# Supplementary material

## Table SA: Data concerning the suitability of suppressed mite reproduction as a trait for resistance selection

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| **Suppressed mite reproduction (SMR)** | |
| Measurement methods: the reproduction rate of *V. destructor* foundresses is measured in brood cells containing pupae at 8–11 (Harbo and Harris, 2005) or 7–12 days post-capping (Büchler *et al*, 2017). The evaluator opens the brood cells and the presence of foundresses and male and female offspring is recorded. SMR is diagnosed when the foundress produced no offspring, only a male offspring or a non-viable male offspring resulting in unmated daughters, or when a delay in oviposition prevented the production of adult mated daughter mites prior to host emergence (Kustermann, 1990; Martin *et al*, 1997). | |
| Suitability as a resistance selection trait | |
| *Pros* | *Cons* |
| * *Brazil*: low mite reproduction in naturally surviving Africanised honey bees possibly contributing to colony survival (Camazine, 1986; Rosenkranz, 1990). * *Canada*: colonies selected for low infestation growth rates for 16 weeks show a lower proportion of reproductive mites (Emsen *et al*, 2012): host-influenced mite reproduction could have an effect on the infestation level. * *Central Europe*: in an *A. m. carnica* population, SMR significantly correlates with infestation levels in adult worker and brood samples (Buchegger *et al*, 2018). * *France*: non-reproducing mites identified in the naturally surviving Avignon population (Locke, 2016b) and in the surviving population from the Toulouse region: in the latter, the trait is linked to host genes from the ecdysone–synthesis pathway (Conlon *et al*, 2019). * *Sweden*: reciprocal crosses between a Gotland population with low mite reproduction and local susceptible lines resulted in a decrease in the rate of successful mite reproduction (at least one viable offspring produced) in all the crosses where at least one parent was of Gotland origin: low reproduction is a highly heritable trait (Locke, 2016a). * *USA*: in a population of colonies with low *V. destructor* population growth rates, the *V. destructor* reproduction rate correlated with an infestation increase (Harbo and Hoopingarner, 1997). SMR was thus chosen for the USDA selection programme. Colonies from this programme showed lower infestation rates when compared to other lines, including colonies of surviving ‘Russian’ stock (Ward *et al*, 2008). Colonies headed by SMR and hybrid queens mated with unselected drones had lower infestation levels when compared to the controls (Harbo and Harris, 2001; Harbo and Harris, 2003). | * *Europe*: no significant correlation between the *V. destructor* reproduction rate and the infestation levels of colonies from different European origins (Büchler, 1990a). * *Germany*: the fertility and fecundity of adult (German) mites infesting Gotland colonies, colonies headed by daughters from USA SMR queens and local *A. m. carnica* colonies did not differ (Weller, 2008). Mites infesting colonies headed by F2 Gotland, *A. m. mellifera*, *A. m. carnica* or *A. m. ligustica* queens did not differ in terms of fertility or fecundity (Odemer, 2019). Between 2013 and 2017, an increase in SMR in a local *A. m. carnica* population selected for low mite reproduction (Büchler, 2019), but high variation in colony values for each year. The genetic contribution through selection to this evolution was not published so far, neither were survival data. * *Italy:* No relation between infestation and the rate of non-reproducing mites in an Italian *A. m. ligustica* population subjected to diverging selection for high and low infestation levels (Lodesani *et al*, 2002).   *USA*: only a third of the variation in the growth rate could be attributed to the proportion of fertile mites together with the ratio of mites infesting brood versus adults (Harris *et al*, 2003). In another study, environmental factors rather than the genetic effects of the host explained the variations in mite reproduction, leading to the conclusion that SMR cannot be improved by selection (DeGrandi-Hoffman *et al*, 2002). Crosses between lines selected for SMR and lines selected for hygienic behaviour towards freeze-killed brood resulted in lower infestation rates in the hybrids when compared to the colonies selected for hygienic behaviour (Ibrahim *et al*, 2004; Ibrahim *et al*, 2007). Surprisingly, no differences in mite fertility or the number of viable offspring produced found between the lines (Ibrahim *et al*, 2007): it cannot be excluded that other traits than the reproduction rate contributed to the differences in infestation rates. |

## Table SB: Data concerning the suitability of Varroa sensitive hygiene as a trait for resistance selection

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| **Varroa sensitive hygiene (VSH)** | |
| Measurement methods: VSH has been measured in various ways. The most precise yet also time-consuming method involves measuring the removal of cells manually infested with *V. destructor* (Bienefeld, 1996b; Boecking *et al*, 2000; Panziera *et al*, 2017). Less effort-intensive methods measure the changes in the infestation rate of the brood frame transitorily inserted into a highly infested colony before being returned to the test colony (Danka *et al*, 2016; Danka *et al*, 2011; Harbo and Harris, 2009; Jungels, 2014; Villa *et al*, 2009; Villa *et al*, 2017). With this method, however, it is impossible to know whether the infested pupae has been removed (VSH) or whether only the mite escaped from the cells opened by the worker (uncapping–recapping, see section 1.1.1.3). A more precise method involving the use of photographs of the inserted brood frame before and after introduction to the test colony to record removed pupae has also been used (de Guzman *et al*, 2015; Oddie *et al*, 2017). It allows for the determination of whether the reduction in infestation measured following the opening of remaining brood cells correlates with brood removal or not. However, this approach does not indicate whether the removed brood was infested or not. For research purposes, the time-consuming analysis of video recordings can help to identify the workers performing the task (Bienefeld *et al*, 2002; Boecking, 1994). This can be useful when later genotyping the individuals involved in removal or using workers to produce drones in experimental selection programmes (Bienefeld *et al*, 2002). A comparison of the different VSH protocols, as was performed for the hygienic tests (see section 1.1.1.4), is currently unavailable to help choose the best protocol, minimise costs and maximise precision. | |
| Suitability as a resistance selection trait | |
| *Pros* | *Cons* |
| * *France*: in colonies with low infestations, honey bees tended to have a lower sensitivity threshold to recognise single-infested cells than honey bees from highly infested colonies (Martin *et al*, 2001). * *Germany*: the removal of infested brood occurred (Boecking and Drescher, 1992) and possibly depended on the viral load of the mites (Boecking, 1994; Schoning *et al*, 2012): VSH may be a defence mechanism against both *V. destructor* and its associated viruses.   *USA*: colonies selected for VSH reduced the infestation levels of foreign brood (-80%) significantly more when compared to F1 colonies (about -30%) and controls (about -0%) (Danka *et al*, 2011). It is not known whether the reduction of the brood infestation rate is due to brood removal or to mites leaving cells opened by workers. In colonies of Russian line, the removal of infested brood is suggested as the main reason for reduced infestation levels when compared to controls (de Guzman *et al*, 2015). In this line, negative correlation (r = -0.25) was measured between the removal of infested brood and the colony infestation level (Kirrane *et al*, 2015): VSH could directly contribute to limiting the infestation level. | * *Germany*: the removal reaction of colonies with high VSH ability towards infested brood is stronger in the case of multiple infestations than single infestation (Boecking and Drescher, 1992), which suggests limited efficiency at low infestation levels. The results of repeated tests on the same colonies correlated with about r = 0.6 (Boecking, 1994); measuring the removal rates after feeding the colonies with sugar water doubled the values when compared to conditions without feeding (Boecking, 1994): values obtained in beekeeping conditions, when many environmental factors are not under control, may result in high variations between evaluation dates. |

## Table SC: Data concerning the suitability of uncapping–recapping as a trait for resistance selection

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| **Uncapping*–*recapping** | |
| Measurement methods: several methods were used to measure the frequency of uncapping*–*recapping. Some studies recorded the percentage of removed mites without the removal of the pupae in artificial infestation experiments (Aumeier *et al*, 2000), whereas recent publications investigated the presence or absence of cocoon silk on the inner side of the cell cap. The absence of silk indicates that the cell has been opened and resealed by workers (Büchler *et al*, 2017; Harris *et al*, 2012). | |
| Suitability as a resistance selection trait | |
| *Pros* | *Cons* |
| * *Europe* and the *USA*: significant correlation between the rate of recapped cells and infestation levels in brood (Buchegger *et al*, 2018; Villegas and Villa, 2006) and adult workers (Buchegger *et al*, 2018): uncapping*–*recapping could be a mechanism used by honey bees to limit infestation. * *France*, *Norway* and *Sweden*: naturally surviving colonies more frequently uncapped and recapped infested cells than local susceptible colonies. Uncapping/recapping is linked to lower mite reproduction in the targeted brood cells (Oddie *et al*, 2018): this mechanism could contribute to colony survival in the studied populations. * *South Africa* and *Brazil*: naturally surviving honey bees presented much higher levels of recapping than naive populations analysed in *Australia* and the *United Kingdom* (Martin *et al*, 2019), so uncapping*–*recapping could have been naturally selected in the resistant populations. | None found so far, although there are few studies on this trait. |

## Table SD: Data concerning the suitability of hygienic behaviour towards dead brood as a trait for resistance selection

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| **Hygienic behaviour towards dead brood** | |
| Measurement methods: the degree of hygienic behaviour of a colony is measured as the removal rate of dead worker pupae by adult workers after a certain amount of time. Brood killing occurs either by freezing a piece of brood comb in a freezer (Kefuss *et al*, 1996; Newton *et al*, 1975) with liquid nitrogen (Spivak and Downey, 1998) or by pinning individual brood cells with a needle (Büchler, 1996; Newton and Ostasiewski, 1986), the latter being less demanding in terms of material and time. These methods appear similar with regards to their ability to quantify hygienic behaviour since significant positive correlations, ranging between 0.54 and 0.96, were obtained (Büchler, 1994; Espinosa-Montano *et al*, 2008; Newton and Ostasiewski, 1986). Thus, the selection output should be independent of the method used, and the ease of implementation can guide the method chosen to assess the phenotype. In Central Europe, however, the pin-test method was recommended to local beekeepers (Hoffmann, 1996a) as it was found to give more repeatable and accurate results (Hoffmann, 1996b). | |
| Suitability as a resistance selection trait | |
| *Pros* | *Cons* |
| * *Argentina*: significant correlation between the removal of experimentally *V. destructor*-infested brood and the removal of pin-killed brood in cells infested by two mites (Del Hoyo *et al*, 2001)). * *Brazil*, Africanised honey bees: strong negative genetic correlation between the removal of freeze-killed brood and the infestation rate of adult honey bees (r=-0.82) (Padilha *et al*, 2013) and between the removal of pin-killed brood and infestation (-0.96) (Pinto *et al*, 2012) and moderate correlation between the removal of freeze-killed brood and the reproduction rate of *V. destructor* (r = -0.48)(Wielewski *et al*, 2012). * *Canada*: untreated colonies selected for hygienic behaviour towards freeze-killed brood better survived in the presence of *V. destructor* when compared to unselected colonies (Guarna *et al*, 2017). Negative correlation (r = -0.13 to r = -0.54) between the removal of freeze-killed brood and infestation rates in brood or on adult workers had previously been identified (Parker *et al*, 2012). * *Ethiopia*: negative correlation between the removal of pin-killed brood and the infestation level on adult bees (r = -0.79) and in brood (r = -0.46) in naturally surviving *A. m. simensis* (Gebremedhn *et al*, 2019) * *Germany*, *A. m. carnica*: negative correlation between hygienic behaviour and the population growth of *V. destructor* (Ehrhardt *et al*, 2010). Arbeitsgemeinschaft Toleranzzucht (AGT, [www.toleranzzucht.de](http://www.toleranzzucht.de)) population: between 2004 and 2007, negative correlation (r=-0.57) between the infestation growth rate and hygienic behaviour (Büchler *et al*, 2008). Bee Research Institute Kirchhain population (Büchler, 1993a): lower infestation rates in colonies selected for hygienic behaviour and grooming when compared to the controls (Büchler, 1997; Büchler, 2000). Positive genetic (r = 0.61 ± 0.51) and phenotypic (r = 0.11) correlation between the removal of pin-killed brood and the removal of *V. destructor*-infested pupae (Boecking *et al*, 2000). Moderate correlation between the removal of pin-killed brood and *V. destructor* infestation, fluctuating depending on the honey bee lines considered (Hoffmann, 1996b). High correlation between mite removal and the removal of pinned (r = 0.65) or freeze-killed brood (r = 0.79) (Büchler, 1994). Significant correlation between the removal of experimentally *V. destructor*-infested cells and the removal of freeze-killed brood infested by two mites (Boecking and Drescher, 1992). * *Kenya,* naturally surviving honey bees: significant correlation found between the infestation level and hygienic behaviour in naturally resistant populations (Muli *et al*, 2014). * *United Kingdom, England*: some highly hygienic colonies had lower infestation rates (Al Toufailia *et al*, 2014). * *USA,* ‘Russian’ stock: colonies showed higher hygienic behaviour than control colonies (de Guzman *et al*, 2002). | * *Argentina*: colonies of European origin were selected for hygienic behaviour via the pin-test method (Palacio *et al*, 2001). Slight differences were found between the selected and non-selected groups in terms of the infestation levels, although no significant differences were visible concerning the survival of the untreated colonies (Merke, 2016). No relation between the removal of pin-killed brood and brood removal in cells experimentally infested with a single mite (Del Hoyo *et al*, 2001). * *Belgium*: no correlation between the removal of freeze-killed brood and the infestation rates of both worker brood and adult workers, the ratio of these infestations or the reproduction rate of mites (Leclercq *et al*, 2018). * *Chile*: no correlation between hygienic behaviour and the infestation level of *V. destructor* (Araneda *et al*, 2008). * *Germany*: no relation between the removal of freeze-killed brood and the removal of cells experimentally infested with a single mite (Boecking and Drescher, 1992). Colonies from the AGT and Kirchhain populations selected for hygienic behaviour did not show better survival when tested in different environmental conditions on the European scale in the absence of mite control when compared with colonies of various origins, most of them not selected for resistance (Meixner *et al*, 2014). In *A. m. carnica*, poor correlation between pin-killed brood removal and the infestation of adult honey bees (Buchegger *et al*, 2018). * *Italy, A. m. ligustica*: no correlation between the removal of pin-killed brood and the infestation level of the colony (Lodesani *et al*, 2002). * *Mexico*, naturally surviving Africanised honey bees: no correlation between hygienic behaviour and the infestation level of *V. destructor* (Medina-Flores *et al*, 2014; Mondragon *et al*, 2005). * *The Netherlands*: In two naturally surviving populations, no high hygienic behaviour towards dead brood (Blacquière *et al*, 2019; Locke and Fries, 2011; Mondragon *et al*, 2005). * *Turkey*, *A. m. anatoliaca*: a survival experiment involving hygienic and non-hygienic colonies with initially equalised mite loads did not show the better survival of hygienic colonies according to freeze-killed brood removal assays (Cakmak, 2010). * *United Kingdom, England*: no relationship between hygienic behaviour and the infestation level in colonies with low or medium hygiene levels (Al Toufailia *et al*, 2014).   *USA*: colonies bred for hygienic behaviour against dead brood were not very effective in cleaning infested cells (Danka *et al*, 2013; Ibrahim and Spivak, 2006). In Minnesota, colonies bred for hygienic behaviour showed lower infestation than controls (Spivak and Reuter, 1998), although they still needed varroacide treatments during the late season to prevent winter losses (Ibrahim *et al*, 2007; Spivak and Reuter, 2001). Similarly, a negative relation between hygienic behaviour and infestation (natural mite fall) was found in another US population selected for hygienic behaviour; however, no significant difference was found for the time of year at which the treatment threshold was reached (Delaplane *et al*, 2005). Another study found no correlation between hygienic behaviour and the infestation level of *V. destructor* (Harbo and Hoopingarner, 1997). |

## Table SE: Data concerning the suitability of a reduced post-capping stage duration as a trait for resistance selection

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| **Reduced post-capping stage duration** | |
| Measurement methods: after the sealing of individual worker cells, the duration of the post-capping stage is monitored at short time intervals either in the hive (Büchler, 1990b; Büchler and Drescher, 1990; Rosenkranz, 1990) or by placing the test comb in an incubator (Bienefeld, 1996a; Oddie *et al*, 2018). The frequency of these observations determines the precision of the assessment of the post-capping duration. The hive method offers the advantage of including colony effects in the analysis; however, the repeated opening of the colony may induce disturbances in the in-hive conditions and so affect brood development. To the best of our knowledge, the two methods have not been compared to date, so their respective impact on the evaluation of the post-capping stage duration is not known. | |
| Suitability as a resistance selection trait | |
| *Pros* | *Cons* |
| * *Germany*: positive correlation (r = 0.48) between the post-capping stage duration and the infestation rate (Büchler, 1990b; Büchler and Drescher, 1990). | * *Germany*: variations in the post-capping stage duration between 270 and 300 hours unlikely to have an effect on the infestation level (Hoffmann, 1996b). * *Norway*: a reduced post-capping stage duration has been identified in a naturally surviving population, although it is unlikely that this trait effectively contributes to the observed survival (Oddie *et al*, 2018). * *Poland*: colonies with *A. m. capensis* ancestry selected for the reduced post-capping stage duration had significantly lower (1.75 *versus* 1.98) *V. destructor* reproduction rates than the unselected controls (Wilde and Siuda, 1997), although this difference was not significant in the following generation. The differences in colony infestation rates when compared to the controls were not significant either (Siuda and Wilde, 1998). This absence of a visible effect on the infestation rate resulted in the end of the selection programme. * *USA*: in contrast to SMR, the post-capping stage duration was only marginally correlated with the infestation rate (Harbo and Hoopingarner, 1997). |

## Table SF: Data concerning the suitability of grooming as a trait for resistance selection

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| **Grooming** | |
| Measurement methods: in the field, grooming is evaluated by sampling the mites falling from the colony onto a board set under a hive with a meshed floor bottom. Mites are collected and body damage, for instance, missing legs or an injured shield, is recorded (Ruttner and Hänel, 1992). The percentage of damaged mites is used as an indicator of the grooming capacity of the colony. | |
| Suitability as a resistance selection trait | |
| *Pros* | *Cons* |
| * *Austria*: significant negative correlation was found between the rate of damaged mites collected under colonies and the infestation levels of brood and adult workers (Moosbeckhofer, 1992), indicating that selecting for colonies showing injured mites could help to limit infestation levels among local *A. m. carnica*. * *Canada*: a higher proportion of damaged mites in colonies selected for low *V. destructor* infestation growth rates when compared to lines selected for high infestation growth rates (Guzman-Novoa *et al*, 2012). Higher daily mite mortality in overwintering colonies whose workers expressed high grooming behaviour in experimental cages when compared to a colony with low grooming workers (Currie and Tahmasbi, 2008). * *Germany:* colonies with a high percentage of damaged mites (above 40%) had a lower increase in their mite population than colonies with less than 30% damaged mites as well as significant negative correlation (r = -0.42) between the proportion of injured mites and the relative infestation increase in spring (Büchler, 1993b). This finding was confirmed by later studies in the Kirchhainer population (Hoffmann, 1996b). Colonies originating from the same selection programme using artificial insemination still had significantly lower infestations than controls in the subsequent generations (Büchler, 2000). * *Mexico*, Africanised honey bees: the proportion of injured mites was one of two variables that correlated best (negatively) with the colony infestation level (Mondragon *et al*, 2005). Other studies highlighted negative correlation between the percentage of injured mites and the mite population growth (Arechavaleta-Velasco and Guzman-Novoa, 2001). * *Tunisia, A. m. intermissa*: grooming was interpreted as contributing to the survival of colonies (Boecking and Ritter, 1993). * *USA*: colonies selected according to the damaged mite rate and tested in different beekeeping conditions showed lower mite populations than controls in some of the test locations (Hunt *et al*, 2016). A preliminary study showed significant positive correlation between the number of injured mites found beneath colonies and the number of mites removed by grooming in caged groups of workers from the same colonies (Andino and Hunt, 2011), indicating than laboratory assays could help to identify colonies with high grooming behaviour. Lower *V. destructor* infestation combined with increased colony survival and the increased expression of a grooming-related gene were later identified in the same selected population when compared to a susceptible control population (Morfin *et al*, 2019). | * *Austria, A. m. carnica*: grooming was identified as a defence mechanism in a line selected for low infestation growth rates (Ruttner and Hänel, 1992). The beekeeper selecting this population mentioned empirical selection progress for high rates of mite injury accompanied by a reduction in the treatment frequency (Markthaler, 2004; Wallner, 1997; Wallner, 2002). However, in a comparison test performed elsewhere in Germany, colonies originating from the lineage selected for grooming showed far higher infestation rates and less damaged mites than the other *A. m. carnica* strains, which were not selected for their proportion of injured mites (Büchler, 1998). This suggests high environmental effects for the grooming trait. * *Canada*: no relation was found between infestation as estimated by natural mite fall and the rate of injured mites in ‘Russian’ stock evaluated in Canada or in Africanised honey bees studied in Mexico (Guzman-Novoa *et al*, 2012). * *Italy*: in a population selected for either low or high *V. destructor* population growth rates, no correlation was found between grooming behaviour and the infestation level (Lodesani *et al*, 2002). * *The Netherlands*: in two naturally surviving populations, no noticeable grooming behaviour was recorded (Kruitwagen *et al*, 2017) * *USA*: no correlation was found between grooming and *V. destructor* population growth (Harbo and Hoopingarner, 1997). |

## Table SG: Data concerning the suitability of the mite infestation level as a trait for resistance selection

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| **Mite infestation level** | |
| Measurement methods: several methods can be used to measure infestation levels. The most precise method involves killing the entire colony (Dietemann *et al*, 2013). In practice, even if the queen could be spared for selection purposes, this method is too costly to be applied. Alternatively, varroacide treatments can be used, although they are destructive towards mites and, therefore, prevent reliable repeated measurements. Mite counts in worker or brood samples and the recording of the natural mite fall beneath the colony are thus preferred for estimating the mite load of the colony (Dietemann *et al*, 2013), and they are employed as selection traits in beekeeping conditions (Erickson *et al*, 2000; Oliver, 2018; Oliver, 2019). The mite population growth rate, for instance, between spring and late summer, may also be used as a selection trait. In research programmes, lineages with either low or high infestation growth rates were selected (Harbo and Hoopingarner, 1997; Kulincevic *et al*, 1992; Lodesani *et al*, 2002), for example, to determine the mechanisms linked to the observed infestation differences (Harbo and Hoopingarner, 1997; Lodesani *et al*, 2002). Similar approaches could also be employed in beekeeping conditions to select for lineages with lower infestation. | |
| Suitability as a resistance selection trait | |
| *Pros* | *Cons* |
| * *Austria*: in the 1990s, a commercial beekeeper selected colonies with low brood infestation growth rates and high natural mite fall. Initially, 12 colonies out of 700 were able to overwinter without treatment in local conditions and to produce similar honey quantities when compared to treated colonies (Ruttner and Hänel, 1992). Some 30–50% of the mites found on the bottom boards of the colony showed signs of injuries, which was interpreted as the result of the active defense behaviour of the worker honey bees (Ruttner and Hänel, 1992). Selection was continued considering the high proportion of injured mites as the breeding goal, with controversial results (Table SF). Another study concluded that selection for late season mite infestation could be feasible, although it would require large tested and selected populations (Boigenzahn and Willam, 1999). * *The Netherlands*: the De Duurzame Bij association ([www.duurzamebij.nl](http://www.duurzamebij.nl)) selects colonies for low cumulative infestation growth rate coefficients based on continuous measurements of the natural mite fall. The programme involves approximately 90 untreated colonies, with mortality rates ranging between 10% and 15% per year (Kok, personal communication). Such a rate is within the range of national colony losses (Brodschneider *et al*, 2016; Van Der Zee *et al*, 2014). | * *Turkey*: colonies with infestation levels under 1 mite per 100 honey bee workers in summer were left untreated and used as a source to requeen more heavily infested and treated colonies (Cakmak and Fuchs, 2013). The proportion of colonies requiring no treatment increased after two years. However, no controls were used to exclude environmental and yearly effects, so genetic progress could not be proven. In addition, collaboration problems with the beekeepers on the island resulted in the relaxing of the selection effort, which led to an increase in infestation rates after the first two years (Fuchs, personal communication). * *USA*: lines with low infestation rates selected in Yugoslavia were tested in the USA and showed barely any difference in infestation levels when compared to susceptible controls (Rinderer *et al*, 1993), despite an estimated heritability for infestation level of 0.3 in the original population (Kulincevic *et al*, 1992). Changes in environmental conditions may have affected the host–parasite interaction. |

## Table SH: V. destructor-infested honey bee populations surviving without acaricide treatments

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| * Avignon and Sarthe, *France*: see section 1.2.1. * Gotland, *Sweden*: see section 1.2.1. * Toulouse, *France*: see section 1.2.1. * *The Netherlands*: see section 1.2.1. * *Norway*: since 1997, untreated and surviving commercial population of Buckfast origin. After high initial losses, significantly lower infestation rates when compared to neighbouring susceptible control colonies (Oddie *et al*, 2017). * *Switzerland*: two groups of non-isolated colonies untreated since 2006 and 2010, respectively, survive despite mite infestations (Dettli, 2018b). Some colonies reduce the infestation of *V. destructor* after peaks in spring or autumn by unknown mechanisms (Dettli, 2018a). * *Ireland*: colonies in North County Dublin untreated since 2010; infestation rates occasionally rose during the beekeeping season, but few colonies were lost. DWV symptoms rarely seen. Signs of resistance or tolerance build-up (McMullan, 2018). * *United Kingdom*: 40 untreated colonies in the Swindon region survive for 20 years despite *V. destructor* infestation and high DWV loads (Gfeller *et al*, 2019; Mordecai *et al*, 2016). In Wales, untreated colonies have been reported to survive for up to 20 years (Gfeller *et al*, 2020). In addition, among the owners of a total of 1573 colonies, the majority of beekeepers do not treat their colonies: between 2010 and 2015, their colony losses were lower than those of beekeepers who treat their colonies (Hudson and Hudson, 2016). In Northern England, in a population kept by a beekeeper, very low infestation rates despite the colonies being untreated since 2002 (Pritchard, 2018). * *Dominica Island*: untreated and infested colonies of *A. m. mellifera* ancestry survive (Rangel *et al*, 2018). No data on colony mortality, on the haplotype of *V. destructor* or on virus infections are available, so the cause of survival is unknown. |

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