

Queen signal bias in ovarian activation in mixed-species colonies of honeybees

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Ovarian activation in workers of queenright and queenless, conspecific and mixed-species colonies of the honeybees, *Apis cerana* and *Apis mellifera* was studied to investigate whether queen signal bias occurs in mixed species colonies of honeybees. And, if so how could chemical communication in honeybees achieve colony homeostasis. Measurements of the mandibular gland pheromones showed that *A. cerana* queens had a significantly higher mean 9-ODA/(9-ODA+10-HDA+10-HDAA) ratio (0.96 ± 0.02) than *A. mellifera* (0.86 ± 0.05) queens. We found that queens of both species inhibit ovarian activation in conspecific workers to the same degree. In contrast, *A. cerana* workers showed significantly greater ovarian activation in queenright mixed-species colonies than in their respective conspecific queenright colonies. Moreover, there was significantly greater and faster ovarian activation in *A. cerana* workers in the mixed-species colonies headed by *A. mellifera* queens than of *A. mellifera* workers in mixed-species colonies headed by *A. cerana* queens. *A. mellifera* workers in conspecific queenless colonies showed significantly greater ovarian activation than those in the mixed-species queenless colonies containing *A. cerana* and *A. mellifera* workers, and conversely in queenless *A. cerana*. The rates and extent of ovarian activation in the two groups of queenless colonies, *A. mellifera* and *A. cerana*, differed significantly. Because *A. cerana* queens have a significantly stronger queen-biased signal than *A. mellifera* queens, we conclude that this interspecific bias of queen signals largely accounts for the greater rate and extent of ovarian activation in *A. cerana* workers in mixed-species colonies headed by *A. mellifera* queens. However, this does not preclude the possibility that interspecific worker-worker interactions in mixed-species colonies contribute to ovarian inhibition.

Keywords: *Apis mellifera*, *Apis cerana*, worker, ovarian activation, pheromones

Predator-prey coevolution: differential behavioural reactions of *Apis cerana* and *A. mellifera* to a predatory wasp, *Vespa velutina*

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The vespine wasp, *Vespa velutina*, specializes in hawking honeybee foragers returning to their nests, which was studied in China using native *Apis cerana* and introduced *A. mellifera* colonies. When the wasps are hawking, *A. cerana* recruits three-fold more guard bees to stave off predation than *A. mellifera*. The former also utilizes wing-shimmering as a visual pattern disruption mechanism, which is not shown by *A. mellifera*. *A. cerana* foragers halve the time of normal flight needed to dart into the nest entrance, while *A. mellifera* actually slows down in sashaying flight manoeuvres. *V. velutina* preferentially hawks *A. mellifera* foragers, when both *A. mellifera* and *A. cerana* occur in the same apiary. The pace of wasp-hawking was highest in mid-summer but the frequency of hawking wasps was three times higher at *A. mellifera* colonies than at the *A. cerana* colonies. The wasps were taking *A. mellifera* foragers at a frequency eight-fold greater than *A. cerana* foragers. The final hawking success rates of the wasps were about three times higher for *A. mellifera* foragers than for *A. cerana*.

Defensiveness of honeybee colonies of *Apis cerana* and *Apis mellifera* (actively balling the wasps but reduction of foraging) against predatory wasps, *Vespa velutina*, and false wasps was assessed. There were significantly more worker bees in balls of the former than latter. Core temperatures in a ball around a live wasp of *A. cerana* were significantly higher than those of *A. mellifera*, and also significantly more when exposed to false wasps. Core temperatures of bee balls exposed to false wasps were significantly lower than those exposed to *V. velutina* for both *A. cerana* and for *A. mellifera*. The lethal thermal limits for *V. velutina*, *A. cerana* and *A. mellifera* were significantly different, so that both species of honeybees have a thermal safety factor in heat-killing such wasp predators. During wasp attacks at the hives measured at 3, 6 and 12 min, the numbers of *Apis cerana cerana* and *Apis cerana indica* bees continuing to forage were significantly reduced with increased wasp attack time. Tropical lowland *A. c. indica* reduced foraging rates significantly more than the highland *c. cerana* bees; but, there was no significant effect on foraging by *A. mellifera*. The latency to recovery of honeybee foraging was significantly greater the longer the duration of wasp attacks. The results show remarkable thermal fine-tuning in a co-evolving predator-prey relationship.

Keywords *A. cerana* . *A. mellifera* . Defense . Balling temperature . Hornet . *Vespa velutina* co-evolution