

Research article

## Nestmate recognition by guards of the Asian hive bee *Apis cerana*

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**Abstract.** When a honey bee colony becomes queenless and broodless its only reproductive option is for some of its workers to produce sons before the colony perishes. However, for this to be possible the policing of worker-laid eggs must be curtailed and this provides the opportunity for queenless colonies to be reproductively parasitized by workers from other nests. Such reproductive parasitism is known to occur in *Apis florea* and *A. cerana*. Microsatellite analyses of worker samples have demonstrated that the proportion of non-natal workers present in an *A. cerana* colony declines after a colony is made queenless. This observation suggests that queenless *A. cerana* colonies may be more vigilant in repelling potentially parasitic non-natal workers than queenright colonies. We compared rates of nestmate and non-nestmate acceptance in both queenright and queenless *A. cerana* colonies using standard assays and showed that there is no statistical difference between the proportion of non-nestmate workers that are rejected in queenless and queenright colonies. We also show that, contrary to earlier reports, *A. cerana* guards are able to discriminate nestmate workers from non-nestmates, and that they reject significantly more non-nestmate workers than nestmate workers.

**Keywords:** *Apis cerana*, guard, worker reproductive parasitism, kin recognition.

### Introduction

Worker reproductive parasitism (WRP) occurs when an insect worker leaves her colony, joins another, and lays eggs there. The importance of WRP as a reproductive option for insect workers is becoming increasingly recognized, as is the necessity of colony-level defense strategies against such parasitism (Neumann et al., 2001; Birmingham et al., 2004; Lopez-Vaamonde et al., 2004; Nanork et al., 2005; 2006; 2007; Hartel et al., 2006a; 2006b; Beekman and Oldroyd, 2008). Much of this research has centered on the honey bee (*Apis* spp.). *Apis* colonies have two primary defense mechanisms against WRP. First, non-nestmate workers are often rejected from the nest entrance in a process known as 'guarding' (Moore et al., 1987; Winston, 1987). Second, worker-laid eggs in queenright colonies (nestmates' and non-nestmates') are recognized as such and are destroyed by the resident workers in a process known as worker policing (Ratnieks and Visscher, 1989; Ratnieks and Wenseleers, 2005; 2008). However, when an *Apis* colony becomes queenless and has failed to raise a replacement queen (i.e. it is hopelessly queenless) the workers must activate their ovaries and cease worker policing in order to successfully raise drone (male) offspring (Miller and Ratnieks, 2001). The cessation of worker policing leaves the queenless colony vulnerable to WRP (Nanork et al., 2005; 2007).

In the red dwarf honey bee, *A. florea*, workers are more likely to join queenless colonies than queenright ones and these non-nestmate workers are more likely to come from other queenless colonies than queenright ones (unpubl. obs. NCC). This suggests that parasitic workers adaptively target queenless colonies, where they have the opportunity for personal reproduction, rather than queenright colonies

where there is minimal chance of successful reproduction due to the effective policing of worker-laid eggs. Non-natal workers in queenless colonies of *A. florea* (Nanork et al., 2005) and the Asian hive bee *A. cerana* (Nanork et al., 2007) have disproportionately higher reproductive success than natal workers.

Non-natal workers have been found in colonies of all *Apis* species that have been investigated (Pfeiffer and Craillshheim, 1998; Paar et al., 2002; Nanork et al., 2005, 2007). Under favourable foraging conditions, i.e. an abundance of nectar-or-pollen-producing flowers, guards of *A. mellifera* colonies are highly permissive, and will allow up to 100% of non-nestmate workers to enter their nest (Downs and Ratnieks, 2000). However, with respect to WRP these non-nestmate workers pose little threat to their host colony, because effective worker policing removes any eggs that they may lay. For example, although 1–5% of *A. cerana* workers have active ovaries in queenright colonies (Oldroyd et al., 2001; Nanork et al., 2007), no males are sons of workers, due to the effective policing of worker-laid eggs (Oldroyd et al., 2001) so the presence of laying workers, non-natal or natal incurs no or minimal costs to the host colony.

When foraging conditions are poor, *A. mellifera* colonies defend themselves against intra-specific robbery by increasing the number and vigilance of guards so that the proportion of non-nestmates that are allowed to enter the colony decreases relative to periods when floral resources are abundant (Ribbands, 1954; Downs and Ratnieks, 2000). Downs and Ratnieks (2000) tested acceptance of nestmates and non-nestmates over a 30 day period; at the beginning 80% of nestmates were accepted, while only 25% of non-nestmates were accepted. As the experiment continued floral resources improved, and by the end of the experiment nearly 100% of test bees were accepted regardless of their origin. Hence, guards adjust their rejection threshold appropriately depending on the likelihood that non-nestmates will attempt to rob the colony (Downs and Ratnieks, 2000).

The proportion of non-natal workers present in colonies of *A. cerana* declines significantly from 4.3% when queenright to 1.8% when queenless (Nanork et al., 2007). In contrast, the proportion of non-natal workers present in queenless *A. florea* colonies increases significantly from 2% when queenright to 4.5% when queenless. Furthermore, *A. florea* shows much higher rates of WRP than does *A. cerana* (Nanork et al., 2005, 2007). It has been proposed that nest architecture may be responsible for this difference, with the cavity-nesting *A. cerana* able to guard the entrance and deter reproductive parasites from entering the colony, whereas open-nesting *A. florea* is less able to defend its nest from conspecifics (Nanork et al., 2007).

In *A. mellifera* guard workers stand at the entrance to their nest and inspect workers entering the colony (Butler and Free, 1952; Herman and Blum, 1981; Moore et al., 1987). The guards use odor cues (e.g. Breed, 1998; Downs and Ratnieks, 1999) to recognize nestmates and non-

nestmates, and guards are often reported to harass and remove non-nestmates.

Very little is known about guarding behaviour in *A. cerana*. Breed et al. (2007) swapped the locations of pairs of *A. cerana* colonies, and reported that there was little sign of aggression when non-nestmate foragers entered each translocated nest. Furthermore, bioassays in which two non-nestmates were paired in an arena revealed that aggression rarely occurred between non-kin pairs of *A. cerana* (Breed et al., 2007). Breed et al. (2007) concluded that nestmate recognition is poorly developed in *A. cerana*, possibly due to the rarity of intra-specific robbery in this species.

Here we explore the possibility that *A. cerana* uses guarding as a defence against WRP by preventing non-nestmates from entering colonies once they have lost their queen. We determined whether *A. cerana* is able to discriminate between nestmates and non-nestmates using an experimental set-up previously used in *A. mellifera* (Downs and Ratnieks, 1999). We compared the vigilance of guards of queenless and queenright colonies, as measured by the proportion of nestmate and non-nestmate workers admitted to the colony. If queenless colonies reject more test workers then the decrease in proportion of non-natal workers in queenless colonies observed by Nanork et al. (2007) is probably caused by the increased vigilance of the queenless guards. If rejection rates remain unchanged, the decrease in non-natal workers is more likely to be due to their removal from the colony after queenlessness or reduced rates of worker drifting into queenless colonies.

## Methods

We utilized 6 *A. cerana* colonies of the black 'Hill' morph of *A. cerana* (Oldroyd et al., 2006), located at the Raman Research Institute, Bangalore, India in November 2007. There was ample pollen and nectar for forage available from plantations of *Eucalyptus camaldulensis*. Due to the honey flow, we provided the colonies with one frame of foundation comb on November 6, 2007 and more as needed. As environmental cues transferred via wax comb are involved in nest-mate recognition (Breed et al., 1988, 1995; Beekman et al., 2002a; D'Ettorre et al., 2006) we avoided using drawn combs. All colonies were housed in standard *A. cerana* hive boxes and were each headed by a naturally mated queen. We applied grease to the stands of each colony, and sat the stands in water to minimize attacks by ants.

We conducted blind tests of guarding behaviour beginning on November 11, 2007 using a procedure adapted from Downs and Ratnieks (1999). We collected approximately thirty workers from the outer comb of a colony using a pooter, disturbing the colony as little as possible. The standard protocol for evaluating guarding behavior (Downs and Ratnieks, 1999) utilizes returning foragers, but we did not follow this method as some colonies were observed to forage for pollen much more than others, and would have resulted in the test not being blind. Nurse bees are usually found on the inner combs where the brood is raised, while foragers tend to be found on the outer combs (Seeley, 1985; Winston, 1987). Thus, by sampling bees from the outer comb we increased the chances of sampling foragers. We transferred the aspirated workers into a sealable plastic bag along with a small folded piece of paper to identify the origin of the sample. We also collected workers from an unrelated (non-nestmate) colony into an identical plastic bag using the same method. We cooled the bees in an ice box so

that they could walk but not fly. We then tested the acceptance of the nestmate and non-nestmate workers by the focal colony. Using forceps we placed a worker on the entrance board of the colony and observed the reaction of the guards. If the test worker was bitten, had its legs, antennae or wings pulled, or was mauled or removed from the colony then this was recorded as rejection. Acceptance required that the test worker be inspected by at least one guard and not be subjected to the above rejection behaviour. We observed each test worker for the duration of any interaction (approximately 5 minutes) before removing it from the entrance board. We then offered the colony a worker from the other bag, continuing to alternate between bags until a total of ten workers from each bag (nestmate or non-nestmate) had been tested. No test worker was used more than once and the observer was unaware of the contents of each bag (nestmate or non-nestmate) until all observations were completed. This protocol was then repeated in each of the other 5 colonies. After observations on day 5 we dequeened half the colonies selected at random and confirmed the presence of the queen in the remaining colonies. We removed queen cells from the queenless colonies on days 9 and 10 and disturbed the queenright colonies to a similar extent. Observations resumed on day 10, when the queenless colonies no longer had larvae and continued until day 14 using the same procedure as above. Each colony acted as both a donor and receiver each day and was randomly paired with a colony each day, thus controlling for the possibility that there was an effect of queenstate of donor bees on the likelihood of acceptance.

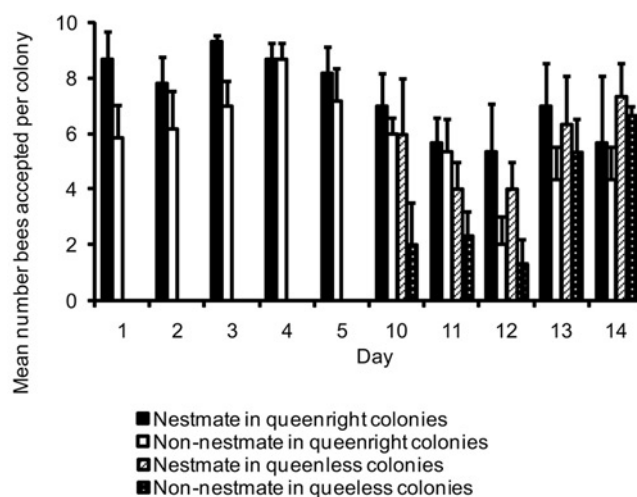
In *A. cerana* laying workers become active within 3 days of dequeening, and worker-laid eggs are observed within 4 days of dequeening indicating that at least some worker-laid eggs are acceptable after 4 days and therefore that worker policing is curtailed (Oldroyd et al., 2001; Nanork et al., 2007). Hence our queenless colonies were vulnerable to WRP during the assays. We did not examine colonies for the presence of laying workers during the experiment as we wished to cause as little disturbance as possible; however after observations were completed on the last day of the experiment we observed worker-laid eggs in all queenless colonies.

### Statistics

Prior to analysis we transformed the data with an  $\text{asin}\sqrt{X}$  transformation (Fowler et al., 1998). We analysed the proportion of accepted workers using a repeated measures ANOVA with day as the within-subject variable, and worker origin (nestmate or non-nestmate) as the main effect. During the period where half the colonies were queenless we analysed the proportion of non-nestmate workers accepted with day as the within-subject variable, and queenstate (queenright or queenless) as the main effect. Mauchly's test was performed to test that the assumption of sphericity (equality of the variances of the differences between levels of the repeated measures factors) was not violated.

### Results

The assumption of sphericity was violated when all days were considered (Mauchly's test:  $W < 0.001$ ,  $\chi^2_{44} = 73.49$ ,  $P = 0.011$ ) and therefore we report the  $F$  statistics calculated with the Greenhouse-Geisser correction to degrees of freedom. Non-nestmate workers were rejected significantly more than nestmate workers when all days were considered (days 1–5 and 10–14; Table 1; Fig. 1), when only days 1–5 were considered ( $P = 0.027$ ) and was marginally significant on days 10–14 ( $P = 0.051$ ). Only days 1 ( $P = 0.043$ ) and 12 ( $P = 0.022$ ) were significant individually. There was a significant effect of day, showing that environmental conditions influence the rate of bee



**Figure 1.** Mean and standard error of the untransformed number of nestmate and non-nestmate bees accepted into queenright and queenless colonies. Half of the colonies were dequeened after observations on day 5. Over all days of the experiment, nestmates were accepted significantly more often than non-nestmates ( $P = 0.005$ ). Queenstate does not affect the proportion of test bees accepted into colonies ( $P = 0.134$ ).

acceptance (Table 1). There was no significant interaction between day and origin (nestmate or non-nestmate), showing that the proportion of non-nestmate workers accepted relative to nestmate workers accepted did not change (Table 1).

Sphericity was not violated when considering days 10–14, when half of the colonies were queenless (Mauchly's test:  $W = 0.168$ ,  $\chi^2_9 = 13.24$ ,  $P = 0.162$ ) and therefore we report the  $F$  statistics with sphericity assumed. There was no statistical difference between the proportion of non-nestmate workers rejected in queenless and queenright colonies (Table 2) and there was no significant effect of day. On day 14 significantly more test bees (nestmate and non-nestmate) were accepted into queenless colonies than into queenright colonies (Table 2;  $P = 0.007$ ). Queenstate did not affect the number of test bees

**Table 1.** Repeated measures ANOVA of the  $\text{asin}\sqrt{X}$  transformation of the proportion of bees accepted for all days (1–5, 10–14) of the experiment. Worker origin (nestmate or non-nestmate) is the main effect. Day is the within-subject variable.

Source	d.f.	M.S.	$F$	$P$	Power
Between-subjects effects					
Origin	1	5662.76	13.08	0.005	0.90
Error	10	433.10			
Within-subjects effects					
Day	3.71	5017.87	7.07	<0.001	0.99
Day x Origin	3.71	510.30	0.72	0.575	0.20
Error (day)	37.09	710.05			

accepted on any other day, however the interaction between day and queenstate (queenright or queenless) was significant (Table 2). The interaction between day, state and origin was not significant and was therefore removed from the model.

**Table 2.** Repeated measures ANOVA of the  $\text{asin}\sqrt{X}$  transformation of the proportion of bees accepted for days 10–14 of the experiment, when half of the colonies were queenless. Queenstate (queenright or queenless) and origin (nestmate or non-nestmate) are the main effects. Day is the within-subject variable.

Source	d.f.	M.S.	<i>F</i>	<i>P</i>	Power
Between-subjects effects					
State	1	207.02	2.71	0.134	0.31
Origin	1	385.09	5.05	0.051	0.52
Error	9	76.30			
Within-subjects effects					
Day	4	61.89	1.51	0.219	0.42
Day x State	4	133.27	3.26	0.022	0.78
Day x Origin	4	38.21	0.93	0.456	0.27
Error (day)	36	40.94			

## Discussion

Our results show that *A. cerana* guards reject non-nestmates significantly more often than they do nestmates. This shows that *A. cerana* guards have the ability to discriminate nestmates from non-nestmates and that they use this ability to prevent non-nestmates from entering their colony in a manner similar to *A. mellifera* (Butler and Free, 1952; Hermann and Blum, 1981; Moore et al., 1987; Downs and Ratnieks, 2000). Breed et al. (2007) and Sasagawa et al. (2002) reported that aggressive interactions between non-nestmates are uncommon when *A. cerana* workers from different colonies are paired in an arena. In light of our results, we suggest that this bioassay is inappropriate for detecting nestmate recognition in *A. cerana*, Downs and Ratnieks (2000) noted that *A. mellifera* guards treated in this manner stopped behaving like guards. Perhaps *A. cerana* workers react strongly to confinement and therefore do not react to the presence of the other bee.

During times of abundant floral resources, guards of *A. mellifera* accepted up to 100% of the nestmates and non-nestmates offered to them (Downs and Ratnieks, 2000). Our experiment was conducted during a time of floral abundance and hence the proportion of bees accepted was high. The difference between the proportion of nestmates and non-nestmates accepted, while being significant when pooled for all days, was significant on only two days out of ten and the difference in terms of the number of bees was small. It is likely that the guarding behaviour would have been less permissive during our experiment had not the environmental conditions been so favourable.

Nanork et al. (2007) showed that after *A. cerana* colonies were dequeened, the mean proportion of non-natal workers declined from 4.3% to 1.8%. We hypothesized that this decline might be associated with heightened guarding activity, which reduces the number of non-natal workers in a colony. However, we show here that there is no statistical difference in aggression toward non-nestmates by queenright and queenless colonies when the data from all days were pooled. In fact, contrary to our expectation, queenless colonies were found to accept significantly more non-nestmate workers than queenright colonies on day 14, suggesting that if anything there may be a trend for queenless colonies to become more permissive of non-natal workers than queenright colonies.

A similar counter-intuitive decrease in the aggression of guards in queenless colonies has been found in *A. mellifera*, where queenless colonies were found to sting a target significantly less than queenright colonies (Delaplane and Harbo, 1987). Furthermore, in South Africa where colonies of *A. m. scutellata* are frequently parasitized by workers from *A. m. capensis* (Beekman et al., 2002b, 2008) queenless colonies do not show an increase in guarding (Beekman et al., 2002b). This is despite the fact that queenless *A. m. scutellata* colonies are more likely to be targeted by *A. m. capensis* workers than queenright colonies (Neumann et al., 2001)

We conclude that the observed decline in the proportion of non-natal workers observed in *A. cerana* colonies after they are dequeened (Nanork et al., 2007) is apparently not caused by increased vigilance by guards at the nest entrance. Thus we suggest that nestmate recognition has no role as a response to WRP in the honey bee and evolved solely to prevent intra-specific robbing.

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