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A Plea for Use of Honey Bees' Natural Resilience in Beekeeping

Tjeerd Blacquière and Delphine Panziera

This plea is about leaving room for nature in ordinary daily beekeeping, but also about leaving room for nature in the reproduction of the bee colonies, i.e. beekeeping without queen breeding and without cultivation of breeds. Our European honey bees (*Apis mellifera*) naturally possess numerous traits including behaviors that make them less vulnerable to diseases and other threats in their environment (Evans & Spivak, 2010; Wilson-Rich, Spivak, Fefferman, & Starks, 2009). It is very important for these properties to be retained in their full genetic width, in order to sustain the colonies' capacities to continuously adapt to new conditions (Neumann & Blacquière, 2017). It is also important that we, as beekeepers, utilize as much as possible these adaptive abilities of the bees (Seeley, 2017a). This means that it may occasionally be better to follow the bees' nature rather than to force the bees to meet our requirements (Brosi, Delaplane, Boots, & de Roode, 2017). Here we present several examples to underpin this statement.

Honey Bees are Endemic

Our honey bee occurs naturally as a wild species in Africa, the Middle East and Europe. Within this wide range, many described subspecies are present and well adapted to local circumstances. Additionally, there is variation within the different subspecies and the bees turn out to be strongly adapted to local conditions on a finer scale. Such local adaptation of "ecotypes" may be adaptation to the weather, to conditions and seasonality of forage, but also to local variation in diseases. A nice example is the "Landes" bee, a regional honey bee within the subspecies "black bee" (*A. m. mellifera*), adapted to the climate and forage conditions of an area in Les Landes, France (Strange, Garnery, & Sheppard, 2007). A few native European subspecies were carried across seas as Europeans settled in new territories such as the Americas, Australia and Asia. By accident, man has also caused the spread of the African Savannah Bee (*A. m. scutellata*) in South, Middle and even North America (Africanized bees, sometimes called "killer bees").

The black honey bee (*A. m. mellifera*) is the indigenous subspecies in our West European environment, with a distribution ranging from the Pyrenees through Western Europe (including the British Isles) far into Russia (De la Rúa, Jaffé, Dall'Olio, Muñoz, & Serrano, 2010). However, beekeepers have introduced for centuries Italian (*A.m. ligustica*), Carniolan (*A. m. carnica*) and Caucasian (*A.m. caucasica*) queens to bring in qualities thought to be better suited for beekeeping (Meixner et al., 2010). As a result, our Western European black honey bee has been repeatedly hybridized with other subspecies. More recently, Buckfast bees also introduced properties (genes, actually alleles) of other honey bee subspecies (African and Middle East subspecies).

The Honey Bee is a Wild Species

Even though they have long been held by humans, honey bees remain a principally wild species (Oldroyd, 2012). While in some countries there are efforts to select and breed honey bees, in many others, bees have hardly been domesticated or have not been domesticated at all. Where there are no active breeding and selection effort, the bees could be considered a wild species. Where more intensive selection and breeding occurs, we don't have the level of domestication of farm animals, but we have semi-domestication, where some attributes of domestication coexist with some attributes of being a wild species. One could for instance perceive the situation in the USA as a case of domestication, where a handful queen breeders supply the whole continent with queens. For true "domestication" however, a prerequisite is the control of the organisms' mating and reproduction by man, as it is the case in our livestock. The honey bee queens' promiscuous mating behavior with more than 15 drones (polyandry) makes the domestication task difficult, unless by using artificial insemination or mating on isolated mating stations, for instance on islands. In addition, this mating with many drones (with ample genetic variation) is also necessary to build a well-functioning colony. There appears to be no difference in the number of drones with which a queen mates between wild and managed colonies (Tarpy, Delaney, & Seeley, 2015), in both cases about 15 to 22. This number of mating events is probably a compromise that yields sufficient genetic diversity, weighed against the risk taken by the queen with each additional mating, and therefore naturally selected as an optimum.

A queen mating on a station with 20 drones originating from a number of "drone-colonies", headed by sister queens, might still run short in genetic variation. The drones might genetically be too similar, and due to this lack of variation the worker bees in the colony would also become too similar. A lack of some essential alleles of immunity-related genes might arise, resulting in a reduced ability to handle pathogens of the entire colony. A recent study (Delaplane, Pietravalle, Brown, & Budge, 2015) showed that mating with much higher numbers of drones using artificial insemination (as this would not be achievable naturally) increased the resilience of the colonies to the varroa mite. Fifteen to twenty drones might be enough for most traits, but in some cases useful alleles might be so rare that 15–20 unrelated drones, or alternatively far more than 20 mating events are needed to come across those rare alleles.

It appears that, as soon as a selective breeding for desired properties such as gentleness, low swarming tendency etc. is stopped, these traits are quickly lost. This suggests that several man selected traits are not directly beneficial to the colony fitness, as they would remain frequent in the gene pool otherwise.

The original traits of the honey bees provide a high level of resilience towards all kinds of diseases and parasites, which allowed beekeepers to keep the bees without the use of veterinary drugs. While in some countries diseases are still handled without medication, the situation has changed drastically with the arrival of the varroa mite in Europe. Varroa is a foreign exotic parasite, against which our honey

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bees had no defense. Unfortunately, as long as we do control the varroa mites in our colonies, there is no selection pressure left, and no resistance will ever evolve: the bees remain as vulnerable as they were upon arrival of varroa.

Understanding: Resistance or Tolerance to Varroa is Required

The majority of the beekeeping community is now aware of the idea that the solution for varroa must also be sought in the resistance and tolerance mechanisms of the bees. This could allow the return to an old-fashioned apiculture free of veterinary drugs. We now also know that the survival of honey bee populations with varroa is possible in nature and in beekeeping operations (Locke, 2016; further examples: Kefuss, Vanpoucke, Bolt, & Kefuss, 2015; McMullan, 2018; Oddie, Dahle, & Neumann, 2017; Panziera, van Langevelde, & Blacquière, 2017), so beekeeping without controlling the mite is no longer an unworldly vision. Only the path to it is controversial: should we go the usual route of breeding and beekeeping (retaining the qualities appreciated by the beekeeper), or should we follow the bees in their hard struggle to survive "in nature"?

The two methods to select varroa resistance or tolerance are:

(1) Targeted selection: We seek and choose (select) properties that counteract the development of varroa, and breed them into our bee stocks. For example, it could be breeding for hygienic behavior against the varroa mite (VSH) (Leclercq, Pannebakker, Gengler, Nguyen, & Francis, 2017; Wilson-Rich et al., 2009), or grooming of mites (Pritchard, 2016). Such breeding requires a highly coordinated approach and controlled mating of the queens with selected drones. At the same time, consideration can be given to preserving the desired characteristics of bees for beekeepers (Uzunov, Brascamp, & Büchler, 2017). This route has already been applied, sometimes with some success (Rosenkranz, Aumeier, & Ziegelmann, 2010). This approach actually takes domestication further. In principle, this can be done on a large scale (where selected queens are made available to beekeepers), but it can also be done locally.

(2) "Natural" selection: We no longer control the mite and thus leave the bee colonies to deal with this suddenly increased parasite pressure. Ideally this results in some kind of remise (most beekeepers would consider ideal an outcome where the bees "win", but that option may be illusory): there is a balance between bees and mites (hosts and parasites), in which both can survive. This route has already proven to be successful several times in nature (Seeley 2007, 2017b) as well as starting from colonies initially managed by beekeepers (Fries, Imdorf, & Rosenkranz, 2006; Kefuss et al., 2015; Le Conte et al., 2007; Oddie et al., 2017; Panziera et al., 2017). We may be able to speak of de-domestication, which is named feralisation. This should be allowed to occur at various locations (with local bee colonies and their mites). Using this approach will also result in bee populations of colonies well adapted to the local environment. Surprisingly, "natural selection" appears to be effective after only a few years of refraining from control of varroa. That the "natural" way of selection through only elimination of the non-fitting phenotypes can result in fast evolution in honey bees was underpinned by a recent study (Avalos et al., 2017) in which defensive Africanized honey bees in Puerto Rico evolved docility in just a decade. This selective sweep was shown to be based on several loci.

In both approaches of selection, the process is continuous and actually never ends. In addition, conditions can change, new pests can occur. In the latter case, method 1 will be constrained to look for new resistance traits and start the selection and breeding process according to the new plague. In method 2, the new pest will increase the selection pressure and will raise new resistance mechanisms without deleting the already acquired adaptations. The feralisation in method 2 might result in the loss of colony traits considered as "beneficial beekeeping characteristics". Obviously, feralisation does not grant the return of lost alleles in the genepool (Johnsson et al., 2016). This is an additional warning against the overuse of selective breeding and domestication in beekeeping practices. It is also an argument for the protection of local subspecies and ecotypes without too much interference by beekeeping.

Theoretically, honey bees could have become fully domesticated and would be unable to survive without human intervention. However, there are strong examples showing this is not the case in the USA (Seeley, 2017b), France (Kefuss et al., 2015; Le Conte et al., 2007), Ireland (McMullan, 2018), Netherlands (Panziera et al., 2017), Sweden (Fries, Imdorf, et al., 2006). An important argument to support the idea that bees are able to survive without help is that, before and after varroa, the life expectancy of wild or feralised colonies was not affected: about five to six years for an established colony (Le Conte et al., 2007; Seeley 2017b), which is also similar to the life expectancy (6.6 years) of wild colonies in Australia, where varroa mites are not present (Oldroyd, Thexton, Lawler, & Crozier, 1997).

The importance of aligning as much as possible with what would happen in nature is crucial for method 2. Hence, let the bees make the most of their own potential in the fight against diseases. A simple example: while bees themselves prevent robbery and thus prevent entry of diseases by active guard bees, the beekeeper should not spread diseases from one colony to another by using, for example, contaminated beekeeping tools. As conspicuous as it seems, many widely accepted and used beekeeping methods counteract honey bees' own resilience strategies.

How Does Resilience Work in Nature?

The theory, almost always verified by empirical data, predicts that invasive parasites cause much damage at the beginning of invasion as the host has not adapted yet to this new threat. But too virulent parasites take the risk of killing their host too quickly, therefore eliminating chances of transmission and leading to their own extinction. On one hand, hosts unable to cope with the parasite burden are killed without reproducing. On the other hand, stronger hosts effectively pass on their genes to the next generation, thereby favoring resistant or tolerant phenotypes in the population. Thus, as time and generations go by, both phenomena lead to a milder virulence of the parasite and a higher resistance or tolerance of the host (Schmid-Hempel, 2011). In regular beekeeping many management measures as well as the choice of selected queens increase horizontal transmission paths and offend the development of a balanced mild host parasite relationship (Brosi et al., 2017).

The host may develop both resistance (the ability to limit parasite burden) and tolerance (the ability to limit the damage caused by a given parasite burden, for example by becoming insensitive to a poison of the parasite, for definitions see Raberg, Graham, & Read, 2009). Both mechanisms can be deployed simultaneously and depend on the presence of the parasite. As long as beekeepers control the varroa mites, no balanced natural relationship can be maintained or arise between the mite and the bees.

Conditions to be Met for the Evolution of a Balanced Host Parasite Relationship

A parasite can be transmitted horizontally or vertically. Horizontal transmission is from one bee to another bee of the same generation, or from one colony to another colony. Vertical transmission means from mother to her offspring, for example through the eggs. Transmission of parasites from the mother colony to an after-swarm is a form of vertical transmission (the after-swarm is a daughter of the original mother-colony). With vertical transmission, adaptations to the parasite, in the genes that the mother passes along to her offspring, will be taken to the next generation (= the same colony with the new queen). There is a good chance that the colony with the daughter queen can handle the transmitted parasite better, as they are already acquainted. Parasites depend on their hosts' survival or on successful transmission to other susceptible hosts. Therefore, when a parasite depends solely on vertical transmission, a mild virulence is crucial.

Reproduction of Colonies: Vertical or Horizontal Transmission of Parasites?

The natural reproduction of honey bee colonies is achieved through the process of swarming in spring. The prime swarm with the old queen with a part of the workers and drones forms the continuation of the original colony, with the "old" parasites and the already existing "relationship" between them. The remaining colony is now led by a new young queen and can be qualified as "new" or "daughter" colony. After the swarm leaves, the original parasites are still present but the genetic identity of the colony slowly changes as the workforce is replaced. Thus, there is a vertical transmission of the parasite (from mother (-colony) to descendant (colony)). The daughter inherited her mother's properties (genes), allowing her and her offspring to deal with the parasite that her mother was able to handle. The colony also inherits genes from the drones that fertilized the queen, which will mostly have originated from other colonies. This new genetic identity, partly inherited and partly acquired might increase the fitness of the colony. The relationship between host and parasite might differ between the mother and the daughter colony, for good or bad.

The situation is similar for the sisters of the young queen which may leave the original colony in after swarms: if they succeed to build a balanced enough relationship, they may survive, if they fail they will die.

The swarm (both prime and secondary swarms) loses or escapes part of the parasites with which the colony "had a relationship", since parasites of the brood do not or barely go with a swarm (*Paenibacillus larvae,* Fries, Lindström, & Korpela, 2006) or quickly disappear possibly caused by the intensive comb building activities of the swarm bees (*Ascosphaera apis*, Aronstein & Murray, 2010). This escape is beneficial for the start and building of the own host (=swarm) parasite relationship, a little respite is welcome because there are already enough challenges for a swarm to survive. In the wild, not even a quarter of the prime swarms survive, even though they found a nest. This can be explained by their inability to build a strong enough population of bees and food supplies for the winter (Seeley, 1995, 2017b).

Not only parasites, but the entire microbiome, the microorganisms living together with and within the bees and the colony, is inherited vertically when a colony swarms. The microbiome may play important roles in the metabolism of the colony as a whole (Özkirim, 2012).

Introduction of a New Queen: Vertical or Horizontal Transmission of Parasites?

It is a beekeeping practice to "rejuvenate" a colony by removing the old queen and introducing a young fertilized (or optionally a virgin) queen. Queens are sometimes bred by grafting larvae from a selected colony into artificial queen cells and, after emergence, getting them to mate with selected drones in a mating station. This rearing of queens from selected grafted larvae is not a common practice in the Netherlands where most beekeepers allow their colonies to rear their own queens, but in surrounding countries it often is (Büchler, Berg, & Le Conte, 2010). What are the consequences of such reproduction/propagation for the transmission and relationship with parasites? While the new queen is introduced into an unrelated colony which might carry different parasites, she might also be bringing her own parasites (plus parasites she may have got from the drones) into this new colony. Thus, this process might raise both vertical and horizontal transmission of parasites. Likewise, the local parasites are suddenly exposed to new genotypes and therefore, at each introduction of a foreign queen, the host-parasite interactions are reset. This disturbance would be minimized by introducing queens originating from the same apiary.

Recently, a study by Salmela, Amdam, and Freitak (2015) showed that the queen could add specific immune primers to eggs. These primers target specific parasites with which the queen has been in contact. This immune mechanism works through the yolk protein vitellogenin and can be considered as an analogue to "vaccination" of the offspring. This inherited immunity obviously loses most of its benefits when a queen is displaced, as a native daughter queen would probably already be better adapted, through her mother's primers and her exposure to the local disease variants, than to the disease variants of a mating station or those of a new colony.

Some Examples of Beekeepers Counteracting Honey Bee Colonies

Parasites can also drift when colonies are placed close to each other, which is horizontal transmission. A recent study by Seeley and Smith (2015) compared the development and mite infestation of colonies placed either in an apiary oriented in a row, or freely dispersed (distance between the colonies ~ 20 to 50 m) in woods surrounding the apiary. The study showed that, regardless of the colony location, colonies that had swarmed had a lower mite infestation than colonies that had not swarmed. This might be explained by the broodless period following the departure of a swarm. In the colonies that had not produced a swarm, the mite infestation increased strongly, and some did not survive the following winter. Remarkably, during the summer, in the colonies that had swarmed (and had a lower infestation), the infestation increased again in the row apiary, but not in the colonies dispersed in the wood. Seeley & Smith explain this by drifting of bees at the row apiary: many workers and drones from the swarmed and non-swarmed colonies mixed together, while this did not occur in colonies placed in the woods. Additionally, mated queens returned more successfully to their original colony when it was placed in the woods. The research shows that beekeepers can greatly stimulate varroa infestation by: (1) preventing swarming (which leads to continuous breeding), (2) putting colonies close together in a row, and (3) keeping colonies already having a high infestation in the same apiary with low infestation colonies (so the infested colonies can collapse and be robbed by neighboring colonies, which will take over the mites). Although these results might not seem spectacularly surprising, the difference in the dynamics of colonies in a row versus scattered colonies is relevant.

Summary

The honey bee is in Europe an endemic and wild species, with regional subspecies and many local adaptations. Although subspecies and populations have been hybridized, and despite some selective breeding, the honey bee still behaves naturally and increases its fitness through continuous local adaptation. In order to evolve more resilience against the varroa mite, a major threat, two ways are open: (1) targeted selection and breeding on a large or regional scale, and (2) natural selection for fitness in the presence of the varroa mite. While the success score for selective breeding is still scant, natural selection has delivered a few described cases of resistance, all in relatively short time periods.

Resilience of an organism towards parasites and diseases can be obtained by resistance (the disease/parasite is hampered in its development and fitness) and by tolerance (the damage caused by the disease or parasite is avoided or restraint). Resistance and tolerance can act concurrently. A balanced relationship between host and parasite can develop through resistance and tolerance, and an important condition to reach such a balance is that the disease or parasite is *vertically* transmitted: from mother to offspring. When a parasite is transmitted horizontally, such a balanced relationship struggles to develop. With natural reproduction of honey bee colonies, parasites are transmitted vertically onto the new generation. Method (2) of natural selection does not interfere with this transmission route. By replication or rejuvenation of colonies with the introduction of foreign queens (method (1)), the transmission is largely horizontal. This applies as well for the transmission of beneficial organisms (symbionts) in the colony.

In addition to reproduction of colonies and selective breeding, many other methods applied by beekeepers conflict with the bee colonies' behaviours and resilience traits against parasites and diseases. Aligning methods to the natural traits of the bees, as well as the decision to start selection, targeted or natural, should be done with prudence to avoid evitable collateral damage.

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