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Queen mandibular gland pheromone influences worker honey bee (*Apis mellifera* L.) foraging ontogeny and juvenile hormone titers

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Abstract

Synthetic queen mandibular gland pheromone (QMP) was applied to honey bee colonies to test two hypotheses: (i) QMP acts like a primer pheromone in the regulation of age-related division of labor, and (ii) this primer effect, if present, varies in three strains of workers that show genetically-based differences in their retinue attraction response to QMP (a pheromone releaser effect). Strains of workers that were high, or low in their response to QMP in a laboratory bioassay, as well as unselected 'wild-type' workers, were fostered in queenright colonies with or without supplemental QMP. Effects of QMP on foraging ontogeny and juvenile hormone III (JH) blood titers in worker honey bees were measured. Bees in QMP-supplemented colonies showed significant delays in foraging ontogeny, and foraging activity was reduced. They also had significantly lower JH titers, although the titer curves were somewhat atypical. There were no differences in foraging ontogeny or JH titers among the three strains. We conclude that (i) QMP can delay the ontogeny of foraging by some mechanism that suppresses JH production, (ii) this QMP primer response is independent of the retinue releaser response, and (iii) QMP can play an important role in regulating division of labour.

Keywords: Apis mellifera; Queen mandibular gland pheromone; Division of labor; Juvenile hormone; Social insects

1. Introduction

The dynamic organization of division of labor is an important attribute for the honey bee (*Apis mellifera* L.) and other highly eusocial insects. A primary advantage of eusocial life is that all labor may be performed concurrently instead of sequentially (Oster and Wilson, 1978). In most of the ants, and many social wasps and bees, workers are differentiated into behavioral groups, an effect of age-related change known as temporal polyethism (Robinson, 1992; Hölldobler and Wilson, 1990; Jeanne, 1991). The adult workers usually progress from tasks performed within to those performed outside the nest.

The honey bee behavioral catalogue is lengthy but all individuals do not perform every possible task at any given age (Robinson, 1992; Winston, 1987). Rather the labor schedule reflects a compromise between task performance and location efficiencies (Seeley, 1982). Tasks have been divided among four basic categories; (i) cell cleaning and capping, (ii) brood and queen tending, (iii) comb building, cleaning and food handling, and (iv) outside tasks such as ventilating, guarding and foraging (Seeley, 1982). The nearly universal characteristic of progression from within- to outside-nest tasks is believed to be adaptive because the most hazardous tasks are delegated to the latter part of a worker's life (Oster and Wilson, 1978). Workers undergo physiological changes with age in such a way that their response threshold to various environmental stimuli changes (reviewed by Robinson, 1992). These behavioral changes are associated with shifts in endocrine gland activity.

Juvenile hormone (JH) titers increase as honey bee workers age (Fluri et al., 1982; Huang et al., 1991, 1994), and treatment with JH mimic, JH, or JH analog will induce precocious foraging (Sasagawa et al., 1989; Robinson and Ratnieks, 1987; Robinson, 1985, 1987; Fluri et al., 1982; Jaycox, 1976; Jaycox et al., 1974). Individual behavioral development may be delayed,

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accelerated or reversed in response to changing internal and external colony environment (reviewed by Robinson, 1992). Accelerated behavioral development (precocious foraging) may be induced as a response to a lack of older forager age bees, retarded behavioral development (overage nurse bees) may be a response to a lack of young bees, and behavioral reversion (from foraging to nursing behavior) may be induced in response to a severe deficit of young bees (Huang and Robinson, 1992; Robinson, 1992; Robinson et al., 1992; Page et al., 1989). Accelerated development is associated with a precocious rise in JH titers, retarded development with an extended duration of low JH titers, and behavioral reversion with a decrease in JH titers (Robinson et al., 1989, 1992). Colony age demography also has a key role in mediating the rate of behavioral development (Huang and Robinson, 1992). The rate of behavioral development is inversely related to the proportion of old bees in a colony (Huang and Robinson, 1996).

The regulation of age-related division of labor is complex and likely involves multiple factors. One possible integrative mechanism for temporal polyethism is queen pheromone. To date, demonstrated queen effects on division of labor have been limited to genetic contributions to worker genotype that influence pollen hoarding (Hellmich et al., 1985; Page et al., 1989), and defensive behavior (Guzmán-Novoa and Page, 1994). Despite known primer pheromone effects of queen mandibular gland pheromone on workers, such as the suppression of reproductive queen rearing and JH biosynthesis (Pettis et al., 1995; Kaatz et al., 1992; Winston and Slessor, 1992), division of labor influences have not been explored.

QMP also elicits a releaser-type behavioral response called retinue behavior, characterized by workers surrounding the queen or a QMP-dosed lure while antennating and removing QMP from the surface with their antennae, proboscides, and forelegs (Slessor et al., 1988, 1990; Kaminski et al., 1990). There is a genetic component to variability in worker retinue response to QMP, and two strains of bees that differ in this trait were selected to examine the role of QMP in colony-level functioning and individual bee behavior (Pankiw et al., 1994, 1995). One strain was highly responsive to QMP in a retinue bioassay (high strain), and another was comparatively unresponsive (low strain) (Pankiw et al., 1994).

The main objective of our study was to examine the influence of QMP on worker foraging ontogeny and JH titers. Extracts of queen mandibular gland pheromone (QMP), and its major component 9-ODA (2-keto-(E)-2-decenoic acid) inhibit the rate of JH biosynthesis in vitro (Kaatz et al., 1992), which could induce a JH-based delay in worker foraging ontogeny. We were interested in confirming and extending these results by measuring both behavioral ontogeny and JH titers in bees living in larger, more typical, colonies. Our primary hypothesis was that workers reared in nest environments with supplemental QMP would display lower JH titers and later foraging ontogeny than in untreated colonies. In addition, we tested for possible genetic variability for the influence of QMP on foraging and JH titers. High and low strain workers were used to determine whether selection based on the retinue response to QMP conferred a correlated response to the proposed influence of QMP on foraging ontogeny and JH titers. Finally, we also determined whether supplemental QMP affect the activity of foragers.

2. Methods

2.1. Bees

Workers that were highly responsive (high strain) or non-responsive (low strain) to QMP were obtained from the third generation of a selection program (Pankiw et al., 1994). Each strain has three sublines to minimize inbreeding within which individual queens were mated according to a closed mating design (Laidlaw and Page, 1986). In this design each queen has a 'hermaphroditic' parent (contributing eggs, and male gametes via her haploid sons), and is one in turn. Queens from colonies with the highest and lowest retinue responses to QMP were chosen to be parents of the next generation. Each queen was instrumentally inseminated with the semen from a single drone (one drone per queen). Workers from each high and low QMP-responding colony were super-sisters with an average relatedness of 0.75 (Laidlaw and Page, 1986).

'Wild-type' refers to Simon Fraser University stock colonies headed by open mated queens, therefore worker relatedness was variable. Retinue behavior for all strain sources were measured two days prior to initiating this study, and assigned to control or QMP-treated colonies. Means and standard errors of the responses were as follows: $X_{\text{High}} = 37.5 \pm 3.4$, $X_{\text{Low}} = 6.6 \pm 1.1$, $X_{\text{Wild}} = 17.8 \pm 1.5$ (see Pankiw et al., 1994 for retinue bioassay methodology).

Bees of known age were obtained by removing combs containing developing pupae from colonies of high-, low- and wild-type strains. The combs were placed in an incubator maintained at 33°C for a 24 h emergence period. The newly emerging adults (N = 100 per strain per colony: grand total of 3600) were marked with colored, numbered tags, a different color for each of the three strains. These bees were used for behavioral analyses. For JH analyses an additional 200 per strain per colony (N = 7200) of newly emerged workers were paint-marked with different colors to designate strain. Sampling bees for JH (a destructive process) would reduce the number of tagged workers being observed for forag-

ing ontogeny, therefore the two marking methods were used, number tagging for foraging ontogeny and activity, and paint marking for JH titer measurement.

All marked workers were introduced to 6 QMP treated and 6 control 4-frame colonies equalized for adult numbers (approx. 10 000), brood area (2 frames), and food stores (2 frames). The experiment was terminated when all tagged workers had foraged or could no longer be found in the colony. Colony assignment for QMP- or control treatment was determined randomly.

2.2. Treatments

QMP-treatment colonies received daily a glass microscope slide loaded with one queen equivalent of QMP, centrally placed on the wax comb frame tops of each colony. A queen equivalent of QMP contains 250 μg 9-keto-(E)-2-decenoic acid (9-ODA), 150 μg 9-hydroxy-(E)-2-decenoic acid, 20 μg methyl p-hydroxybenzoate, and 2 μg 4-hydroxy-3-methoxyphenylethanol (Slessor et al., 1990) in 10 μl isopropanol. The amount of 9-ODA found in a queen at any one time ranges from 0.2 to 1.8 times the queen equivalent used here, so the added amount of QMP was well within what could be expected to be naturally available to colonies (Pankiw et al., 1996). Control colonies received glass microscope slides daily loaded with 10 μl 2-propanol. Colony assignment for QMP- or control treatments was determined randomly.

2.3. Behavioral measurements

Entrance counts were conducted to measure the activity of tagged and untagged foragers. Hive entrances were partially blocked with wide mesh screen to slow forager entry into the colony, allowing the observer to distinguish the identity of each forager. Measurements were taken for 5-min intervals, four times daily, twice in the morning and twice in the afternoon, beginning 5 days after worker introductions. Tag numbers were called out and tape recorded or written down by another person. Observations were conducted blindly with respect to treatment and strain.

Colony entrances were blocked completely twice daily, once in the morning and once in the afternoon for 15 min after entrance counts were completed. The identity of the tagged workers at blocked entrances was recorded. The date of the first foraging trip was considered to be the date that a marked worker was first seen outside the hive during entrance observations. While a small number of these first flights may have been orientation rather than foraging flights, previous studies suggest that error because of this factor is insignificant (Winston and Katz, 1982; Winston and Punnett, 1982).

Census data were collected to correct for differential mortality for the purposes of statistical analysis. Censuses were conducted on the 1st, 15th and 35th day after worker introductions to determine whether possible treatment or strain differences were based on differential mortality among the focal bees. Censuses were conducted by scanning each face of each frame, as well as the interior of the hive body. The identification of tagged workers was recorded.

2.4. Sampling scheme for JH titer determination

One worker from each strain (high, low and wild-type) was collected randomly from each frame face of the four frames in the hive. A total of eight workers per strain per colony per treatment was collected and placed in a Ziploc® plastic bag, and stored temporarily in a container of ice. In the laboratory, five workers per strain per colony per treatment were used to obtain blood (hemolymph) samples. The additional three workers served as back-up workers in the event that a proper sample of blood could not be obtained. The sampling regime, 0, 7, 14, 21 and 28 days after emergence, was chosen to follow temporal polyethic progression from nursing to older forager tasks, as established in previous studies (Robinson, 1992). Sampling was performed blind with respect to behavior. This was because we wanted to have no assumptions about whether individual bees, or bees in different treatment groups were at the same stage of behavioral development - this issue is central to the hypothesis being tested. Collections took place prior to 10 a.m. to ensure against excluding the collection of any workers that may be outside the nest; during the course of this experiment no foraging took place before 10 a.m. The summer weather pattern during the course of this experiment consisted of rainy conditions interspersed with brief warm sunny periods and cool nights (average night temp. 8°C, average a.m. temp. 15°C and average p.m. temp. 19°C).

2.5. Control studies for measurement of JH titer

These experiments were performed the following summer (1994) because levels of JH in foragers in this study were found to be lower than in other studies which used the same JH RIA (Huang and Robinson, 1995; Huang et al., 1994). We therefore performed two types of analysis to explore two possible sources of variation. First, it was determined whether blood samples were contaminated with foregut contents using an established high performance liquid chromatography (HPLC) assay (Hayse et al., 1992). Hemolymph collection involved puncturing the membrane beneath the third tergite and collecting the hemolymph. A wound directed ventrally could puncture the crop contaminating the sample with sucrose. Honey bee hemolymph contains trehalose but no detectable sucrose (Woodring et al., 1993). HPLC analyses were thus conducted to test for the presence

of sucrose in hemolymph samples (M.S. Kuhlenschmidt, unpublished); no sucrose was found in the hemolymph samples of 1993 (N = 6).

Second, we determined whether JH titers of foragers could vary depending on whether foragers were sampled within or outside the nest. Into four 4-frame colonies (approx. 10 000 workers) 100 paint-marked, newly emerged workers were introduced (as above). Twenty-eight days later 20 workers per colony were captured and paint-marked as returning foragers, then ten were collected from within the colony the following morning before foraging began and the remaining ten (marked) workers per colony were collected as returning foragers at the colony entrances (Huang et al., 1994). Hemolymph collection and JH analysis were performed as above.

2.6. Measurement of JH titer

JH analysis took place at the University of Illinois, Urbana–Champaign. Hemolymph samples packed in dry ice were shipped from Simon Fraser University by overnight courier. Hemolymph was collected from cold anaesthetized workers and mixed with 500 μl acetonitrile and stored at – 70°C until shipment. JH titers were measured for bees with a chiral-specific radioimmunoassay (RIA) (Hunnicutt et al., 1989). Huang et al. (1994) demonstrated the specificity of the assay for adult worker honey bees. Each sample contained hemolymph from an individual bee.

JH was extracted twice by adding 1 ml 0.9% NaCl and 1 ml hexane. An aliquot of extracted JH was then added to a 200 μl mixture of JH antibody (1:28 000 dilution) and radiolabeled JH III (8000 dpm, NEN, 629 Gbq-mmol^{-1}). After a 2 h incubation at room temperature, unbound radiolabeled JH was separated from bound JH by incubation with dextran-coated charcoal for 2.5 min. Radioactivity in the supernatant (containing radiolabeled JH bound to antiserum) was quantified by liquid scintillation spectrometry (Beckman LS6000IC). A standard curve was created for each RIA run with known amounts of racemic JH III (Sigma). The data from the standard curve were fitted to a five parameter model (Prentice, 1976). Curve fitting was done by non-linear regression (KaleidaGraph, Synergy Software). JH titers were then calculated using the five parameters. Previous results (Huang et al., 1994) indicate that results from this RIA agree with those obtained with either the Strambi or Goodman JH RIAs, both of which have been validated with gas chromatography/mass spectroscopy (Goodman et al., 1990; de Kort et al., 1985). All solvents used were HPLC grade, obtained from either EM Science, Fisher Scientific, or J.T. Baxter Chemical Company. Glassware was baked at 500°C for 3.5 h prior to use to minimize JH adsorption (Strambi et al., 1981).

Prior to JH determination samples were recoded so that worker age, genotype and treatment were not apparent to the person performing the RIA. In addition, titer determinations were made on the same day from 75 of the 150 samples collected per colony. This was done so that differences among age, genotype or treatment, could not be attributed to interassay variation of the RIA. Although inter- and intra-assay variations were similar (both about 10%, Huang and Robinson, 1996), our way of 'blocking' the treatment combinations further minimizes any variation due to different RIA runs.

2.7. Statistical analyses

All results are presented as means and standard errors.

2.7.1. Foraging ontogeny and foraging activity

Data were log transformed prior to an analysis of variance so that variances would be independent of means, a necessary assumption for the analysis of variance (Sokal and Rohlf, 1995).

2.7.2. JH titer measurements

To increase precision for comparing the average effects of treatments on strains and interactions, the data were analysed based on a split-plot design (Sokal and Rohlf, 1995). In the 'control' experiment JH titers of foragers sampled in the hive or as returned were compared with a *t*-test (Sokal and Rohlf, 1995).

3. Results

3.1. Foraging ontogeny

Exposing workers to colony environments with supplemental QMP resulted in delayed foraging (Fig. 1). There were no differences ($F = 3.23$, $df = 2$, $P > 0.05$) among the QMP-responding strains within treatments so data within treatments were pooled for analysis (Control: high strain 20.5 ± 0.5, low strain 21.0 ± 0.8, wild strain 22.3 ± 1.0 - QMP treated: high strain 23.3 ± 0.8, low strain 24.7 ± 0.8, wild-type 25.4 ± 0.5). Workers in QMP-treated colonies foraged significantly later compared to control colonies, with an average delay of 2.7 days later ($F = 42.74$, $df = 1$ $P < 0.0001$) (Fig. 1).

3.2. Foraging activity

The number of tagged workers returning from foraging flights was significantly lower ($F = 5.3$, $df = 1$, $P < 0.05$) in QMP treated colonies than control colonies (Fig. 2). There were no within-treatment differences among the high, low or wild-type QMP-responding strains ($F = 3.1$, $df = 2$, $P > 0.05$), (Control: high strain 2.0 ± 0.03 5 min^{-1}, low strain 1.9 ± 0.01 5 min^{-1}, wild-type 2.3 ± 0.02 5 min^{-1}; QMP treated: high strain 1.3 ±

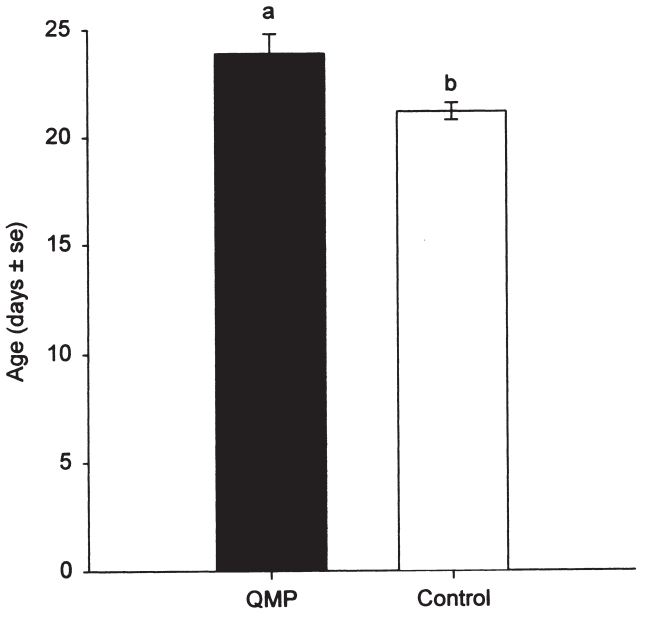

Fig. 1. Mean foraging age of control and QMP-treated colonies. Workers in control colonies began foraging at significantly younger ages than workers in QMP-treated (N = 6 QMP and Control colonies, $P < 0.05$).

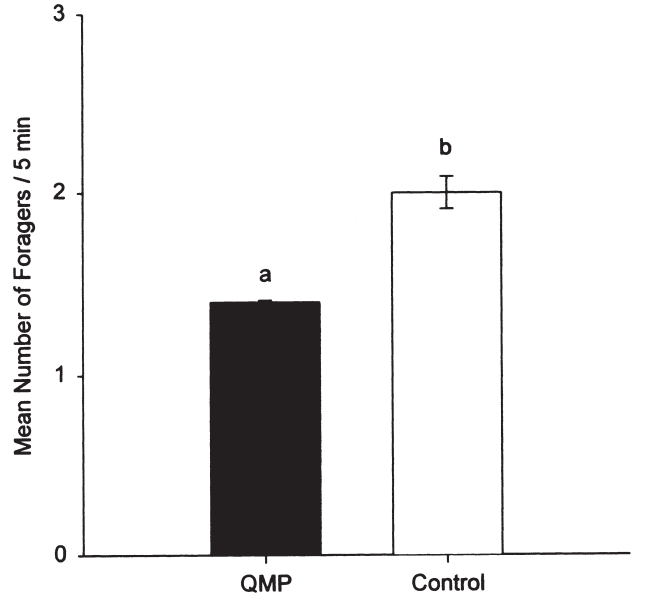

Fig. 2. The mean number of incoming marked foragers per 5 min was significantly greater in control versus QMP treated colonies ($P < 0.05$).

0.02 5 min^{-1}, low strain 1.5 ± 0.03 5 min^{-1}, wild-type 1.6 ± 0.03 5 min^{-1}). The mean ratio of non-pollen to pollen foragers was 2.7 for control colonies and 2.5 for QMP colonies, the difference was not significant (Kruskall–Wallis, $\chi^2 = 2.9$, df = 1, $P > 0.05$).

3.3. JH titers

Split-plot analysis of variance indicated there were significant differences among treatments (F = 6.21, df = 1, $P < 0.01$) (Fig. 3), no differences among strains (F = 1.44, df = 2, $P > 0.24$), and no treatment × strain interaction (F = 2.19, df = 2, $P > 0.11$).

Further analyses of variance were performed using means of colony-level means, to avoid a pseudo-replication error (i.e. treatment N = 6 colonies), and pooled strains (because there was no strain effect from split-plot analysis of variance). This analysis revealed an overall treatment effect (F = 6.40, df = 1, $P < 0.01$). Analysis of variance to examine treatment differences on days 0, 7, 14, 21 and 28 indicated that day 14 contributed the most to treatment differences (F = 74, df = 1, $P < 0.0001$) (Fig. 3).

3.4. Inside nest vs returning forager JH titer

There were no differences in JH titers between workers collected in the nest and foraging workers (148.8 ± 15.9 ng ml^{-1}, and 157.0 ± 12.4 respectively, $t = 0.3$, df = 1, $P > 0.8$). These results indicate that there was no effect of worker location on JH titer, so that the relatively low JH titers detected in foragers (Fig. 3) could not be attributed to sampling method. JH titers of foragers collected in 1994 were higher than those collected in the main experiment and also were similar to results

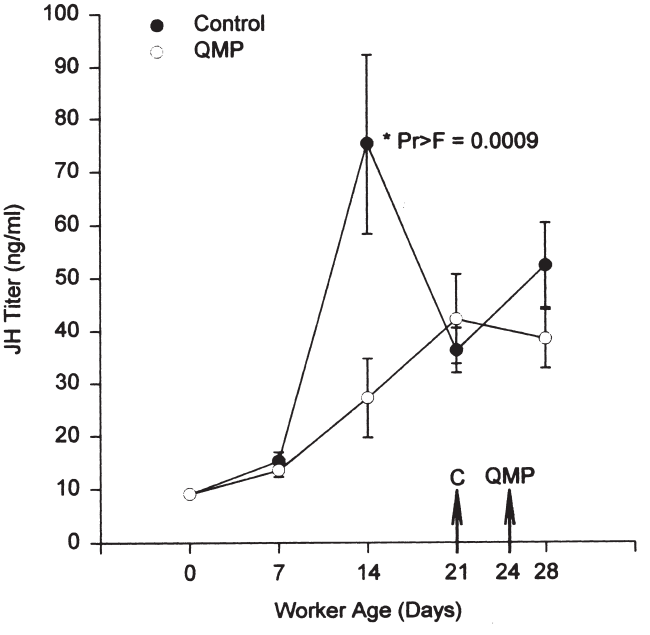

Fig. 3. JH titers (Mean ± SE) for worker honey bees in control (N = 6) and QMP-treated (N = 6) colonies. JH titers of control colony bees were significantly greater ($P < 0.01$) than QMP-treated colony bees. Day 14 contributed most ($P < 0.001$) to the overall difference. Arrows with C and QMP indicate mean foraging age for control and QMP-treated workers, respectively.

from previous studies (Huang et al., 1994; Huang and Robinson, 1995).

4. Discussion

These results provide the first demonstration that a social insect queen pheromone can act as a modulator for division of labor. QMP treatment delayed the age at which foraging began and associated with this delayed foraging ontogeny were lower JH titers for workers in QMP-treated colonies compared to control colonies. We also found no genetic-based difference in the QMP inhibition of JH titers and foraging ontogeny, at least in the strains tested.

QMP functions to moderate the rate at which workers progress from within-nest tasks to outside-nest tasks. A modulator such as QMP may impose a labor schedule that promotes efficiency in task performance by physiologically delaying a shift to the next age caste. QMP also may lengthen transition phases from age caste to age caste, resulting in worker task response thresholds that overlap age castes, thereby producing a worker generalist capable of behavioral plasticity. In addition, the presence of the queen-based inhibitor may prevent all of a colony's young workers from developing too rapidly towards foraging in the event of a sudden loss of older workers due to predation, rapid weather changes or other factors, detaining some for within-hive tasks.

QMP may be most influential in suppressing JH titers and foraging in small rather than large colonies because the (queen) source is more accessible. QMP is dispersed throughout the nest via transmissions from worker to worker (Naumann et al., 1991, 1992) signalling queen presence to the colony. Removal of the queen from the nest or inhibition of QMP transmission as a result of high worker numbers (a dilution effect) results in queen rearing, normally inhibited by QMP (Pettis et al., 1995; Winston et al., 1989, 1990, 1991). The queen's pheromonal inhibition of new queen rearing by workers is a primer effect of QMP, in which the endocrine or reproductive systems may be altered physiologically. QMP is most effective in inhibiting queen rearing activities among less populous colonies (Winston et al., 1991), and QMP is detectable in a greater proportion of workers in unpopulous colonies (Naumann et al., 1993). Although there is no link between the two known QMP primer effects, swarming suppression and delayed foraging ontogeny, it seems reasonable to assume that QMP transmission mechanisms would be similar for both. Thus, the QMP effects we found here may diminish as colonies become more populous, and worker-based inhibitory factors might become more significant. Studies of QMP and worker inhibitory factors in colonies of different populations and age structures would be useful to further explore this subject.

QMP treatment also caused a decrease in colony foraging activity, possibly due to the accumulative effect of individual workers beginning to forage at later ages. Huang and Robinson (1996) have shown that older worker bees inhibit the rate of behavioral development of younger bees and hypothesized that this effect is mediated by a socially transmitted factor. We have shown that QMP also inhibits behavioral development. In addition, Kaatz et al. (1992) demonstrated lower JH titers and biosynthesis in caged workers exposed to a queen (extracts of QMP and synthetic QMP), and Y. Le Conte and G.E. Robinson (unpublished observations) have found delayed foraging and decreased JH titers in workers from colonies with queens compared to queenless colonies. Thus, QMP appears to act as an 'inhibitor' in addition to the inhibitory effects of older workers found by Huang and Robinson (1996). However, this interaction may be complex; Jaycox (1970) found more foraging of workers from colonies with a queen than from queenless colonies, suggesting that the presence or absence of queen pheromone could be a different issue than quantity of queen pheromone in the nest.

Our results also suggest that QMP influences foraging ontogeny by inhibiting JH titers, consistent with previous results demonstrating a causal relationship between JH and foraging ontogeny (reviewed by Robinson, 1992). The JH titers for foragers in the 1993 experiment were low compared with other studies using bees of similar age; JH titers typically increase from middle age to foraging age and plateau at levels above 100 ng ml^{-1} only after foraging commences (Huang et al., 1994, 1991). These low values do not appear to be an artifact of our sampling procedure because the control experiments in 1994 showed typical high JH titers for foragers and, no differences in JH titers between foragers collected in the hive and those returning to the hive. Also, the drop in JH levels following the single JH peak observed on day 14 was unusual. This peak JH titer on day 14 (Fig. 2) may have 'set' control workers to a physiological foraging state predisposing relatively earlier foraging (Huang and Robinson, 1995). In contrast, a comparable JH peak was not observed among QMP treated workers, but rather we observed a slower, continuous increase (Fig. 2).

We suspect that the reason for the low JH titers in 1993 foragers was cool (average night temp. 8°C, average a.m. temp. 15°C, average p.m. temp. 19°C), rainy conditions interspersed with brief warm sunny weather that prevailed throughout the duration of this experiment, in contrast to 1994 when temperatures were consistently 20°C–25°C during the day. During seasonally cool and cold periods, or experimentally induced cold in which foragers are less active or inactive, JH titers decline to pre-foraging levels (Huang and Robinson, 1995). Decreases in JH in the fall, and increases in JH in the spring may be attributed to seasonal changes in tempera-

ture as suggested by Bühler et al. (1983). Characteristically, overwintering foragers have low JH titers (Huang and Robinson, 1995; Fluri et al., 1977), associated with prolonged longevity. Despite low JH titers and extended longevity, overwintering foragers apparently do not survive to the spring in temperate climates (Huang and Robinson, 1995). However, summer foragers presented with adverse climatic conditions must be capable of taking advantage of brief periods of favorable weather, and then possibly waiting long periods for another foraging opportunity. The functional significance of low JH titers in summer foragers may induce greater longevity and lower consumption rates of limited resources. This behavioral and physiological plasticity in JH levels and foraging ages may be principal factors in honey bee ecological success. Given the atypical pattern of JH titers in 1993, it remains plausible that QMP could influence foraging ontogeny by an as-yet to be discovered process that does not involve JH.

We did not detect strain variability for QMP inhibition on foraging ontogeny and JH. Strains selected for QMP retinue response did not respond significantly differently to QMP primer influences on ontogeny of foraging and JH titers. Evidently the QMP-induced releaser retinue response does not confer a correlated response to this primer influence, and the primer effect does not appear to have a similar genetically variable nature, at least in the strains we tested.

In summary, QMP delays foraging ontogeny in worker honey bees, and this is associated with lower JH titers. QMP should be included with worker genotype (reviewed by Page and Robinson, 1991; see also Giray and Robinson, 1994) and colony age demography (Huang and Robinson, 1992, 1996) as a factor that influences temporal polyethism. The integration of QMP (and perhaps other honey bee pheromones such as worker or brood pheromones), genetics and the environment, into models for the plasticity of division of labor will undoubtedly lead to a refinement in our understanding of the mechanisms regulating temporal polyethism.

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