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Recapping behavior in *Apis cerana*: does it contribute to resistance against *Varroa* spp.?

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ABSTRACT

The invasion of the ectoparasitic mite *Varroa destructor* into European honey bee, *Apis mellifera*, populations has contributed to the collapse of most wild populations and economic losses in beekeeping operations. Understanding how some *A. mellifera* populations survive infestation by this parasite is of great fundamental and practical interest and has led to numerous studies of potential resistance mechanisms. One such mechanism is the uncapping and recapping of comb cells containing infested brood by nurse bees. Recapping has been observed in most surviving populations, but its link to *V. destructor* resistance remains unclear. Investigating the occurrence of recapping in the Eastern honey bee, *Apis cerana*, the original host of the parasite, could provide a better understanding of the evolution and function of this behaviour in the *Apis* genus. Here, we determined the frequency of recapping in two *A. cerana* populations in China and Thailand at different stages of brood development and compared them with a sympatric *A. mellifera* population in China. The species, which differ in their susceptibility to infestation, did not show significant differences in recapping frequency. A specific association between recapping and resistance to *Varroa* spp. in *A. cerana* is therefore not supported. We discuss possible functions and evolutionary scenarios for this behavior.

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Apis cerana; *Apis mellifera*; recapping; resistance; *Varroa* spp

Introduction

Much of the increase in honey bee, *Apis mellifera*, colony losses experienced by beekeepers in the last decades and the near eradication of the wild *A. mellifera* populations of European origin is due to infestations by an invasive lineage of the ectoparasitic mite *Varroa destructor* (Le Conte et al., 2010; Dietemann et al., 2012; Traynor et al. 2020; Hristov et al., 2021). This mite shifted from its original and co-adapted host *Apis cerana* to *A. mellifera* when the latter was introduced into the former's distribution range (Rosenkranz et al., 2010; Traynor et al. 2020). Because of this new parasite, the survival of *A. mellifera* stock of European origin depends on annual varroacide treatments (Rosenkranz et al., 2010; Bubnič et al., 2021; Jack & Ellis, 2021; Hernandez et al., 2022). However, some populations of *A. mellifera* survive infestation without treatments (Locke, 2016; Mondet et al., 2020). Several resistance traits affecting mite survival or reproduction have been proposed as the cause for their ability to survive in the presence of the parasite (Locke, 2016; Guichard et al., 2020; Mondet et al., 2020). These observations led to selection attempts to increase the frequency of these traits in the stocks and increase their ability to resist *V. destructor* infestation, as a solution to the "Varroa problem" that was considered more sustainable than the use of varroacides (Dietemann et al., 2012). However, these attempts showed limited success (Guichard et al., 2020; Le Conte et al., 2020) and a better understanding of resistance mechanisms and traits is still needed to promote progress in resistance selection (Dietemann et al., 2012; Guichard et al., 2020). Recently, recapping, which consists in adult workers opening and closing again the brood cells in which the parasite reproduces, has

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received renewed attention after it was first described in the 1990s (Boecking & Spivak, 1999). Recapping, was proposed as a key resistance mechanism in *A. mellifera* (Oddie et al., 2017). This trait was subsequently observed in most surviving *A. mellifera* populations but has no direct effect on *V. destructor* reproduction (Harris et al., 2012; Oddie et al., 2018; Martin et al., 2020; Hawkins & Martin, 2021) and its expression varies widely within susceptible and surviving populations (Grindrod & Martin, 2021; Oddie et al., 2021). Thus, the contribution of this behaviour to *V. destructor* resistance remains unclear and controversial (van Alphen et al., 2019; Hawkins & Martin, 2021; Oddie et al., 2021).

To better understand the relationship between recapping and *V. destructor* resistance and adaptive value in *Apis* spp., it is necessary to investigate its occurrence in *A. cerana* (Grindrod & Martin, 2023), the original and co-adapted host of *V. destructor* (Traynor et al., 2020; Lin et al., 2021). Previous quantification of recapping in *A. cerana* did not allow deriving a representative picture of the different contexts in which this behavior may be expressed because i) only brood cells experimentally infested with live or dead mites were considered, ii) were therefore based on the presence versus absence of previously introduced mites, and iii) did not distinguish recapped cells from those in which the brood had been removed by hygienic behavior (Rath & Drescher, 2010, Tewarson et al. 1992, Rosenkranz et al., 1993). We therefore quantified the proportion of recapped brood cells in *A. cerana*, irrespective of their infestation status using the presence or absence of silk under the wax cap (Oddie et al., 2018). Using this method, the recapping rates of two populations of *A. cerana* could be compared with the recapping rate in sympatric *A. mellifera* colonies to one of these populations and with figures available in the literature for *A. mellifera*. The *A. cerana* populations studied belonged to the morphocluster IV (Radloff et al., 2010) from Chiang Mai, Thailand, hosting mainly *V. jacobsoni* (Dietemann et al., 2019), and to the morphocluster I (Radloff et al., 2010) from Hangzhou, China, which hosts *V. destructor* (Lin et al., 2021). Our aims were i) to assess whether the expression of this behavior differed according to the contrasting levels of resistance of the original and new host species to *Varroa* spp. and ii) to gain insight into the possible causes of this behavior. For the latter aim, we determined whether recapping rates were associated with the developmental status of the brood occupying the recapped cells of both species. If recapping rates reach a plateau before the end of the developmental period, it is likely that causal factors occur before a certain stage is reached or are associated with a brood damage threshold (as for example in the case of hygienic removal of *V. destructor*-infested brood, Lin et al., 2018; Spivak & Danka, 2020). Alternatively, if it is observed to increase until imago emergence, the probability for occurrence increases with time and is not tied to a particular stage (e.g., increasing probability of mechanical damage to the cap over time or infection outcomes independent of brood developmental stage).

The similarity of the recapping rates measured in *A. cerana* and *A. mellifera* and the increased rates of recapping along host development are discussed in relation to the role of this behavior in the resistance to *Varroa* spp. infestation.

Materials and methods

Honey bee colonies used

In March 2020, four *A. cerana* colonies of the mainland lineage morphocluster IV were screened in Chiang Mai, Thailand. From April to May 2020, six *A. cerana* colonies of the mainland lineage morphocluster I and seven *A. mellifera ligustica* colonies kept in the same apiary on the campus of Zhejiang University, Hangzhou were used. The *A. mellifera* colonies were treated with fluvalinate against *V. destructor* and *Tropilaelaps* sp. to ensure their survival. The *A. cerana* colonies did not require such treatment.

Recapping diagnosis and data recording

The cells screened for recapping were randomly selected on worker brood combs. A mean number (SD, range) of 105 (42, 63–161) worker cells for *A. cerana* in Thailand, 209 (11, 195–228) for *A. cerana* in China and 224 (26, 198–267) for *A. mellifera* in China were examined for recapping. To determine whether a cell was recapped, the cap was carefully lifted in one piece with fine tweezers. If all or part of the silk cocoon spun by the larvae had been removed during uncapping, the cells were classified as recapped (Oddie et al., 2018). Occasionally, the caps showing missing silk were perforated (Figure 1). In some cases, perforated caps with no missing silk (except where the hole was located) were observed. These cells may have been in the process of uncapping and were not considered as recapped. To quantify the occurrence of this phenomenon, these cells were counted separately in Thailand. Recently capped cells containing larvae are still in the process of cocoon spinning, making it difficult to determine the recapping status. Therefore, cells containing larvae were excluded from the analysis. As workers only had two days to recap cells containing prepupae, these were excluded from the comparison of recapping rates among populations and species. However, for completeness, they were included in the comparison of recapping rates between host developmental stages. To allow comparisons of brood development between host species with

Figure 1. Experimentally opened cells showing an intact wax cap (left) and a cap with a partially missing silk layer and a hole (right), indicating that the cell was uncapped and partially recapped.

Figure 2. Developmental stages *A. cerana* workers. From left to right: larva, prepupa, white-eyed pupa, pink-eyed pupa, purple-eyed pupa, yellow thorax pupa, grey thorax pupa, pre-emergent adult, adapted from Human et al. (2013).

a different pupal developmental time (one day shorter in *A. cerana*, Oldroyd & Wongsiri, 2009), the host development stage was assessed rather than the number of days after cell capping. The developmental stages of *A. cerana* (Figure 2) were determined after removing the brood from the recapped cells and by analogy with those of *A. mellifera* (Human et al., 2013).

Recapping of *A. cerana* drone cells was not expected to occur due to the natural occurrence of holes in the caps (Boecking et al., 1999) and of the entombing behavior, through which unhealthy individuals remain sequestrated in their cells (Rath, 1999) and was therefore not investigated.

In Thailand, the *V. destructor* infestation rate of the cells screened for recapping was determined after removing the brood from the cells and inspecting both cells and brood for the presence of adult or immature mites (Dietemann et al., 2013).

Data analysis

We used generalized linear mixed models run in R 4.2.1 (R Core Team, 2022) with package lme4 (Bates et al., 2015) to investigate the factors associated with recapping rates in the three populations studied: *A. cerana* Thailand, *A. cerana* China, and *A. mellifera* China. The number of recapped and non-recapped cells was modeled with honey bee population as a fixed factor and colony identity as a random factor. Overdispersion was assessed with blmeco 1.4 (Korner-Nievergelt et al., 2015) and overdisp_fun (Bolker et al., 2022) to verify that the observed variance was not higher than the variance predicted by the model. Significance levels for fixed factors were obtained using the package car 3.1–0 (Fox & Weisberg, 2018). Pairwise comparisons between populations were performed using emmeans 1.8.0 (Lenth et al., 2022) with Tukey's adjustment for multiple comparisons.

The relationship between recapping and brood developmental stage in *A. cerana* and *A. mellifera* in China was modeled in the same way, with brood developmental stage and honey bee species as fixed factors and colony identity as a random factor. The full model included the interaction between the fixed factors. Whether this interaction was needed in the final model was assessed by comparing the Akaike and Bayesian Information Criteria of models including and excluding this term.

The packages ggplot2 3.3.6 and ggforce 0.3.4 were used for plots.

Results

Recapping rates

Recapping of worker brood occurred in both *A. cerana* populations screened. Mean recapping rates (SD) of *A. cerana* worker brood in Thai ($N = 4$) and Chinese ($N = 6$) colonies were 42.2% (16.3%) and 17.9% (8.9%), respectively, and were not significantly different (Figure 3, Table S1). In China, the recapping rates of *A. cerana* and *A. mellifera* colonies were not significantly different, with a mean (SD) of 20.3% (18.9%) for the latter (Figure 3, Table S1). No overdispersion was observed (Table S1). Recapping rates were not significantly

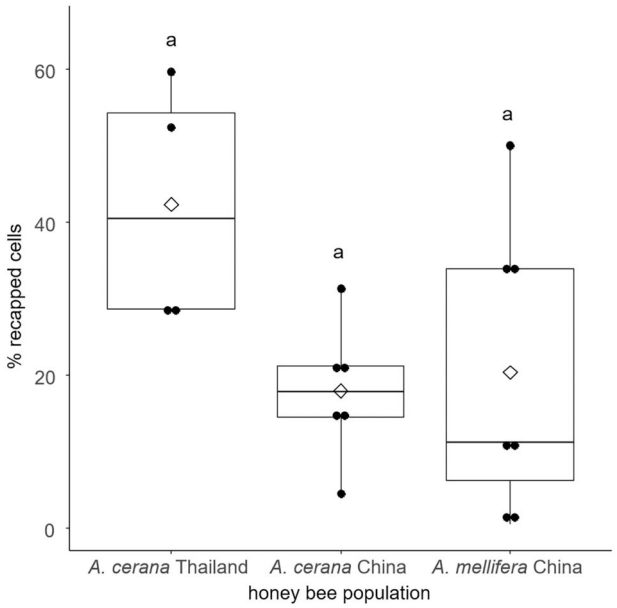

Figure 3. Percentage of recapped cells in the three populations studied: *A. cerana* in Chiang Mai, Thailand and *A. cerana* and *A. mellifera* in Hangzhou, China. Diamonds denote the mean, horizontal lines the median, boxes the first and third quartiles and black dots are the data points. Different letters indicate significant differences; see Table S1 for details of the statistical output.

different across all three populations, but were close to significance (Chi-square = 5.5, df = 2, $p = 0.06$).

Approximately one-fifth (mean = 18.5%, SD = 4.0%, range = 14.4 – 23.2%) of the cells examined in the Thai *A. cerana* colonies showed a perforation without silk missing under the rest of the cap.

The infestation rates of *A. cerana* worker brood in Thailand had a mean (SD, range) of 0.6 (0.7, 0.0–1.4) mites per 100 workers. One of the two infested cells found had been recapped.

Variation in recapping rate during brood development

The interaction term species*developmental stage did not improve the model and was therefore discarded (Table S2). The data show that in Hangzhou, China, the recapping rate was not significantly different between the honey bee species (Chi-square = 0.2, df = 1, $p = 0.66$), but that it varied significantly with brood development stage (Chi-square = 90.8, df = 6, $p < 0.001$). No overdispersion was found (Table S3). Recapping rates increased as brood development progressed (Figure 4 for the two species pooled) to reach a mean (SD) of 40.9% (31.2%) and 27.8% (26.7%) in pre-emergence adults in *A. cerana* and *A. mellifera*, respectively (Tables S4 and S5).

Discussion

Differences in recapping rates between *A. cerana* and *A. mellifera* colonies varied widely within in a similar range. As a result, the Thai and Chinese *A. cerana* and *A. mellifera* populations studied did not differ significantly in recapping rates, with *A. mellifera* having mean recapping rates intermediate between the two *A. cerana* populations and individual values at both extremes of the range measured in the study. In both species, the rate of recapping increased as brood development progressed.

One-fifth of the cell caps in Thai *A. cerana* colonies were perforated but did not lack silk beyond the hole itself. These cells may have been in the process of being uncapped and not yet recapped. Their presence was not reported in *A. mellifera*. This difference in the occurrence of holes in the caps between the species suggests that the uncapping/recapping process is slower in *A. cerana* than in *A. mellifera*.

The Thai *A. cerana* colonies showed a mean recapping rate of 42% (Figure 3), which is intermediate between the mean rates reported for *A. mellifera* populations surviving *V. destructor* infestation and susceptible populations (Martin et al., 2020; Grindrod & Martin, 2021). By contrast, with an average of 20% of cells recapped (Figure 3), the recapping rates in Chinese *A. cerana* colonies were lower than in Thai colonies of this species, although not significantly so, with a p-value just above the 0.05 threshold (Table S1). A larger sample size may have produced a significant difference. The variation in recapping rates between and within the two *A. cerana* populations studied could be due to several reasons. As we only measured recapping rates at a single time point, we may not have captured a representative moment of recapping activity in these colonies. Such variation could be due to different triggering factors such as cryptic pathogen infections or unidentified environmental factors. Tewarson et al. (1992) found a fairly constant recapping rate in *A. cerana* colonies over two to three months in two years, but as they did not distinguish recapping from hygienic behavior and as variations could occur over longer periods, seasonal changes in recapping rates should be investigated in more detail.

We found no evidence that *Varroa* spp. infestation triggered recapping, as few of the cells screened in the Thai *A. cerana* colonies were infested, consistent with the rates reported by Wang et al. (2020) in this population. However, a causal relationship between *Varroa* spp. and the recapping behavior cannot be excluded, as the mite foundresses could have escaped after the cells were uncapped and before they were recapped (Rosenkranz et al. 1993). To verify their previous presence in a cell they left, the occurrence of mite dejections should be verified, which was not done in this study. However, the recapping rates observed are inconsistent with the rare presence of mites in the brood examined. Although mites leaving their cells after uncapping may infest other cells about

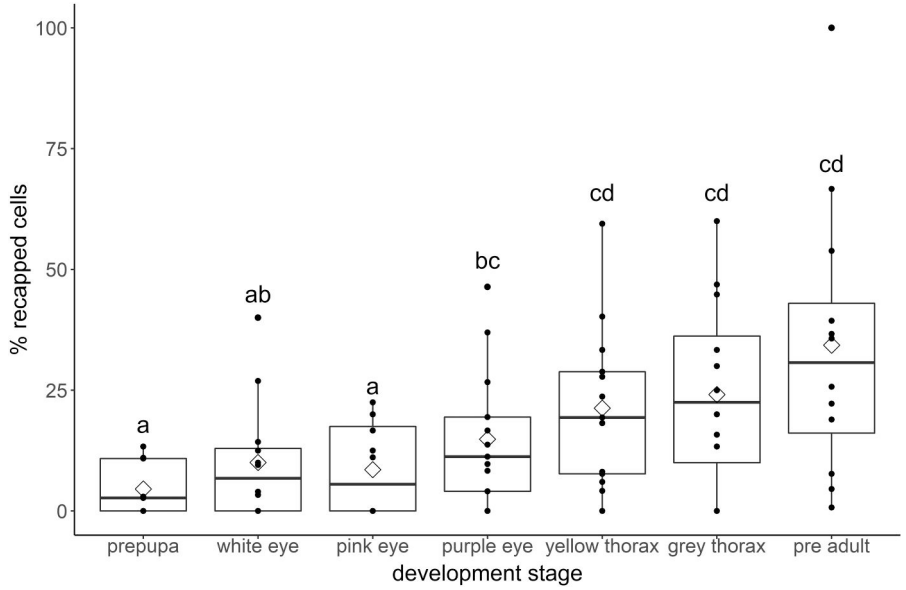

Figure 4. Adjusted probabilities for recapping rate in *A. cerana* and *A. mellifera* in Hangzhou, China, according to brood development stage. The GLMM showed no significant differences in the recapping rate between the two species and data were pooled. Different letters indicate significant differences, see Table S2 for details of the statistical output. Pre adult stands for pre-emergence adults. Diamonds denote the mean, horizontal lines the median, boxes the first and third quartiles and black dots are the data points. Plots and analyses for each species separately are presented in Tables S4 and S5.

to be capped, the resulting serial recapping events triggered by individual mites are unlikely to result in more than 40% of the cells being recapped. Infestation by *Varroa* spp. as the sole trigger for recapping and subsequent hygienic removal (Rath, 1999; Grindrod & Martin, 2021) is also unlikely because recapping rates increased steadily as brood development progressed. Because hygienic removal induced by *V. destructor* peaks three days after capping and then levels off (Lin et al., 2018), a plateau in recapping rates should have been observed instead of a constant increase until imago emergence. As there was no significant difference in the relationship between recapping rates and developmental stage between *A. cerana* and *A. mellifera* (Table S3), the previously reported weak correspondence between *V. destructor* and hygienic removal in *A. mellifera* is supported (Guichard et al., 2020, Spivak & Danka, 2020).

The weak proximal relationship between *Varroa* spp. infestation and recapping in *A. cerana*, the relatively low recapping rates measured in *A. cerana* close to the average recapping rates of *A, mellifera* susceptible populations (Grindrod & Martin, 2021), and the overlap in recapping rates between *A. cerana* and *A. mellifera* (Figure 3) do not support the hypothesis of a strong and specific relationship with *V. destructor* resistance in *A. cerana*.

Pathogens other than *V. destructor* could cause *A. cerana* to nurse bees to open and recap brood cells to inspect their contents. It is, therefore, necessary to investigate whether viruses and bacteria or combinations of pathogens can cause recapping. Such an effect is likely since, for example, DWV infection levels have been reported to correlate with the intensity of hygienic removal in *A. mellifera* (Schöning et al., 2012). Differences in infection levels and other environmental factors (e.g., varroacidal treatments in *A. mellifera*) could explain the observed variation in recapping rates among colonies and populations examined in our study and others. The role of physical damage to *A. cerana* caps should also be considered as a cause of recapping. Because the caps made by *A. cerana* are very thin and much more fragile than those of *A. mellifera* (unpublished data), they can be easily damaged. The likelihood of damages requiring repairs increases with time and could explain the increasing recapping rates observed during brood development (Figure 4).

The cause and function of recapping in *Apis* spp. are still poorly understood (Guichard et al., 2023). Because of the high recapping rate observed in *A. cerana* worker brood in the virtual absence of *Varroa* spp. infestation, it is unlikely that this behavior has evolved specifically as part of a *Varroa* spp. resistance mechanism and could be triggered by various as yet unidentified causes of brood disturbance (e.g., viral or bacterial infection, Rath, 1999; Spivak & Danka, 2020) or wax cap damage (this study). Nevertheless, recapping may have been co-opted in *A. mellifera* to contribute to colony survival to *V. destructor* infestation (Oddie et al., 2018; Spivak & Danka, 2020; Grindrod & Martin, 2021; Oddie et al., 2021) or may be linked to another resistance mechanism through a pleiotropic effect. As the expression of resistance factors may vary in time and space (Moro et al., 2021; von Virag et al., 2022), measurements of recapping in *A. cerana* and *A. mellifera* should be repeated at intervals in individual colonies in different populations. In addition, its triggering

factors should be identified to gain a better understanding of the function, adaptive value and evolution of this behavior in the genus *Apis*.

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Disclosure statement

No potential competing interests were reported by the authors.

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Data availability statement

Raw data are provided in supplementary material Tables S6 and S7.

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