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ORIGINAL PAPER

The pheromones of laying workers in two honeybee sister species: *Apis cerana* and *Apis mellifera*

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Abstract When a honeybee colony loses its queen, workers activate their ovaries and begin to lay eggs. This is accompanied by a shift in their pheromonal bouquet, which becomes more queen like. Workers of the Asian hive bee *Apis cerana* show unusually high levels of ovary activation and this can be interpreted as evidence for a recent evolutionary arms race between queens and workers over worker reproduction in this species. To further explore this, we compared the rate of pheromonal bouquet change between two honeybee sister species of *Apis cerana* and *Apis mellifera* under queenright and queenless conditions. We show that in both species, the pheromonal components HOB, 9-ODA, HVA, 9-HDA, 10-HDAA and 10-HDA have significantly higher amounts in laying workers than in non-laying workers. In the queenright colonies of *A. mellifera* and *A. cerana*, the ratios (9-ODA)/(9-ODA + 9-HDA + 10-HDAA + 10-HDA) are not significantly different between the two species, but in queenless *A. cerana* colonies the ratio is significant higher than in *A. mellifera*, suggesting that in *A. cerana*, the workers' pheromonal bouquet is dominated by the queen compound, 9-ODA. The amount of 9-ODA in laying *A. cerana* workers increased by over 585% compared with the non-laying workers, that is 6.75 times higher than in *A. mellifera* where laying workers only had 86% more 9-ODA compared with non-laying workers.

Keywords *Apis cerana* · *Apis mellifera* · Pheromonal bouquet · Laying worker · Queenless

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Introduction

In honeybee colonies, the queen is the only female individual capable of sexual reproduction. Pheromones secreted by the queens' mandibular gland can have an inhibitory affect on the ovarian activation of workers (Slessor et al. 1988; Winston et al. 1989; Winston and Slessor 1992). The major components are 9-ODA, 9-HDA, 10-HDA, 10-HDAA and HOB (Crewe 1982; Plettner et al. 1996, 1997). However, when a colony loses its queen, the subsequent lack of queen pheromones allows many workers to activate their ovaries and lay unfertilized eggs, which normally develop into haploid males (drones) (Crozier 1975).

The proximate mechanisms that regulate worker ovary activation in the honey bees are well understood. Queens produce a variety of pheromones from multiple sources whose combined action inhibits ovary activation in workers. Chief amongst these are the pheromones secreted by the queen's mandibular glands (Butler 1959). Mandibular gland secretions of queens have a high proportion of 9-ODA, whereas the glands of workers produce secretions that are richer in 10-HDA (Plettner et al. 1995, 1996). Thus, the ratio of 9-ODA/(9-ODA + 10-HDA + 10-HDAA) is a measure

of how "queen-like" a mandibular gland bouquet is (Moritz et al. 2000; Hoover et al. 2005; Schäfer et al. 2006), and the more 9-ODA circulating in a colony, the less likely *A. mellifera* workers are to activate their ovaries (Hoover et al. 2003).

Ovary activation in workers appears to be accompanied by subtle changes in exocrine gland secretions. Dufour's gland secretions of laying workers differ from those of non-laying workers, especially in wax-type esters (Katzav-Gozansky et al. 1997, 2001; Sole et al. 2002). Furthermore, in some ants (Peeters et al. 1999; Liebig et al. 2000) and wasps (Sledge et al. 2001), ovary activation is correlated with changes in cuticular hydrocarbon profiles and may be used as cues by which workers recognise ovarian activation in other workers (Liebig et al. 2000). However, this seems unlikely since ovarian activation and pheromones only covary (Hepburn et al. 1988; Plettner et al. 1993). False queens are laying workers that show queen-like characteristics in that they do not work and attract a court of workers as a queen would (Sakagami 1958).

The chemical complexity of the pheromone bouquets of queens and workers has been suggested as evidence that an evolutionary arms race for reproductive dominance has occurred (Katzav-Gozansky 2006). Often, laying workers produce a mandibular gland secretion with a composition very similar to that of the queen (Crewe and Velthuis 1980). As a consequence, these workers elicit behavioural patterns and prime physiological responses in other subordinate workers that otherwise would only be observed in response to the presence of the queen (Velthuis et al. 1990). These workers are known as 'false queens'(Sakagami 1958) or 'pseudoqueens' (Velthuis et al. 1990). Pseudoqueens can suppress ovary activation in other workers, elicit retinue behaviour and escape worker policing. They also suppress the production of a queen-like pheromone signal in other workers (Moritz et al. 2000). Pseudoqueen development is particularly frequent in the Cape honeybee, *Apis mellifera capensis* (Neumann and Moritz 2002). Workers of this subspecies may develop a queen-like mandibular gland secretion, which, within a few days, is dominated by the queen substance (9-ODA) (Simon et al. 2001). Since both queens and workers use the same biochemical pathways to produce either queen (9-ODA) or the worker substances (10-hydroxydecanoic acid, 10-HDAA; and 10- hydroxy-(E) 2-decenoic acid, 10-HDA) (Plettner et al. 1996, 1997), a worker's likelihood to be reproductive is detectable at the level of pheromone production. Reproductively dominant workers have been shown to swiftly develop a 9-ODA-dominated mandibular gland pheromone (Moritz et al. 2000; Zheng et al. 2010).

Curiously, however, workers of the Eastern hive bee *A. cerana* which is the honeybee sister species of *A. mellifera* have been reported to have high rates of ovary activation even under queenright conditions (Tan et al. 2009). Sakagami and Akahra (1958) reported that 10–20% of *A. cerana* workers in queenright colonies contained mature eggs in their ovaries (Sakagami and Akahra 1958). In queenless colonies, there are reports of up to 70% of workers having activated ovaries (Blanford 1923; Tan et al. 2009), much higher than workers of *A. mellifera* (about 40%: Page and Erickson 1988). Furthermore, unlike *A. mellifera*, *A. cerana* workers may continue to lay after the introduction of a new queen (Sakagami 1958).

The apparently high degree of reproductive conflict in *A. cerana* provides a valuable opportunity to further investigate the evolutionary arms race between queens and workers over worker reproduction in *Apis*. We compared the changes in pheromonal bouquet composition in both sister species and under queenright and queenless conditions. We predict that on an average the *A. cerana* workers have a more queen-like pheromonal bouquet than *A. mellifera*. This would also provide evidence of an ongoing evolutionary arms race for reproductive dominance in this species.

Workers over worker reproduction in *Apis*. We compared the changes in pheromonal bouquet composition in both sister species and under queenright and queenless conditions. The apparently high degree of reproductive conflict in *A. cerana* provides a valuable opportunity to further investigate the evolutionary arms race between queens and workers over worker reproduction in *Apis*.

Materials and methods

Study site

The experiments were conducted at the test apiary of Yunnan Agricultural University, Kunming, China in the spring of 2009. Pheromone composition analysis was conducted at Pretoria University, South Africa.

Colonies

Three colonies of *Apis cerana* and three *A. mellifera* colonies containing each two frames of brood and two of honey and pollen were used in the experiment. Six workers from all six colonies were collected and the ovarian status evaluated, confirming that these workers had ovaries of stage 1 (Hess 1942; Pirk and Boodhoo et al. 2010; Pirk et al. 2011). The heads of these workers were extracted in 200 µl dichloromethane (Sigma HPLC Grad, ≥99.9%) in GC bottles. Then, these colonies were de-queened and checked daily for the appearance of queencells, which were removed. This continued until the workers began to lay and multiple eggs began to appear in individual cells. From each colony about 100 indoor workers were sampled randomly and

dissected to check for ovary activation until six worker bees with fully developed ovaries, indicating that they were actively laying individuals. The heads of these workers were removed and kept as above process.

Pheromones

These samples were stored in 200 µl dichloromethane for at least 24 h to extract compounds of the mandibular gland. Half of the extracts were then evaporated to dryness under a stream of nitrogen and the other half was stored as a backup. The residues were redissolved in 10 µl of an internal standard (octanoic acid and tetradecane in dichloromethane) and 10 µl of bistrimethylsilyltrifluoroacetamide (Sigma). One microlitre of this solution was injected into an HP 6890 gas chromatograph fitted with a split–splitless inlet and a 25 m × 0.32 mm methyl silicone-coated fused silica capillary (HP 1). Helium was used as carrier gas at a flow rate of 1 ml per min. The temperature of the oven was maintained at 60°C for 1 min, and then increased to 100°C (at a rate 50°C per min) and then to 220°C at a rate of 3°C per min. The final temperature was maintained for 10 min. Chromatograms were recorded and peak areas determined using HP CHEMSTATION software (March 2006).

The mandibular gland compounds were identified based on the retention times of synthetic compounds and on their retention times when compared with the internal standards. The 'queen substance' (9-ODA) and the 'worker substance' (10-HDA) were quantified using peak areas and the relative mass ratios calculated relative to tetradecane. A standard solution containing the 9-ODA and 10-HDA were run daily to ensure that relative mass ratios were within the limit of the variability found in the series of standard runs. We calculated the following quantitative ratios: ratio = (9-ODA)/(9-ODA + 9-HDA + 10-HDAA + 10-HDA) (Moritz et al. 2000; Hoover et al. 2005; Schäfer et al. 2006).

Statistics

Independent *t* tests were used to test for differences in the absolute amounts (µg) of the constituents in the pheromones between non-laying workers and laying workers of *A. mellifera* and *A. cerana*. Homogeneity of variances and normality of the data were examined using Levene's test and Shapiro–Wilk's test (Johnson and Wichern 2002). Heterogeneity was stabilized after a square-root transformation of the data. All tests were performed using Statistica© (StatSoft 2009).

Results

Eighteen samples of laying workers (LW) and non-laying workers (NLW) were tested in *A. cerana* for its pheromone, which included HOB, 9-ODA, HVA, 9-HDA, 10-HDAA and 10-HDA. Highly significant differences in the absolute amounts (µg) of most pheromonal compounds were observed between LW and NLW (*t* test: HOB: $t = 4.942$, $p < 0.001$; 9-ODA: $t = 2.700$, $p = 0.011$; HVA: $t = 3.037$, $p = 0.004$; 10-HDAA: $t = 3.873$, $p < 0.001$ and 10-HDA: $t = 2.238$, $p = 0.031$), except 9-HDA ($t = 1.488$, $p = 0.146$) (Table 1).

Table 1 Mean amount (µg) and standard errors (mean ± SE) of six major mandibular gland compounds, total amount and ratio = (9-ODA)/(9-ODA + 9-HDA + 10-HDAA + 10-HDA) of NLW and LW in *A. cerana*

	Mean ± SE		*t*	*p*
	NLW	LW		
HOB	0.017 ± 0.006	0.160 ± 0.038	4.942	<0.001
9-ODA	0.014 ± 0.003	0.096 ± 0.034	2.700	0.011
HVA	0.003 ± 0.001	0.026 ± 0.010	3.037	0.004
9-HDA	0.188 ± 0.035	0.525 ± 0.168	1.488	0.146
10-HDAA	0.002 ± 0.001	0.063 ± 0.020	3.873	<0.001
10-HDA	0.086 ± 0.024	0.238 ± 0.059	2.238	0.031
Amount	0.309 ± 0.050	1.103 ± 0.232	3.513	0.001
Ratio	0.097 ± 0.034	0.089 ± 0.022	0.177	0.861

Table 2 Mean amount (µg) and standard errors (mean ± SE) of six major mandibular gland compounds, total amount and ratio = (9-ODA)/(9-ODA + 9-HDA + 10-HDAA + 10-HDA) of NLW and LW in *A. mellifera*

	Mean ± SE		*t*	*p*
	NLW	LW		
HOB	0.320 ± 0.133	0.049 ± 0.020	2.177	0.037
9-ODA	0.068 ± 0.009	0.127 ± 0.017	2.842	0.001
HVA	0.005 ± 0.004	0.057 ± 0.025	2.660	0.012
9-HDA	1.213 ± 0.237	2.044 ± 0.312	2.124	0.042
10-HDAA	0.422 ± 0.160	3.250 ± 1.007	2.785	0.009
10-HDA	0.558 ± 0.254	5.204 ± 1.837	2.562	0.015
Amount	2.587 ± 0.622	10.733 ± 2.995	2.647	0.013
Ratio	0.056 ± 0.014	0.033 ± 0.006	1.536	0.135

In 18 *A. mellifera* samples, all absolute amounts (µg) of mandibular gland compounds were significantly different between LW and NLW (*t* test: HOB: $t = 2.177$, $p = 0.037$; 9-ODA: $t = 2.842$, $p = 0.001$; HVA: $t = 2.660$, $p = 0.012$; 9-HDA: $t = 2.124$, $p = 0.042$; 10-HDAA: $t = 2.785$, $p = 0.009$ and 10-HDA: $t = 2.562$, $p = 0.015$) (Table 2).

The increase in 9-HDA when comparing non-laying workers with laying workers in *A. cerana* is 179.3%, whereas it is only 68.5% in *A. mellifera*. Similar for 9-ODA, where in *A. cerana*, it increased by 585.7% and only 86.8% in *A mellifera* (Tables 1, 2).

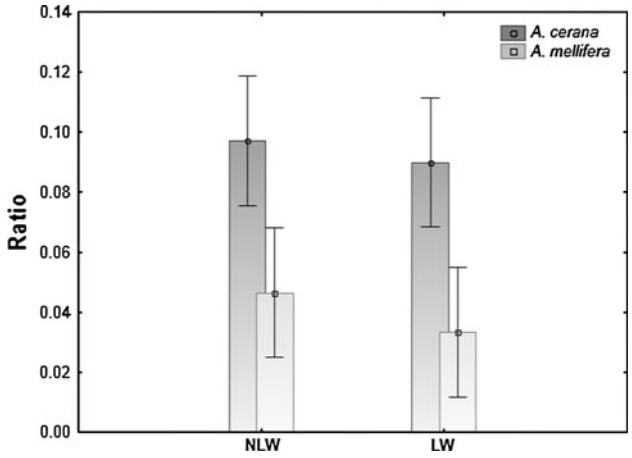

Fig. 1 Mean and standard errors (mean ± SE) of the ratio 9-ODA/(9-ODA + 9-HAD + 10-HDA + 10-HDAA) in non-laying workers (NLW) and laying workers (LW) of *A. cerana* and *A. mellifera*

The ratio (9-ODA)/(9-ODA + 9-HDA + 10-HDAA + 10-HDA) between NLW and LW in *A. cerana* was not significantly different ($t = 0.177$, $p = 0.861$), nor in *A. mellifera* ($t = 1.536$, $p = 0.135$) (Tables 1, 2). There was no significant difference in the ratio of NLW between *A. cerana* and *A. mellifera* ($t = 1.045$, $p = 0.304$), but the ratio of LW of *A. cerana* was significantly higher than *A. mellifera* ($t = 2.447$, $p = 0.019$) (Fig. 1).

Discussion

Our results show that in both species, certain pheromone bouquet components have significantly higher total amounts in LW as compared to NLW. In particular, the queen compounds 9-ODA and 9-HDA of *A. cerana* were about seven and three times higher respectively, whilst in *A. mellifera* these compounds were only about twice as high in LW compared with NLW (Tables 1, 2). This is consistent with the previous studies which showed that *A. cerana* has a significantly higher queen bias (9-ODA presence) than *A. mellifera* (Keeling et al. 2001; Pirk et al. 2011 for *A. cerana*; Crewe and Velthuis 1980 for *A. mellifera*). When comparing NLW with LW in both species, *A. cerana* and *A. mellifera*, showed no significant differences in the ratio (9-ODA)(9-ODA + 9-HDA + 10-HDAA + 10-HDA), in both species the 9-ODA compound amount increased significantly in the LW, as did most of other pheromone components.

Similarly to previous studies (Moritz et al. 2004), our results suggest that the compounds used to calculate the ratios are indeed sensitive indicators of the biosynthetic investment in queen substance. In queenless colonies of both *A. mellifera* and *A. cerana*, some workers become highly reproductive (Sakagami 1954), and produce queen-like pheromones (Sole et al. 2002). These pheromones inhibit reproductive development of other workers. The importance of these pheromones is founded on their multiple functions in signalling reproductive status and allowing individuals to prevent reproduction by their nestmates (Velthuis et al. 1990; Moritz et al. 2000; Simon et al. 2005; Dietemann et al. 2007).

Our study is consistent with the previous work showing that social regulation in *A. cerana* is more easily disturbed than in European *A. mellifera* (Tan et al. 2009). In queenright European *A. mellifera* colonies, <0.8% of workers had activated ovaries; this increased to 39.4% in queenlees and broodless colonies (Tan et al. 2009). The queen dominates reproduction and the vast majority of workers are unable to attempt reproduction when she is present. In contrast, over 4.6% of workers in queenright *A. cerana* colonies had active ovaries and this increased to 72.1% in queenlees and broodless colonies (Tan et al. 2009). We suggest that the fast activation of queen-like pheromonal bouquet of some *A. cerana* workers, comparable to *A. m. capensis* (Zheng et al. 2010) allows them to compete with each other in egg reproductive dominance in queenless colony. Workers of a queenless colony not only compete with fellow nestmates but also non-nestmates (Nanork et al. 2007). Therefore, workers are selected to become reproductive dominant comparable to *A. m. capensis* (Moritz et al. 2008) to out-compete fellow workers when it is time to reproduce. Indeed that could explain why the pheromonal production is significantly higher in *A. cerana* as compared to the European *A. mellifera*, the former workers have to "control" more.

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