Juvenile Hormone Does Not Affect Division of Labor in Bumble Bee Colonies (Hymenoptera: Apidae)

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ABSTRACT Juvenile hormone (JH) is involved in the regulation of division of labor in honey bee colonies, but it was not known whether JH plays a similar role in other social bees. Topical application of 250 μg of the JH analog methoprene or injection of 250 μg JH I did not affect worker foraging or nest activity in colonies of the primitively eusocial bumble bees *Bombus* (*Pyrobombus*) *impatiens* Cresson and *B.* (*P.*) *bimaculatus* Cresson. Because bumble bees do not exhibit strong age polyethism, these results are consistent with findings in honey bees that JH influences only the performance of age-dependent tasks.

KEY WORDS Insecta, *Bombus,* juvenile hormone, division of labor, age polyethism

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THE ECOLOGICAL SUCCESS of social insects is attributed in large part to the ability of colonies to perform several different tasks simultaneously with groups of specialized workers (Oster & Wilson 1978, Wilson 1987). The mechanisms of this division of labor among workers are not well understood.

Age polyethism occurs in many highly eusocial bees, the honey bees (Apinae), and stingless bees (Meliponinae). Workers perform different ensembles of tasks as they age (reviewed in Michener 1974, Seeley 1985, Winston 1987; also see Sommeijer 1984). Young workers perform tasks such as brood and queen care and nest maintenance within the nest, and older individuals forage.

Bumble bees (Bombinae) share a common origin with the Apinae and Meliponinae (Kimsey 1984, Michener & Sakagami 1987) but are primitively eusocial and exhibit a different pattern of division of labor. Cameron (1989) recently reported that workers of *Bombus griseocollis* De Geer do not exhibit strong age polyethism. Following a period (about 36 h) of "callow behavior" upon emergence, characterized almost exclusively by brood incubation, workers may engage in nest or foraging activities at virtually any age (Cameron 1989). However, patterns of worker behavior change as the colony ages (Cameron 1989). Brian (1952), Free (1955), and Goldblatt & Fell (1987) have shown that worker size influences the tendency to forage or engage in nest activity; the larger bees most likely become foragers. The mechanisms regulating bumble bee behavioral plasticity and the integration of worker activities under changing colony conditions are not known.

Juvenile hormone (JH) affects the morphological differentiation of worker ants and termites (reviewed by Nijhout & Wheeler 1982). JH also plays a role in the temporal division of labor among workers in the honey bee, *Apis mellifera* L. A rising titer of JH associated with aging of the worker bee (Hagenguth & Rembold 1978, Fluri et al. 1982, Robinson et al. 1987) is involved in the regulation of age polyethism (Jaycox et al. 1974; Jaycox 1976; Fluri et al. 1982; Robinson 1985, 1987a,b,c; Sasagawa et al. 1986). Low levels of JH are associated with nest activities, and higher titers help trigger the onset of foraging among older bees. The intrinsic rise in JH is modulated by environmental factors that accelerate or retard behavioral ontogeny of workers. Extrinsic regulation of JH is a mechanism enabling honey bee colonies to respond to changing conditions by altering the proportions of individuals engaged in various tasks (Robinson et al. 1989).

For several reasons, we tested the hypothesis that JH also controls division of labor in bumble bees. First, knowledge of the social organization of *Bombus* is important to our understanding of the evolution of division of labor in the social bees, because *Bombus* is intermediate in degree of sociality within the Apidae. Second, preliminary observations by van Doorn (1987) suggested that JH did not regulate division of labor in *Bombus terrestris* (L.). Third, because division of labor in *Bombus* does not appear to be age-based as it is in *A. mellifera,* this comparative study should show if JH plays a part in the division of labor only of those social bees that have age polyethism.

Materials and Methods

We observed the effects of experimentally increasing adult worker JH levels on nest activity

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(i.e., brood care and nest maintenance) and foraging behavior, two of the principal activity classes in a bumble bee colony. We tested whether treatment early in life affects the likelihood of initiating nest activity or foraging, or the continued performance of these tasks.

Observation Colonies. Colonies of *Bombus* (*Pyrobumbus*) *bimaculatus* Cresson and *B.* (*P.*) *impatiens* Cresson were established during the summer of 1987 in Columbus, Ohio, from queens collected in the spring within a 125-km radius. Colonies were maintained (Plowright & Jay 1966) in observation shelters that allowed free flight outside. Ten *B. impatiens* and 11 *B. bimaculatus* colonies (queen, workers, and brood clump) were each transferred into a clear Plexiglas observation box (33.5 by 23.0 by 24.5 cm) after the first workers emerged. Workers from up to three different broods per colony were observed throughout the season. In *B. impatiens* colonies, we observed 3–8 bees per colony from the first brood, 2–13 from the second, and 13–28 from the third (total observed = 142). In *B. bimaculatus* colonies, these values were 2–8, 10–11, and 6–13 bees, respectively (total observed = 76).

Treatments. *Experiment 1: Effects on Initiation of Nursing and Foraging.* Callow workers that had emerged naturally in the nest were individually marked on the thoracic dorsum with a colored, numbered plastic disk (Opalithplättchen) and topically treated with either 250 μg of the JH analog (S) methoprene (Zoecon Corporation, Palo Alto, Calif.) dissolved in 5 μl acetone or with 5 μl acetone alone (control). Although there is recent evidence for different acceptor sites for JH homologs and analogs (Prestwich 1987), methoprene has shown JH-like activity in many different insects (Staal 1975), including honey bees (Robinson 1985, 1987b,c; Robinson & Ratnieks 1987; Sasagawa et al. 1986). A dose of 250 μg was used for bumble bees because the same dose strongly affected the behavior of similarly sized honey bees (Robinson 1985, 1987b). Workers were marked and treated without anesthetization and returned to their nests within 20 min of removal. To allow for the possible effects of age on treatment efficacy, we determined the precise age of each focal bee to within several hours by scanning each colony for worker emergence 8–10 times/d and once every night between 2200 and 2300 hours. Similarly aged individuals were paired, one receiving methoprene and the other, acetone alone. Size variation among callows within a brood were minor and not a factor in our pairing. A total of 218 bees was treated in this experiment.

Experiment 2: Effects on the Continuation of Nursing and Foraging. We identified 10 foragers and six nurses in a colony of *B. impatiens* by observing 22 workers from three broods for 8 h over 2 d. Five pairs of foragers and three pairs of nurses, grouped by similarity in age and size, were treated as in Experiment 1: one member of each pair received 250 μg methoprene and the other, acetone alone (Experiment 2a). Size was a factor when pairing workers in this experiment because variation can occur among broods (S.A.C., unpublished data). In Experiment 2b, we injected 250 μg JH I dissolved in 5 μl triolein oil or pure triolein oil (control) into two identified foragers and six nurses from a different *B. impatiens* colony, and into four foragers and four nurses from a *B. bimaculatus* colony. Injections were made through the intersegmental membrane between the fifth and sixth metasomal terga with a finely drawn glass microcapillary pipette. Bees were cooled and held in position with modeling clay on a cold table (1–2°C) before they were injected.

In all experiments, treatments were administered from coded vials to allow unbiased observations of behavior.

Observation Methods. *Experiment 1.* The activity of each marked bee was recorded once during each of four to eight daily scans of each colony. Each bee was located during a scan and observed long enough (usually several seconds) to discern and record her activity. Bees were identified as nest bees or foragers according to the following criteria (Cameron 1985, 1989): nest bees fed and incubated brood and engaged in nest maintenance. Bees returning to the nest with nectar or pollen on at least two consecutive flights were classified as foragers. Individuals away from the nest were presumed to be foraging if they were previously identified as such; scans made late each night verified whether they were still alive. Observations began from one to several hours after treatments. We recorded the date and time of each behavioral observation so that we could quantify, to within a few hours, the age at which foraging began and the latency from treatment to the onset of foraging for each labeled bee. It was important to measure latency from treatment to foraging because the age at which some workers were treated varied by several hours despite our efforts to minimize these differences. Individuals were observed within one to several hours of treatment over a 14-d period, during which 4,611 observations was recorded.

Experiment 2. Observations were made on nest bees and foragers 5–20 d old. Two-hour scans were made once a day to determine any switches in activity (from nest activity to foraging or vice versa). Individuals were observed for 7 d after treatment in Experiment 2 (unless they died earlier), for 233 observations in Experiment 2a and 130 in Experiment 2b.

Experiment to Test for Methoprene Mimicry of JH Activity in Bombus. To clarify our interpretation of the results of the experiments described herein, we tested whether methoprene can cause JH-like effects in *Bombus*. New queens (1–2 wk old) of *B. fervidus* emerging naturally in a wild colony in late summer were topically treated with 250 μg methoprene or acetone alone ($n = 14$ for each treatment). The results of these treatments

Table 1. Effects of methoprene on behavior of *B. fervidus* gynes

Gyne no.	Treatment	Activities[a]			
		Forage	Nest	Guard	Total
1	Methoprene	7	2	0	
2	Methoprene	1	2	1	
3	Methoprene	0	2	0	
4	Methoprene	0	2	0	
5	Methoprene	0	1	0	
6	Methoprene	1	1	0	
7	Methoprene	0	1	0	
8	Methoprene	0	1	0	
9	Methoprene	0	1	0	
10	Methoprene	0	1	0	
11	Methoprene	0	1	0	
12	Methoprene	9	1	2	
13	Methoprene	1	0	0	
14	Methoprene	1	0	0	
Total		20	16	3	39
15	Acetone	1	1	0	
16–28	Acetone	0	0	0	
		1	1	0	2

$F = 9.96$; $P < 0.0002$; Hotelling–Lawley multivariate *t* test.

[a] Values represent observed counts for each activity.

were compared with Röseler's (1977a) finding that newly emerged *Bombus* queens (gynes) injected with 50 μg JH I exhibit worker behavior instead of entering diapause. Behavioral observations on treated gynes began within one to several hours after treatment and continued 1–3 h daily for 10 d. Gynes were observed for the worker activities of foraging, nest activity, and guarding (see Cameron 1989).

Statistical Analyses. Foraging, guarding, and nest activity of gynes treated with methoprene or acetone were analyzed for treatment effect using multivariate analysis of variance (MANOVA), implemented in the GLM procedure from SAS (SAS Institute 1982). The Hotelling–Lawley test, a multivariate *t* test, was used to test the hypothesis of no overall treatment effect. *T* tests (Experiment 1) and Mann–Whitney *U* tests (Experiment 2) were used for intergroup comparisons of methoprene or JH I- and acetone-treated workers.

Voucher specimens of *B. bimaculatus* and *B. impatiens* are deposited in the Snow Entomological Museum at the University of Kansas, Lawrence.

Results

Methoprene is active in gynes of *B. fervidus*. Gynes treated with methoprene exhibited a significantly higher frequency of worker behavior than acetone-treated gynes (Table 1). All 14 gynes treated with methoprene were observed performing workerlike behavior at least once, compared with only a single acetone-treated gyne. Two treated gynes were observed guarding; this behavior has never been observed in untreated *Bombus* gynes. These results are similar to those obtained with JH I treatments of *B. terrestris* (Röseler 1977a).

Table 2. Effects of methoprene on the ontogeny of worker foraging behavior in *B. impatiens* and *B. bimaculatus* workers

Parameter	Species of *Bombus*			
	B. impatiens		*B. bimaculatus*	
	Methoprene	Acetone	Methoprene	Acetone
	Age at first foraging, h			
Mean	116.2	121.3	96.9	76.7
SE	8.9	12.7	19.6	19.1
n	23	26	6	4
	$P > 0.7$			
	Latency from treatment to onset of foraging, h			
Mean	99.1	106.7	62.2	54.7
SE	10.0	13.2	17.7	12.0
n	23	26	6	4

$P > 0.6$; two-tailed *t* test.

There were differences between species in the rate of behavioral development; untreated *B. bimaculatus* workers began foraging at significantly ($P < 0.001$, one-tailed Mann–Whitney *U* test) younger ages than *B. impatiens* workers (Table 2). However, methoprene did not affect the ontogeny of worker foraging behavior in either species. There was no significant difference between methoprene-treated and control workers in the mean age at which workers began foraging or in the mean latency from treatment to onset of foraging in *B. impatiens* (Table 2). The same trend was evident in *B. bimaculatus* (Table 2). However, because of high mortality, we were unable to obtain a large number of pairs to test our results with sufficient power. We conducted power analyses (Snedecor & Cochran 1976) to determine the probability of detecting effects of methoprene on foraging behavior in *Bombus* that are as large as those detected by Robinson (1985) for honey bees. The probability of detecting effects of methoprene (using the results of Robinson [1985] to estimate size of effect and variance) is >0.95 for *B. impatiens* and <0.80 for *B. bimaculatus*.

Neither topical applications of methoprene nor JH injections resulted in a switch from nest activity to foraging or vice versa. After treatment, workers treated with methoprene and JH I continued to forage and engage in nest activity at the same high level as that of the acetone-treated workers (Tables 3 and 4). Only two of the treated nest bees (#40 methoprene, #24 JH I) and one of the nest bee controls for JH I (#42) showed any appreciable change in behavior, foraging in 43–56% of the observations during the 7-d observation period (Table 4). Some of the JH-treated nest bees disappeared the day after treatment, but none of the others showed increases in foraging activity relative to the control nest bees (Table 4). *P* values reported in Tables 3 and 4 are based on pooled observations of workers treated with methoprene and JH I and pooled observations of the control workers. Pooling is justified because no statistically significant dif-

Table 3. Effects of methoprene and JH I on persistence of foraging in *B. impatiens* (i) and *B. bimaculatus* (b) workers over a 7-d period after treatment

Methoprene			Control			JH I			Control		
Foragers[a]	% Time foraging	*n*	Foragers	% Time foraging	*n*	Foragers	% Time foraging	*n*	Foragers	% Time foraging	*n*
25i	100	3	27i	95	21	32i	66	6	40i	92	13
22i	95	20	31i	88	17	15b	100	4	16b	100	4
36i	67	15	26i	88	26	17b	100	2	21b	87	15
			32i	100	18						
			39i	100	23						

[a] All foragers are identified by bee number.
n, number of observations. $P > 0.20$; two-tailed Mann–Whitney *U* tests.

ferences in foraging or nest activity were found in comparisons between workers treated with methoprene and JH I or between control groups ($P > 0.05$; two-tailed Mann–Whitney *U* test).

Discussion

Our results suggest that division of labor in bumble bee colonies is not controlled by JH. A dose of 250 μg methoprene did not affect the ontogeny of worker foraging behavior but was able to induce effects in larger sized gynes comparable with those caused by JH treatment (Röseler 1977a). Effects on gyne behavior were evident within 16 h and persisted for up to 10 d, whereas no effects were observed in workers beginning 16 h after treatment. This suggests that methoprene was still present in workers, at least during the initial period of our observations. Our observations were sufficiently detailed to detect species differences in the ontogeny of foraging behavior, suggesting that treatment effects, if they existed, also would have been detected. Although the same methoprene dose we used for bumble bees strongly influenced the behavior of honey bees that are of similar size and mass (Robinson 1985, 1987b,c), perhaps a larger quantity is needed to penetrate the more extensive pilation of *Bombus* workers. Our dose of injected JH I was much higher, however, than endogenous titers of JH in *Bombus* (Röseler & Röseler 1978, 1986) and it, too, failed to elicit a behavioral effect. Although this conclusion is based on small sample sizes, it is consistent with the results of methoprene treatment and with a report that injection of 50 μg JH I did not cause observable changes in the timing of foraging behavior in *B. terrestris* (van Doorn 1987). Together, these results suggest that even if there are differences in the endogenous JH titers of nurses and foragers as suggested by Röseler (1977b), they may not influence the division of labor. Quantitative analyses of JH titers (Bergot et al. 1981, Strambi et al. 1981, Rembold & Lackner 1985) of workers engaged in different tasks are needed to confirm our findings. JH titers in bumble bee prepupae have been successfully measured (Strambi et al. 1984).

Our results, coupled with the finding that workers of *Bombus griseocollis* do not exhibit strong age polyethism (Cameron 1989), are consistent with reports that JH affects only age-dependent tasks of honey bees (Robinson 1987b). Although *B. impatiens* and *B. bimaculatus* were not examined specifically for age polyethism in our study, our observations suggest that worker size was the major factor governing foraging and nest activity. In both species, only the largest individuals in the colony were foragers, engaging in both foraging and nest activities on the same day. The same is true of *B. griseocollis* (Cameron 1985, 1989).

In *B. griseocollis*, virtually all major activities can be performed by workers of any age following a period of callow behavior limited to brood incubation, a probable consequence of incomplete morphological development. However, individuals

Table 4. Effects of methoprene and JH I on persistence of nest activity in *B. impatiens* (i) and *B. bimaculatus* (b) workers over a 7-d period after treatment

Methoprene			Control			JH I			Control		
Nest[a] activity	% Nest activity	*n*	Nest activity	% Nest activity	*n*	Nest activity	% Nest activity	*n*	Nest activity	% Nest activity	*n*
17i	100	19	21i	100	6	34i	100	3	38i	66	6
40i	55	14	41i	94	17	37i	100	3	42i	44	16
43i	87.5	16	44i	95	19	39i	100	3	18b	100	10
						12b	100	11	23b	100	3
						24b	57	7			

[a] All bees engaged in nest activity are identified by bee number.
n, number of observations. $P > 0.20$; two-tailed Mann–Whitney *U* tests.

that emerge at different times of the season and under different colony conditions display distinct patterns of task performance (Cameron 1985, 1989). Division of labor in other species of bumble bees is based, in part, on worker size; foragers are among the largest bees in the colony and nest bees are smaller (Brian 1952, Free 1955, Garófalo 1978). In general, division of labor in bumble bees probably is not based on a stereotyped pattern of behavioral development within the lifetime of a bee, and a timing mechanism such as JH provides apparently is not involved. The physiological mechanisms underlying worker division of labor in bumble bee colonies are still not known.

We are left with the question of the commonality of hormonal regulation of division of labor in the social insects. The role of JH in the differentiation of morphologically distinct castes of social insects is well known (reviewed by Nijhout & Wheeler 1982). The regulation by JH of division of labor among workers in species without physical castes may be limited to *Apis,* or to species with well-developed age polyethism. Alternatively, JH may not regulate both worker reproductive maturation and division of labor in a species. In *Bombus,* JH regulates reproductive behavior in gynes and workers (Röseler 1975, Röseler & Röseler 1977, van Honk et al. 1981) and does not appear to be involved in division of labor. In *Apis,* JH underlies division of labor, but elevated levels of JH do not appear to play the role usual in insects in the reproductive development of queens (Hrdy & Slama 1963, Engels & Ramamurty 1976, Kaatz 1987) or in the oviposition behavior of egg-laying workers (G.E.R., C. Strambi, A. Strambi, unpublished data). Studies of other primitively eusocial and highly eusocial species are needed to determine the generality of this regulatory mechanism. Premier candidates are stingless bees, a highly eusocial group that shares a common ancestry with *Apis* and *Bombus,* and the swarm-founding polybiine wasps, such as *Polybia occidentalis* (Oliviera), that have large colonies and strong age polyethism (Jeanne et al. 1988).

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