



A destructive host-shift

A comparative review of resistance mechanisms
in the novel and original hosts of *Varroa*
destructor

Elin Sjögren Englund

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Swedish University of Agricultural Sciences, SLU

Faculty of Natural Resources and Agricultural Sciences • Department of Ecology

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Elin Sjögren Englund

Supervisor: Barbara Locke Grandér, SLU, Department of Ecology

Assistant supervisor: Nicholas Scaramella, SLU, Department of Ecology

Examiner: Eva Forsgren, SLU, Department of Ecology

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Swedish University of Agricultural Sciences

Faculty of Natural Resources and Agricultural Sciences

Department of Ecology

Abstract

Apiculture has a major antagonist in *Varroa destructor*, the ectoparasitic mite that has become the most prominent driver of colony losses for the European honey bee, *Apis mellifera*. This was not always the case, as *V. destructor* is native to Asia and originally only infested the Asian honey bee, *Apis cerana*. As these two species have co-evolved, *A. cerana* colonies can coexist with the mite, in contrast to colonies of *A. mellifera*, which die within 2-3 years, unless treated.

This review explores the differences in the coevolved and the novel parasite-host relationships and tries to determine what factors have made *V. destructor* so successful in *A. mellifera*. The resistance of *A. cerana* is multi-variate, but the two behaviors that are considered the most important are social apoptosis, which denies *V. destructor* from worker brood infestation, and grooming, which reduces mite populations when drone brood is not produced. *A. mellifera* lacks the former and is less effective at the latter.

Many effects of resistance behaviors and factors on varroa infestation are not quantified, making comparisons between them difficult. There are also many factors that remain largely unexplored by the scientific community such as entombing of drone brood, bee damage on mites, swarming, absconding and colony size, that could have an effect. This obscures what behaviors really have an effect in Varroa resistance.

As we look into the future of the Varroa-honey bee relationship, there is hope in resistant variants of *A. mellifera*. However, whether resistant behaviors are compatible with market needs remains to be seen, as current treatments for Varroa control continue to be effective.

Keywords: *Varroa destructor*, *Apis cerana*, *Apis mellifera*, host-shift

Table of contents

1.	Introduction	5
1.1	Varroa <i>destructor</i> and the host-shift	5
1.2	Varroosis and viruses	6
1.3	Solutions and treatment	7
1.4	Scope	7
2.	Conditions for Varroa reproduction in the two species.....	8
2.1	Reproductive success	8
2.2	Social apoptosis in worker brood	9
2.3	Mutual destruction and entombing in drone brood	11
3.	Grooming and dispersal mites	12
3.1	Grooming	12
4.	Transmission between colonies.....	14
4.1	Mite density and dispersal	14
4.2	Swarming and absconding.....	15
5.	The potential for co-evolution in the novel host.....	17
5.1	Resistant bees	17
5.2	Adaptability and plasticity of <i>V. destructor</i>	18
6.	Conclusion.....	19
	References	20
	Acknowledgements.....	28

1. Introduction

Invasive species is a major threat to biodiversity, and bring with it both economic and ecological damage (IPBES, 2019). As highly specialized organisms, parasites are usually restricted to the distribution range of their hosts, but some manage to shift hosts and become invasive (Neumann & Elzen 2004; Singh et al. 2013; Kuchta et al. 2018; Theodosopoulos et al. 2021). This can be a consequence of new allopatric conditions, where a parasite get access to a host-species closely related to its original host (Engelstädter & Fortuna 2019). Honey bees have exchanged several invasive parasites in the last century as a result of global export and beekeeping of the European honey bee *Apis mellifera* (Neumann & Elzen 2004; Roberts et al. 2015; Steinhauer et al. 2018; Sakamoto et al. 2020). The most notable of these is the mite *Varroa destructor*.

1.1 *Varroa destructor* and the host-shift

When *A. mellifera* was imported to East Asia in the late 19th century for its superior honey production, it came into contact with its close relative, the Asian honey bee *Apis cerana* (Sakai & Okada 1973; Ruttner & Maul 1983). This artificial sympatric distribution led to increased contact between the two species and an opportunity for the ectoparasitic mite *Varroa destructor* to shift hosts from *A. cerana* to *A. mellifera* (Anderson & Trueman 2000; Techer et al. 2022). The first documented infestation of *V. destructor* on *A. mellifera* occurred in Japan in 1957 (Crane 1984). The mite has since spread outside of its natural distribution range, due to human-mediated translocation of infested honey bee colonies, into all continents except Antarctica and Australia (Rosenkranz et al. 2010).

V. destructor and *A. cerana* have coevolved into a stable parasite-host relationship, where *A. cerana* colonies are usually infested with mites, but have low mite quantities and most importantly, do not die from infestation (Wang et al. 2020). In contrast, the relationship between *A. mellifera* and *V. destructor* has proven to be detrimental. As most infested colonies die within 2-3 years unless beekeepers treat them, *V. destructor* has become one of the most important drivers of colony losses globally (Rosenkranz et al. 2010; Steinhauer et al. 2018). Wild and feral populations of *A. mellifera* are assumed to have declined since the introduction

of *V. destructor*, but there is not enough data on their abundance to draw conclusions (Kohl & Rutschmann 2018).

V. destructor was presumed to be the closely related mite *Varroa jacobsoni* until 2000, when it was first described as a separate species (Anderson & Trueman 2000). Consequently, all literature published before 2000 refer to the mite as *V. jacobsoni*. The two species are closely related but infest different subspecies of *A. cerana*, which has put them on different evolutionary trajectories (Techer et al. 2019). *V. destructor* infest *A. cerana* in most of mainland Asia, except India, and *V. jacobsoni* infests Indian, Malay, Indonesian and Filipino populations (Anderson & Trueman 2000; Chantawannakul et al. 2016; Techer et al. 2019). It is only in Thailand that their infestation of *A. cerana* overlap (Techer et al. 2019). Until recently *V. destructor* was the only Varroa species that parasitized *A. mellifera*, but in 2008 a host-shift in *V. jacobsoni* was discovered on Papua New Guinea (Roberts et al. 2015). *V. destructor* has however proven to be the more harmful of the two.

1.2 Varroosis and viruses

V. destructor is a brood parasite that reproduces on the pupating bee and use adult bees for dispersal. As *A. mellifera* has no native brood parasites, it is ill-equipped to deal with this new invasive parasite (Eickwort 1994). The mite feeds on the fat body of its host, an organ unique to insects which is important for embryogenesis, immune function and hormonal regulation (Arrese & Soulages 2010; Ramsey et al. 2019). Varroa infestation causes decreased homing ability, higher mortality, and altered response to stimuli in the individual bee (Kralj & Fuchs 2006; Kralj et al. 2007; Yang & Cox-Foster 2007). It's however not the mite itself that causes the most damage to bee colonies.

The most devastating effects of the *V. destructor* mite is in fact due to its role as a vector for multiple honey bee viruses. Deformed Wing Virus (DWV), is the most common varroa mite-associated virus and considered to be one of the major drivers of colony loss (Yang & Cox-Foster 2007; Dainat et al. 2012; Wilfert et al. 2016). It is transmitted to developing pupae by the feeding of the mite during its reproductive phase and infected bees emerge as adults with symptomatic deformed wings and a shortened life-span (Bailey & Ball 1991; Dainat et al. 2012). It has even been suggested that *A. mellifera* can survive Varroa infestation in the absence of DWV, as *A. mellifera* populations in Papua New Guinea infested with *V. jacobsoni* without DWV, show resilience (Roberts et al. 2020). The increased prevalence of DWV caused by *V. destructor* has brought on a trickle-down effect of DWV onto wild pollinators such as bumble bees, as *A. mellifera* functions as a reservoir for the virus (Fürst et al. 2014; Wilfert et al. 2016). Therefore, the spread of *V. destructor* has the potential to be a threat to not only apiculture, but to pollinator diversity as well.

1.3 Solutions and treatment

There are of course methods for varroa control. Chemical treatments like synthetic acaricides and organic acids are the most effective against colony losses (Haber et al. 2019). All synthetic acaricides have however been shown to induce resistance in Varroa (Haber et al. 2019). There are other methods that take advantage of the reproductive biology of varroa, like drone frames and reproduction breaks, but these has proven less effective (*ibid.*). Which brings us to the possibility of resistant bees, that could have the potential to be a no effort, cost-effective solution. If *A. cerana* can handle the mite, why couldn't *A. mellifera*?

This review intends to explore the differences between how the original and novel host cope with *V. destructor* and in doing so try to understand the evolutionary context of this mite, why it has become so successful in its new host and identify the knowledge gaps in the original host-parasite system. Finally, this review will shortly speculate about the emergence of resistant populations of *A. mellifera* in Europe and North America and the possibility of coevolution between *A. mellifera* and *V. destructor*.

1.4 Scope

A. mellifera and *A. cerana* have wide distribution ranges, high diversity with many subspecies and occur both as wild or feral colonies and as kept colonies in apiaries. This introduces potentially confounding effects as climate, genetic diversity and apiculture may modify Varroa infestation and bee behavior (Martin & Medina 2004; Giacobino et al. 2016; Loftus et al. 2016). These effects are studied to some degree in *A. mellifera*, but less so in *A. cerana*. Furthermore, there are many haplotypes of *V. destructor*, only two of which, the Korean and Japan haplotypes, parasitizes *A. mellifera*. These haplotypes have variants with differences in reproductive success in both *A. cerana* and *A. mellifera* (Beaurepaire et al. 2015; Lin et al. 2021). As these discoveries are quite new, there is still little data on specific differences between these genetic variants and how these affect their infestation of the honey bees. With this in mind, this review will focus on susceptible variants of *A. mellifera*, *A. cerana* within the native range of *V. destructor*, and their behavioral responses to the Korean haplotype of *V. destructor*.

2. Conditions for Varroa reproduction in the two species

The abundance of mites in a colony are directly correlated to the survival of a colony, as viral titers of DWV increase with its mite vector (Francis et al. 2013). In *A. cerana*, mite populations stabilize at less than 800 mites in a colony, whereas mite populations in *A. mellifera* grow until the colony collapses. This is considered to be mostly an effect of differential mite reproduction in *A. mellifera* and *A. cerana* (Martin & Medina 2004).

V. destructor reproduces on pupating bees. To succeed, it needs to infest the brood cell before it's capped by a nurse bee. As the mite has no acoustic or visual perception, it relies on chemical cues to orient itself (Dillier et al. 2006). The same pheromone that acts as a cue for nurse bees to cap the cell, also acts as a kairomone that induces Varroa to infest the cell just before capping (Le Conte et al. 1990). There is a difference between chemical attraction between new and original host, as Varroa is more attracted to the cuticular hydrocarbons of *A. mellifera* brood than *A. cerana* brood (Li et al. 2021). Whether this preference is a consequence of adaption in *A. cerana* to become less attractive, or a response of Varroa to higher fitness in *A. mellifera* is not known.

In *A. cerana*, the mite infests both worker and drone brood, but can only reproduce in drone brood successfully, as opposed to in *A. mellifera*, where the mite can reproduce on both types of brood (Koeniger et al. 1981). Mites are up to 12 times more likely to infest drone cells than worker cells in *A. mellifera* in natural conditions (Fuchs 1990). This is because drone cell openings are physically larger and drones receive more visits by nurse bees (Boot et al. 1995; Martin 1995a; Calderone & Kuenen 2003). It seems that Varroa cannot chemically distinguish worker and drone brood, meaning it is unlikely that the mite has a direct preference for drone brood (Calderone & Lin 2001).

2.1 Reproductive success

The foundress mite begins laying its eggs 70 hours after infestation at intervals of 30 hours, with one male egg laid first, and the rest being female offspring (Martin 1994). The male mates with its sisters within the brood cell, unless there are

daughters from another foundress mite (Traynor et al. 2020). The female mites take 130 h to fully mature, which limits how many mite offspring can be produced in each brood cell before the pupating bee emerges as an adult (Martin 1994). In *A. mellifera* this limits production to a maximum of 3 females in worker brood and 5 in drone brood (Martin 1994, 1995a). *A. cerana* drone brood has a similar developing time to *A. mellifera* drones, and hence the mite can produce a maximum of 5 females (Martin 1995a). Mean reproductive success is 2.1-2.2 female mites/cell in *A. mellifera* and *A. cerana* drone cells and 1.0-1.5 female mites/cell in *A. mellifera* worker cells (Martin 1995b). This difference in brood types could be an effect of lower infertility rates in mites on drone brood in addition to the longer duration of drone development (Martin 1995a). Although the drone brood only constitutes 5-15 % of the total brood in a colony and are only produced during swarming season, the higher reproductive success in drone brood has shown to have a positive effect on mite population size later in the season in *A. mellifera* (Fuchs 1990; Kraus et al. 2007).

Infestation of multiple foundresses in a single brood cell is the only way to introduce genetic exchange, but competition restricts successful reproduction, more so in *A. mellifera* than in *A. cerana* (Boot et al. 1997). This is mainly due to competition in feeding between offspring (Martin 1995b). Overall, *A. cerana* have a higher percentage of multiple infestations than *A. mellifera*, as there is fewer brood cells to parasitize (Wang et al. 2020).

2.2 Social apoptosis in worker brood

The most important characteristic of the stable parasite-host relationship between *A. cerana* and *V. destructor* is the social apoptosis of worker brood (Rath 1999). This behavior is analogous to apoptosis in multicellular organisms, where a damaged cell goes through programmed cell death for the benefit of the organism as a whole. Eusocial insects can similarly take benefit in sacrificing individuals for the good of the colony. *A. cerana* sacrifices its worker brood to kill off infesting Varroa, reducing the mites' reproductive resource to drone brood only. This colony level resistance mechanism is a consequence of both brood sensitivity and nurse bee vigilance.

Even a benign wounding, simulating Varroa chelicerae without any injection of Varroa saliva, kills about 15 % of *A. cerana* worker brood and induces a brood removal by nurse bees of 40 % of disturbed brood, a sensitivity not present in *A. mellifera* (Page et al. 2016). In addition, the salivary compound Varroa saliva toxic protein (VTP) is toxic to *A. cerana* larvae, causing abnormal development in 70 % of brood and death (Page et al. 2016; Zhang & Han 2018). In *A. mellifera* worker brood, VTP instead increase titers of DWV causing a higher rate of adults with deformed wings, handicapping the colony (Zhang & Han 2018). These different

outcomes are likely caused by differences in the immune response to VTP (Balakrishnan et al. 2021).

The Varroa mites can continue to infest and reproduce on the *A. cerana* brood, even as it develops abnormally (Lin et al. 2018). It is instead the *A. cerana* nurse bees that prevent mite reproduction by removing abnormally developed larvae, cleaning out 90 % of infested worker cells (Rath & Drescher 1990; Lin et al. 2018). As *A. mellifera* has a lower degree of abnormal development, 20 %, in response to Varroa infestation and is less efficient at cleaning out dead or abnormal brood, the removal response from worker bees to infested worker brood is much lower at less than 20 % (Rath & Drescher 1990; Lin et al. 2016, 2018).

In addition to cleaning out and thereby prohibiting Varroa proliferation, *A. cerana* has been observed cannibalizing dead brood and thereby retaining energy within the colony (Rath & Drescher 1990). Cannibalism has been shown to be a transmission route for DWV and increase spread of the virus within *A. mellifera* colonies (Posada-Florez et al. 2021). As *A. cerana* is faster at hygienic behavior than *A. mellifera*, the bees who clean out infested cells have a decreased risk of getting infected by viruses, as there is less time for proliferation (Lin et al. 2016). Cannibalism should therefore have less impact on DWV spread in *A. cerana* colonies than in *A. mellifera*.

To mitigate the cost of killing brood, the social apoptosis is complemented with a mite removal behavior in *A. cerana*. When an infested cell is noticed, a worker bee can remove the cell cap, clean out accessible mites, and then recap it (Rath & Drescher 1990; Rosenkranz et al. 1993). This behavior is triggered by the presence of both dead and alive mites, and has been observed in 40 % of mite infested worker cells (*ibid.*). *A. mellifera* has been observed doing this in 10 % of infested brood (Rosenkranz et al. 1993). Whether *A. mellifera* clean out mites to this degree is questionable, as the mites in this experiment were sourced from *A. cerana* colonies and may have been more easily detected than if they would have been sourced from *A. mellifera* colonies.

A possible key to how *A. cerana* can invest so much time and effort in its brood is that the proportion of workers per brood cell is higher than in *A. mellifera*, with a proportion of 1.32 and 0.88, respectively (Kraus et al. 1998). The investment can however be said to pay off when the consequences of infested workers in *A. mellifera* are considered.

A. mellifera worker brood that has been infested during development show behavioral alterations in nursing, foraging and other hive chores, and are overall less active in all life stages (Annoscia et al. 2015). The biggest difference is in the reduction of nursing and foraging behaviors, with the latter likely being caused by their shorter lifespans (Annoscia et al. 2015). Given that workers do all the work to maintain the colony, this change in activity is detrimental to brood rearing and colony balance in general, weakening the colony. It could also have a negative

effect on the already low resistance behaviors of *A. mellifera*, such as mite and brood removal. These negative effects do not occur on *A. cerana* since Varroa only reproduce on drone brood.

2.3 Mutual destruction and entombing in drone brood

The drone cells of *A. cerana* and *A. mellifera* differ physiologically, which has consequences for how they interact with Varroa infested drone brood. In the *A. cerana* drone cell the workers remove the wax cap after the cocoon is spun, exposing the hard conical cell cap of the cocoon (Hänel & Ruttner 1985). The cell cap is impervious to workers and can only be broken through by the apical tooth of the emerging drones, which presents the possibility of a mutual destruction scenario (Koeniger et al. 1983; Davis & Prabhuswamy 2000).

If mites kill or weaken drones too much, they will die in a tomb of their own making (Koeniger et al. 1983). This is especially the case for multiply infested brood cells, as 70-80 % these drones either die or lack the strength to emerge (Rath 1999). Depending on the rate of multiple infestations, this has been estimated to affect up to $\frac{1}{4}$ of the reproductive Varroa population in *A. cerana* (Rath 1999). Workers of *A. cerana* can also kill drone brood by actively entombing them. Gas exchange in drone pupae occurs through a central pore in the hard cell cap (Rath 1992). If worker bees detect abnormal brood, they seal the pore with wax, killing both the brood and mites inside (Boecking 1999). On the one hand, these negative feedback mechanisms suppress high mite rates in drone brood, but on the other hand, bees cannot clean out mites to save brood. Given that drones constitute all mite reproduction in *A. cerana*, this behavior could have a considerable negative impact on Varroa populations, but it has not been quantified in natural conditions.

A. mellifera have no trouble perforating and removing its drone cell caps, as they lack the hard conical cell cap of *A. cerana* (Davis & Prabhuswamy 2000). Hence, *A. mellifera* do clean out about 32 % drone brood (Martin 1995a). However, this is independent of infestation rates, and it is unclear whether the cleaned-out cells have higher infestation rates than the remaining cells (*ibid.*).

3. Grooming and dispersal mites

After reproduction in the cell the mites emerge with the new bee. In their dispersal phase, mites have a high preference for nurse bees, which are a cohort of bees with the specialized task to care for larvae and cap the cell with wax when the larvae are mature for pupation (Piccolo et al. 2010; Xie et al. 2016). Infesting nurse bees increases the likelihood of the mite being introduced to the next available brood cell, where it can reproduce (Xie et al. 2016). But there aren't always brood cells available.

V. destructor has evolved in a seasonal context, where drone brood are only available for short periods of the year. *A. cerana* only produce drones in the reproductive season, hence the mite has to be able to sustain itself in a dispersal state for months by attaching itself to workers and eating from their fat bodies (Chinh et al. 2005). Unlike the larvae, the adult workers have means to detect and remove intruders.

To protect itself, *V. destructor* has a high placement preference on the left side of the bee abdomen, where there is a reduced risk for grooming (Delfinado-Baker et al. 1992). To reduce detection, the mite mimic the cuticular hydrocarbons of its host, thus masking itself as part of the bee (Kather et al. 2015). After the host-shift, the mites on *A. cerana* and *A. mellifera* diverged in their mimicry, making mites sourced from *A. cerana* better at mimicry than mites from *A. mellifera* in mimicking both species (Le Conte et al. 2015).

3.1 Grooming

The grooming behavior of *A. cerana* and *A. mellifera* differs in both frequency, efficacy, and behavior. *A. mellifera* use self-grooming to some extent whereas *A. cerana* display both self-grooming and social grooming at higher rates (Peng et al. 1987; Büchler et al. 1992; Fries et al. 1996; Diao et al. 2018). The social grooming of *A. cerana* is stimulated by a shaking “dance”, after which a nearby worker uses its mandibles to comb through the infested bees hairs to remove the intruder (Büchler et al. 1992). As a result of these differences *A. cerana* is more successful than *A. mellifera* in removing mites (Büchler et al. 1992; Fries et al. 1996; Diao et al. 2018). Among mites that has been removed through grooming, mites from *A.*

cerana display a higher degree of damage than in *A. mellifera*, 29 % and 12 % respectively (Fries et al. 1996).

The differential grooming behaviors in *A. cerana* and *A. mellifera* is not necessarily applicable to all species of parasites. When comparing the grooming of *A. cerana* and *A. mellifera* in response to the tracheal mite *Acarapis woodi*, native to *A. mellifera*, the roles are reversed. *A. mellifera* shows a higher grooming response than *A. cerana* (Sakamoto et al. 2020). *A. cerana* is not necessarily intrinsically better at grooming, but specifically better adapted to Varroa mite infestation.

Many experiments that have compared grooming behavior between *A. mellifera* and *A. cerana* have exclusively taken mites from *A. mellifera* colonies, which can exaggerate the grooming rate and efficiency of *A. cerana* (Büchler et al. 1992). There is however still a difference between *A. mellifera* and *A. cerana* in the successful removal of mites, even when *A. cerana* bees are infested with mites from *A. cerana* colonies (Büchler et al. 1992). No studies on mite damage in *A. cerana* have however used *A. cerana* as a mite source, making these damage rates unreliable. All studies on grooming have been done in a lab setting where mites have been actively placed on bees, making it difficult to quantify the real effect of grooming in a natural environment. Given how long *V. destructor* is in dispersal in *A. cerana*, it would be surprising if this behavior is as effective as it is reported to be in some studies, as the mite then should go extinct.

4. Transmission between colonies

The dispersal phase is also when the mites have the opportunity to spread to other colonies, taking advantage of the bee behaviors of robbing, drifting and swarming. Infesting a new colony typically increases the fitness of the individual mite, as *V. destructor* has a density dependent reproduction success (Fuchs 1992). As infestation is widespread in both species, dispersal does not seem to be a limiting factor in the success of *V. destructor* in apiaries (Wang et al. 2020). There is however very little data on feral and wild populations, but given the high colony density in apiaries, it would be expected that infestation rate is lower in sparse, wild populations. Dispersal rates and distances of *V. destructor* are largely unexplored, but one study show that spread is as efficient at 1 km as 1.5 km (Frey et al. 2011).

In apiaries, *A. mellifera* can have colony sizes up to 50 000, with a median colony at 20 000, contrasting the 6 000 to 7 000 bees in wild *A. cerana* colonies (Seeley et al. 1982; Costa-Leonardo et al. 2008; Döke et al. 2019). Whether this is of consequence for Varroa infestation is not studied, but in *A. mellifera* there is a difference in infestation in small and large hives, where smaller hives are less likely to die due to Varroa infestation (Loftus et al. 2016). Whether the small colony sizes of *A. cerana* mitigates Varroa severity is unknown, but this should be researched further.

4.1 Mite density and dispersal

The main difference in mite dispersal in *A. mellifera* and *A. cerana* is a consequence of mite density, which influence the spread of Varroa through robbery and drift. Dispersal through robbery can be caused by high mite quantities, as the prerequisite for robbery is that the colony is in bad health and unable to defend itself from other colonies trying to invade and rob it of its honey. Robbing is a common way of Varroa spread in *A. mellifera* and introduces a high number of mites to the robbing colony (Peck & Seeley 2019). As Varroa has less impact on *A. cerana* colonies, this causal effect should be weaker.

Honey bees can also switch colonies, called drifting, and thereby introduce a smaller amount of mites to neighboring colonies. Dispersal through drift is likely more common in *A. mellifera* than in *A. cerana*, namely because there is a density-

dependent effect on mite choice of phoretic host, as the mite cannot differentiate between the typically preferred nurse bees and forager bees in high mite densities (Cervo et al. 2014). This increases the likelihood of the phoretic host being a forager and thus the likelihood of dispersal through drift (Cervo et al. 2014). Although *V. destructor* can't induce drifting behavior in its forager host, the normal level of drift does spread Varroa between hives (Neumann et al. 2000; Goodwin et al. 2006). As *A. cerana* again does not have as high mite densities, this mode of dispersal is less likely.

4.2 Swarming and absconding

The last possible transmission route is by swarming. When a colony grows large enough and outgrows its hive, it divides. This is called swarming and can be likened to reproduction of colonies, where the old queen leaves with a swarm to establish a new colony. In preparation for swarming, the queen lays drone eggs and some female larvae are developed into new queens instead of worker brood, but then brood rearing is reduced to a halt (Winston 1987:188). The reduction of brood rearing lasts a total of 4 weeks from when the old queen prepares for swarming until the new queen starts reproducing (ibid.). As there are no available brood during this time, mite reproduction is prevented.

When the colony swarms, about 65-75 % of mites are left behind in the old colony on workers and in brood, whereas 25-35% leave with swarm (Wilde et al. 2005; Loftus et al. 2016). This would leave the remaining colony with higher mite-bee ratio, and the swarm with a lower mite-bee ratio. In studies where only the swarm effect on Varroa infestation has been measured, there has been no significant difference in Varroa infestation in swarming and non-swarming colonies in either swarms or swarming colonies (Fries et al. 2003). Small and frequently swarming colonies have however been shown to be less affected by Varroa (Loftus et al. 2016).

V. destructor coevolved with *A. cerana* in wild conditions, which are quite different than for kept *A. mellifera*, which are often subjected to swarm control to increase honey production (Forster 1969). The swarming of *A. cerana* is inconsistent in its distribution range, but a general feature is that even small colonies swarm, independent of crowding (Hepburn 2011). As small, frequently swarming colonies of *A. mellifera* are less sensitive to Varroa, this should also be true for *A. cerana*.

Similarly, the difference in migration patterns between *A. mellifera* and *A. cerana* could have an impact on Varroa populations in the two species. *A. cerana* tend to leave their nest site permanently and search for a new one during dearth periods, a behavior called absconding (Hepburn 2011). *A. mellifera* abscond to a much lower degree (Hepburn 2011). When the hive is about to be abandoned the

Varroa reproduction should be temporarily inhibited as brood rearing decrease in preparation for absconding (Dulta et al. 1988). The Varroa that are not in their dispersal phase are left behind, but as drones are not produced during dearth periods, this might not be a substantial number of mites. There is however evidence pointing to this type of nonreproductive swarming behavior as an adaption to pathogens and parasites (Diao & Hou 2018). As there are few studies on both absconding, swarming and their effects on Varroa, this requires more research.

5. The potential for co-evolution in the novel host

The reviewed difference in the bees' resistances to Varroa have great impact on the dynamics between parasite and host. To reduce the negative effects that *V. destructor* has on apiculture, a long-term solution would be a variant of *A. mellifera* that show as high resistance to *V. destructor* as *A. cerana* does. The question is if a stable parasite-host relationship can evolve either on its own or mediated by artificial selection. Although there are populations of *A. mellifera* where natural selection has led to increased resistance, there are some processes inhibiting the emergence of reliably resistant bees.

5.1 Resistant bees

In the relative short time that *A. mellifera* and *V. destructor* have coexisted, some populations have developed resistance to Varroa. A few European populations have a recapping behavior, which at least correlates with a reduced mite reproduction of 10-30 % (Oddie et al. 2018). The behavior entails removing the cell cap and then recapping, which is suspected to disturb Varroa reproduction (*ibid.*). Social apoptosis has also been observed in resistant variant from Russia, albeit at very low levels (Ihle et al. 2022). Small colony sizes, reduced development time for brood, grooming behaviors and frequent swarming are also characteristics found in resistant populations (Locke 2016; Loftus et al. 2016).

In Europe and North America resistant variants are still sparse. This becomes a problem as resistant genes will dilute, as queens will mate with several drones not sharing resistant genes (van Alphen & Fernhout 2020). In one population that had previously shown resistance by removal of infested brood, the behavior had disappeared within three years (Moro et al. 2021). This indicates that resistance mechanisms can be unstable. Furthermore, the use of acaricides and other means of Varroa control have impeded the natural course of selection, as survival in susceptible populations have been made artificially high (van Alphen & Fernhout 2020). But even with stable resistance, these resistant variants still need to prove useful to beekeepers and be able to compete with treated susceptible bees in the market. Whether they can do so, remains to be seen.

5.2 Adaptability and plasticity of *V. destructor*

Even with resistant variants, that still leaves the mite, which is by no means a passive traveler on its host. As implied by the developed resistance to acaricides in *V. destructor*, it has the capacity for rapid adaption to its surroundings. This could have further implications for *A. mellifera* with resistant traits, as *V. destructor* could have greater capacity than previously thought to adapt (Eliash & Mikheyev 2020).

Hybridizations between *V. jacobsoni* and *V. destructor* have been shown to be a potential inflow of genetic diversity into *V. destructor*, which could prime the species for faster adaption (Dietemann et al. 2019). In Asia, there has also been observations of additional host-shifts from other haplotypes of *V. destructor*. This could increase the gene-pool of *V. destructor* infesting *A. mellifera*, which has until now basically been two specific haplotypes with low genetic diversity (Solignac et al. 2005; Navajas et al. 2010). In 2013 there were two additional haplotypes discovered in Serbia, creating even more potential for genetic diversity (Gajic et al. 2013). These factors could complicate the work of breeding bees for high resistance. As long as *A. mellifera* continue to be in contact with the genetic reservoir populations of *A. cerana*, there will be a risk of new host-shifts and hybridizations.

6. Conclusion

While we try to find and develop stable resistant variants of *A. mellifera*, there is still much that's unknown in the original host-parasite system. If a population model could be created for *V. destructor* on *A. cerana*, where the different resistance behaviors, physiological factors and their effect are quantified, it would give a direction for what to look for in *A. mellifera* bees in terms of resistant traits. This research should be done with *V. destructor* mites from *A. cerana* colonies, so that the true thresholds for resistance can be determined. However, as infestation of worker brood has so wide-reaching consequences for the *A. mellifera* hives, reduced impact on worker brood is likely the most important factor to select for. Resistance is however multi-variate in the original host, implying that redundancy in resistant behaviors could be an important buffer for mite adaption.

There are many shared traits of *V. destructor* resistance in susceptible *A. mellifera* and resistant *A. cerana*, but frequencies and efficacy matter. When breeding for resistance, it is important to keep in mind that some resistance traits could entail unintended consequences for honey production and colony management. Smaller colony sizes and swarming would fall into this category.

Only time will tell how well *V. destructor* will adapt to new resistances in *A. mellifera*, but with continued genetic inflow from Asia, long term resistance can be hard to maintain. *A. mellifera* is right now a never-ending, non-adapted resource, as it is artificially boosted by human care, but treatment is needed to keep colonies alive. Alas, it is not ecologically or economically viable to let nature run its course, as bees are a far too important livestock that both nature and man depend on.

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