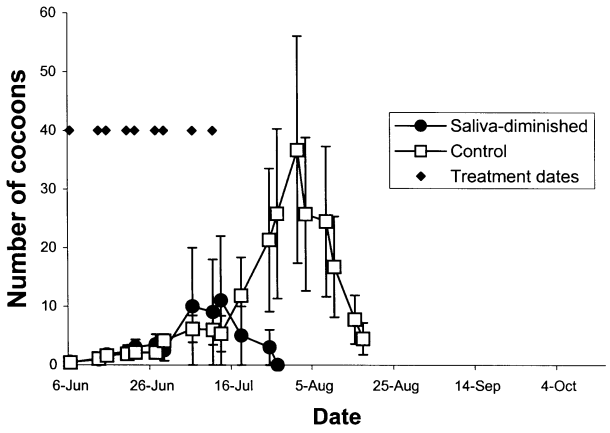

Fig. 6. Mean ± SE of number of pupae per colony for saliva-diminished and control colonies of *Polistes metricus* in 1995. Sample sizes at each data point are the values of Fig. 2. Treatment colonies had trophallactic saliva taken from fifth-instar larvae on dates from 6 June to 11 July shown by the symbols at Y = 40.

In year 2, saliva-diminished nests produced fewer pupae per nest than did control nests (ANOVA $F = 14.236$, 1 d.f., $P < 0.05$; Fig. 6). Saliva-diminished nests produced no pupae at all in August.

Offspring

In year 1, there was no difference in the number of adult females present, including the queen, for honey-supplemented vs. control nests (ANCOVA $F = 0.08$, 1 d.f., $P =$ NS; Fig. 7). This data set was also truncated to begin on 14 June because any effects on this variable would not be expected until after the emergence of the first offspring; ANCOVA for

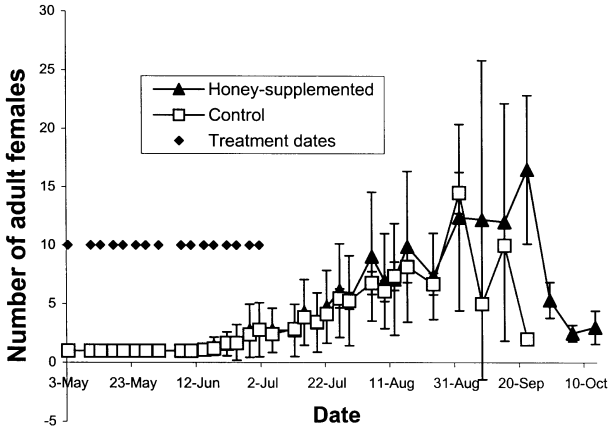

Fig. 7. Mean ± SE of the number of adult females present at the nest for honey-supplemented and control colonies of *Polistes metricus* in 1994. Sample sizes at each data point are the values of Fig. 1. Treatment colonies received honey droplets as food supplementation twice weekly from 3 May until 1 July on dates shown by the symbols at Y = 10.

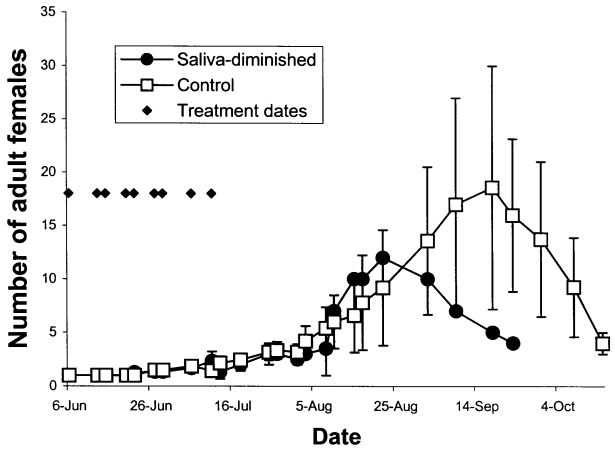

Fig. 8. Mean ± SE of the number of adult females present at the nest for saliva-diminished and control colonies of *Polistes metricus* in 1995. Sample sizes at each data point are the values of Fig. 2. Treatment colonies had trophallactic saliva taken from fifth-instar larvae on dates from 6 June to 11 July shown by the symbols at Y = 18.

the truncated data set confirmed no difference ($F = 1.06$, 1 d.f., P = NS). ANOVA of between-subjects effects for the honey supplementation showed a difference of female offspring present over time ($F = 21.52$, 27 d.f., $P < 0.001$) as well as a significant interaction of time × location ($F = 2.79$, 54 d.f., $P = 0.005$). Offspring first appeared on three honey-supplemented and three control colonies on 14 June. By 17 June, offspring were present in 11 of 34 honey-supplemented colonies vs. six of 31 control colonies, but that difference was not significant ($\chi^2 = 1.418$, 1 d.f., P = NS).

In year 2, a treatment effect on mean number of adult wasps present, including the queen, was not significant (ANOVA, $F = 15.927$, 1 d.f., $P = 0.057$), although numbers of wasps present at honey-supplemented nests exceeded controls in late August and September (Fig. 8).

Discussion

Year 1 survivorship results correspond to those of Klahn (1981), who found no difference in colony survivorship attributable to supplemental feeding. The significant between-site differences in colony survivorship in the present study reflect a more suitable habitat at the unmowed site for predators such as raccoons, deer mice, and birds. No predation was observed but its occurrence was often verified by damaged nests on the ground at the base of the nest box pole. Placing screen mesh over nest box openings in a 1998 study at the same site resulted in lengthy survival of many colonies (J. H. Hunt, unpublished), confirming the proposed role for vertebrate predators in colony loss. Predation also occurred in year 2, but the major source of failure in the saliva-diminished colonies was abandonment by the queen during the first 2 weeks of treatment.

Rossi and Hunt (1988) found no difference in nest size in early July as a consequence of supplementation, and there was no significant difference in colony size between supplemented and control colonies at that same time in the year 1 experiment reported here. Honey-supplemented colonies subsequently reached larger nest sizes than did control colonies but this response occurred after the end of the treatment period, i.e. the late emergence phase colony-level demographic difference was in response to nourishment difference that occurred primarily during the pre-emergence and early emergence phases of the colony cycle. This result confirms the finding by Klahn (1981) that 'food supplementation during [the pre-worker] period can increase colony reproduction later'. Rossi and Hunt (1988) also found that honey-supplemented colonies produced first offspring significantly earlier than did control colonies. Although there was a similar trend in the data reported here, the difference was not significant.

The number of cells in a paper wasp nest is typically a positive correlate of the number of females present [e.g. Hermann and Chao (1984); using *Mischocyttarus mexicanus cubicola* (de Saussure)]. In the honey supplementation experiment, however, larger nest sizes were achieved without a larger number of attendant wasps, indicating that nest size may reflect variables other than, or in addition to, the number of wasps present. Mead *et al.* (1994) and Miyano (1998) both documented lower brood abortion under *ad libitum* caterpillar nourishment; Miyano also recorded a higher oviposition rate by the queen. Either of these factors could foster higher rates of new cell initiation, and both Mead *et al.* and Miyano reported larger nest sizes for higher nourishment colonies. Karsai *et al.* (1996) modelled nest size increase and final nest size of *Polistes dominulus* using only queen oviposition rate, larval development time, and oophagy rate, but not the number of wasps present, as model inputs. Although data on brood abortion and oviposition were not collected, the nest size data suggest that reduced brood abortion and/or increased oviposition rate could be responses to honey supplementation similar in kind and consequence to responses revealed by the previously published caterpillar supplementation studies and by the Karsai *et al.* model.

Honey-supplemented colonies produced more pupae than did control colonies, but the number of adult females present at nests did not differ due to treatment. This means that a lower frequency of emerged adult females remained at the nest in honey-supplementation colonies than in control colonies, which is evidence that early-season offspring with high fat levels (Rossi & Hunt, 1988) pursued roles other than worker roles at higher frequencies than did early-season offspring with lower fat levels. Thus, the honey-supplemented colonies produced a higher frequency of reproductive offspring. The apparent lower frequency of workers and corresponding higher frequency of reproductives among the brood of the honey-supplemented colonies support the argument of West-Eberhard (1987, 1988, 1996), Hunt (1991, 1994), and O'Donnell (1998) that caste

(worker/gyne) differentiation in *Polistes* reflects nutrition-based differences during larval development.

Possible alternatives to working include founding new colonies during the season of emergence (Page *et al*., 1989; Hunt, 1991) and entering early quiescence (Reeve *et al*., 1998). *Polistes* gynes in seasonal environments spend the unfavourable season in quiescence before nest founding at the onset of the following favourable season (Hunt *et al*., 1999). During year 2 of the study, two female *P. metricus* of unknown provenance sat adjacent to one another in an otherwise unoccupied nest box from late July until early September. They seemed in every way to be in early quiescence.

Larvae of saliva-diminished colonies were reduced visibly in vigour after only two treatments, and foundresses began to disappear from nests after two treatments. Foundresses may have simply abandoned their nests, or foundresses of saliva-diminished nests may have been forced to visit flowers to gather nectar for self-nourishment (Hunt *et al*., 1982), where they faced higher rates of predation by predators such as spiders and robber flies. The need to forage for self-maintenance could also have resulted in reduced larval provisioning, leading to reduced vigour of the larvae.

Polistes metricus colonies at the study site typically produce exclusively reproductive offspring beginning in mid July and continuing into September. Only four saliva-diminished colonies produced any offspring, and only two saliva-diminished colonies (vs. six control colonies) survived into August and one saliva-diminished colony (vs. five control colonies) survived into September. It thus seems likely that the saliva-diminished colonies produced few, if any, reproductive offspring. This striking result lends support to a long-ago proposed central role for larval trophallactic saliva in the cohesion of the colony (Roubaud, 1916) and, therefore, the success of the colony. The saliva is nutrient-rich (Ikan & Ishay, 1966; Maschwitz, 1966; Hunt *et al*., 1982; see also Hunt, 1988) and can serve as nourishment to the adults that drink it (Ishay & Ikan, 1968; Spradbery, 1973). A significant colony-level role for larval trophallactic saliva now seems certain.

In both years of this study, higher values for final colony size, numbers of pupae, and colony survivorship were recorded for colonies with relatively higher nourishment: supplemented colonies in year 1 and control colonies in year 2. The apparent fitness consequences strongly support a significant role for nourishment variables in the reproductive success of *Polistes metricus* colonies. Honey supplementation resulted in a greater number of offspring (measured as pupal cocoons) but a lower frequency of workers, which would have remained and been counted at the nest. Thus honey-supplemented nests produced both a greater number and higher frequency of reproductive offspring than did control nests. Diminishment of larval saliva resulted in the production of few total offspring and probably no reproductive offspring at all. These results show that nourishment can be a significant component of natural selective forces acting on colony demographics and fitness outcomes in *Polistes metricus*.

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