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ORIGINAL RESEARCH ARTICLE

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A future resistance breeding strategy against *Varroa destructor* in a small population of the dark honey bee

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In scientific literature, host resistance of *Apis mellifera* against its parasite *Varroa destructor* is often presented as a potential solution to enable a sustainable relationship between both species and secure pollination and beekeeping services. Surprisingly, there are only few studies investigating the interest of beekeepers for this topic. In this paper, we propose a method to assess the desirability of resistance as part of a breeding goal, with a particular focus on small closed populations. The Swiss population of *Apis mellifera mellifera* is taken as case study. The general importance of this selection objective as well as the variability of the acceptance of beekeepers are studied. Thereafter, the willingness to pay for resistance is assessed to highlight possible compromises beekeepers could accept between different qualities they expect from their honey bees. Finally, the main characteristics of the breeding program desired by the beekeepers are presented. In our example, beekeepers are generally in favour of resistant honey bees even if differences in the expected breeding goals were identified. The majority is interested in a breeding strategy to select for resistant stock even though honey bees would produce less honey, swarm more often or be less gentle, showing a clear desirability for resistant traits. Furthermore, we noticed that beekeepers prefer locally selected honey bees displaying a broad genetic diversity. The presented method can be easily applied to evaluate the acceptance of new breeding objectives and to assess the potential of future strategies focusing on resistance against *V. destructor* in breeding programs involving beekeepers and research institutes.

Keywords: *Apis mellifera*; *Varroa destructor*; resistance breeding; closed population; breeding goal; desirability

Introduction

In a context of recurrent colony losses, the ectoparasitic mite *Varroa destructor* is described as one of the main threats to the Western honey bee *Apis mellifera* worldwide (Guzman-Novoa et al., 2010; Kraus & Page, 1995; Le Conte, Ellis, & Ritter, 2010; Neumann & Carreck, 2010; Ritter, Leclercq, & Koch, 1984).

Currently, the control strategies of *V. destructor* mainly rely on chemical treatments (Rosenkranz, Aumeier, & Ziegelmann, 2010). However, they can hardly be considered as sustainable solutions, since risks of contamination of honey bee products (Emsen & Dodologlu, 2009; Wallner, 1999), risks of detrimental effects on honey bees (Tihelka, 2018) or risks of build-up of parasitic resistance (Elzen, Baxter, Spivak, & Wilson, 2000; González-Cabrera et al., 2016; Spreafico, Eördegh, Bernardinelli, & Colombo, 2001) exist.

Host resistance breeding is a long-term strategy in animal breeding, which is performed in diverse livestock species (Gama, Carolino, Santos-Silva, Pimenta, & Costa, 2006; Shook, 1989; Stear & Wakelin, 1998; Zvinorova et al., 2016). The general aim is to generate a breeding progress of the host in order to reduce the parasitic load (Råberg, Graham, & Read, 2009) and thereby stabilize the host-parasitic relationship.

To investigate whether resistance of *A. mellifera* against *V. destructor* could be a long-term solution, a possible strategy can be to verify whether different conditions are fulfilled. A previously described approach (Stear, Bishop, Mallard, & Raadsma, 2001) suggests that it should be sustainable, i.e., likely to reach a stable host-parasitic relationship, feasible, i.e., offering possibility to select for resistance and desirable, i.e., accepted by the actors as a part of the breeding goal of the selection program.

Surprisingly, there is only few data on the acceptance of resistance breeding strategies against *V. destructor* among beekeepers (Kim, Westra, & Gillespie, 2006; Leiby, 2014). Some networks performing collective selection, as Arbeitsgemeinschaft Toleranzzucht in Germany (http://www.toleranzzucht.de) or Buckfast networks on the European scale (Jungels, 2003) already defined the selection of resistant honey bees against *V. destructor* as their main breeding goal, assembling beekeepers sharing the same interest. Nevertheless, it also seems essential to select for resistant honey bees in single, closed populations. Such populations often predate the arrival of *V. destructor* and the motivations of their beekeepers for resistance breeding may not be as homogenous as in dedicated selection groups created

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ex nihilo. The different subspecies of *A. mellifera*, for instance, are of particular interest for their local adaptations, their genetic specificities and their heritage value (De la Rua, Jaffe, Dall'Olio, Munoz, & Serrano, 2009; Meixner et al., 2010; Strange, Garnery, & Sheppard, 2007). Like in other species (Labatut, Bibé, Aggeri, & Girard, 2012; Lauvie & Couix, 2012; Verrier, 1992), these closed populations are often commonly kept and selected by breeders, who need to agree on their breeding objectives and preserve sufficient genetic diversity.

In this study, we chose the example of the native subspecies of *A. mellifera* in Switzerland, *Apis mellifera mellifera* (Parejo et al., 2016; Soland-Reckeweg, Heckel, Neumann, Fluri, & Excoffier, 2009). In this population, a small closed breeding program aims to provide the beekeepers with local *A. m. mellifera* queens having good performances for beekeeping. It is managed by the association mellifera.ch, based on 35 original motherlines and occurs on gyne supersedure. Matings are performed in five mating stations located in the Swiss Alps, evaluated by genetic analysis to provide at least 95% of pure matings, and about 200 queens are evaluated per year in a network of testing apiaries. Queen breeders and testers build the core of the selection program, but other members of mellifera.ch also take advantage of the program as they can use mating stations with males of selected origins to have self-bred queens mated. Currently five breeding values are calculated per tested queen: honey yield, defensive behaviour, calmness during inspection, swarming drive and a so-called Varroa index. General brood health and racial conformity to population standards of *A. m. mellifera* are also evaluated. The data recording of mellifera.ch shows only little evolution in breeding values related to *V. destructor* over the last decade, which leads to the question if and how it would be possible to be more efficient.

In our work, by using the example of mellifera.ch, we propose a methodology to evaluate the desirability (Stear et al., 2001) of resistance breeding against *V. destructor* by means of an online survey. First, we assessed the current breeding objectives of the beekeepers including non-market values. As the majority of Swiss beekeepers are non-professionals (Fluri, Schenk, & Frick, 2004), these values were identified as susceptible to play a major role to understand the breeding goal. In a second step, the willingness to pay (Breidert, 2006) for resistance against *V. destructor* was estimated in order to evaluate the interest for the implementation of the selection strategy in the breeding program. After these two steps, the beekeepers had the possibility to express on how such a breeding strategy should be implemented in the context of their small and native population. Our survey focussed on management of a small closed population selected within its native range, namely *A. m. mellifera* in Switzerland. Therefore, we expected a relatively low numbers of responses, for instance in comparison to past studies on beekeepers in the United States (Underwood, Traver, & López-Uribe, 2019). The local specificities of the studied population raised specific organisational issues for a successful collective selection, which needed to be identified to enable the sustainability of this small local breeding program. The method proposed here can also be adapted to bigger populations.

Material and methods

Survey, data collection and analysis

The study was performed using an online questionnaire (Google forms), which was e-mailed to 413 members of mellifera.ch in December 2017. These beekeepers may either have actively taken part in the breeding program, or reared their own lines of *A. m. mellifera* with possible use of the mating stations of the association. The questionnaire was available for one month and a reminder was sent after two weeks. A total of 42 questions was proposed to the respondents. The first part of the questionnaire summarized general questions about the beekeeper and his/her situation, and questions about his/her management of *V. destructor*, which supplied information about the particular Swiss case but are not be described in this study. The detailed questionnaire is presented as Supporting Material (Supplemental Material 1). The following questions and their results presented below focussed on the importance of resistance in the breeding goal, the utility of resistance and how resistance breeding could be implemented in the breeding program.

Depending on the questions, beekeepers were expected to give a number (e.g., number of hives), tick choice-boxes (e.g., treatments performed), express preferences (e.g., select between two breeding strategies) or express a view (write a statement in own words, e.g., to justify the willingness or not to have own bees genotyped).

Whereas many questions directly resulted in quantitative responses, data obtained from open questions (e.g., justifications, opinions and definitions) were qualitative and analysed using a conventional content analysis approach (Erlingsson & Brysiewicz, 2017; Hsieh & Shannon, 2005). Responses were analysed using codes chosen to fit the statements as precisely as possible. The codes were gathered in similar categories and themes to progressively refine the ideas or highlight nuances in the statements (Erlingsson & Brysiewicz, 2017). The frequencies of the different categories were finally used for the quantitative data analysis.

Assessing the mean breeding goal and variability of expectations in the beekeeper's group

In order to define the breeding goal of beekeepers of mellifera.ch, the respondents were asked to express their view on selection and beekeeping criteria. They independently evaluated honey yield, low defensive behaviour, low swarming drive, brood health, resistance to *V. destructor*, calmness during inspection, racial conformity and genetic diversity between 1 (not important) and 5 (very important), without trying to rank the criteria. These criteria could be analysed as qualities beekeepers expect from their honey bees. A mean breeding goal for the association was estimated from the results by classifying the different criteria according to their grades. Moreover, in order to take into account the variability of the responses between the beekeepers, the latter were allocated in five groups using an unsupervised classification approach (see method below).

Evaluating the utility of resistance against *V. destructor*

In the second part of the questionnaire, the utility of resistance against *V. destructor* for beekeepers was evaluated. As beekeepers are mostly non-professionals in Switzerland (Fluri et al., 2004), resistance was considered as a non-market trait. Their willingness to pay for a host-resistance selection strategy was therefore estimated by a choice-based conjoint analysis (Breidert, 2006). In successive questions, they were invited to choose between their current non-resistant honey bees and resistant honey bees showing different honey yields (from highly productive to unproductive), beekeeping abilities (variable defensive behaviour and swarming drive), different racial (pure *A. m. mellifera* or not) and geographical origins (local or non-local honey bees).

Implementing resistance breeding in the selection program

The beekeepers were asked to define how they would implement resistance breeding in their breeding program if they wanted to breed efficiently for resistance against *V. destructor*. To do so, questions on the general organisation of selection, on selection intensity and on the importance of resistance against *V. destructor* in the breeding index were proposed to investigate how the expectations of beekeepers could be included in their selection practices.

Statistical approach

Statistical analyses were performed using R (R-Core-Team, 2018). The presence of differences of importance between the selection criteria was tested using a Friedman's test. To make pairwise comparisons between the criteria and identify criteria of significantly different importance, *p*-values of the absolute rank sum differences of the pairs of Friedman rank sums were obtained according to a proposed method (Eisinga, Heskes, Pelzer, & Te Grotenhuis, 2017) and adjusted by using the Holm method (Holm, 1979).

The beekeepers were allocated into different clusters based upon self-evaluated breeding criteria using an unsupervised clustering approach. We calculated Euclidean distances between all beekeepers with the R function dist and generated a hierarchical cluster dendrogram using the ward.D2 method from the R function hclust (Murtagh & Legendre, 2014). Based on the groups defined from the clustering, a heatmap of the mean importance for the different criteria per group was created, displaying the mean values and standard deviations.

To highlight between-group differences in the evaluation of the utility of resistant *A. m. mellifera*, Kruskal-Wallis tests were performed to identify group effects. For responses where a significant group influence (p-value <0.05) was found, pairwise Wilcoxon tests were carried out to assess the differences between the single groups (the *p*-values were adjusted by using the Benjamini-Hochberg (BH) method). Responses where significant (p-value <0.05) between-group differences appeared are presented in the results.

Results

A sample of 99 Swiss beekeepers (owning a total of 2823 colonies of *A. m. mellifera*) returned the questionnaire after one month. The gross response rate was 24%, but according to estimations from the association, it had to be taken into account that about 100 beekeepers to whom questionnaires were sent were not taking actively part in the association activities. Respondents were mainly small-scale beekeepers (only 4 of them owned more than 50 colonies) with various experience in beekeeping (from less than 4 years to more of 40 years of beekeeping practices). A detailed description is presented in Table 1.

Breeding goals

The sampled beekeepers were invited to express their opinion on the importance of several phenotypic or genotypic criteria related to their activity. The responses for the importance of honey yield, low defensive behaviour, low swarming drive, brood health, resistance to *V. destructor*, calmness during inspection, racial conformity and genetic diversity are presented in Figure 1. Significant differences in terms of importance between the criteria were identified (Friedman rank sum test, Friedman chi-squared = 203.41, df = 7, p-value $< 2.2\text{e-}16$). *P*-values of the absolute rank sum differences of the pairs of Friedman rank sums (Eisinga et al., 2017) were used to make pairwise comparisons between the criteria.

Across all beekeepers, brood health was the most important criterion, whilst honey yield, as well as low swarming drive and calmness during inspection, were of lower interest. Resistance against *V. destructor* was in

Table 1. Repartition of beekeepers having replied to the survey according to their number of hives and their beekeeping experience.

Number of respondents per beekeeping operation size class	
Size class	*Beekeepers having replied to the survey*
1 to 5 colonies	5
6 to 10 colonies	12
11 to 20 colonies	36
21 to 30 colonies	18
31 to 40 colonies	15
41 to 50 colonies	9
51 to 100 colonies	2
More than 100 colonies	2
Number of respondents per experience class	
Experience class	*Beekeepers having replied to the survey*
0 to 4 years	19
5 to 10 years	30
11 to 20 years	16
21 to 40 years	28
41 years and more	6

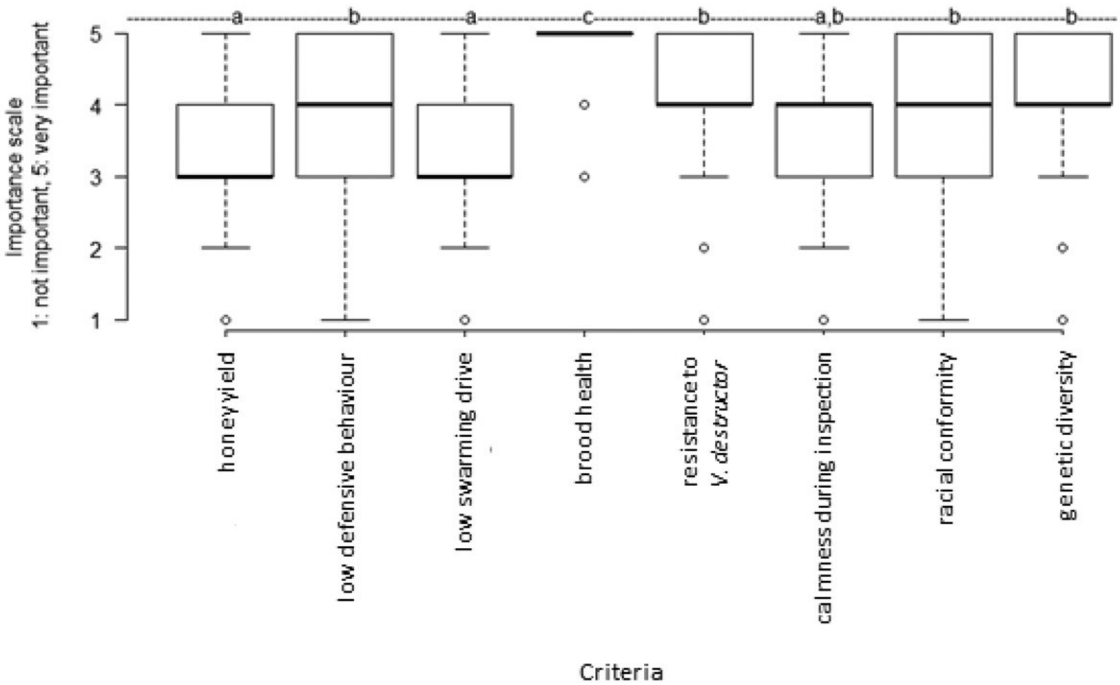

Figure 1. Importance of separately evaluated breeding-related criteria rated on a scale from 1 (not important) to 5 (very important) for 99 respondents to the survey. Importance significantly varies according to criteria (Friedman rank sum test, Friedman chi-squared $= 203.41$, df $= 7$, p-value $< 2.2e\text{-}16$). Different letters indicate significant (p-values <0.05, p adjust method: Holm) differences between the importance of criteria, following the calculation of the p-values of the absolute rank sum differences of the pairs of Friedman rank sums.

between with a high level of importance (mean 4.11, standard deviation 0.96).

Beekeepers were clustered (unsupervised clustering) according to their preferences. We identified five different groups, which show different levels of interest for one or several criteria (Figure 2). The groups were numbered from 1 to 5, and clustering occurred as follow: (1),((2,3),(4,5)). Group 3 ($n_3 = 39$) gathered most of the beekeepers, followed by group 1 ($n_1 = 23$) and three smaller groups (2, 4 and 5 with resp. $n_2 = 10$, $n_4 = 11$ and $n_5 = 16$).

The mean responses and the standard deviation of each group for the importance scores are presented in Figure 3. Beekeepers across all groups attributed high scores to brood health, but rated the other criteria differently.

If we focus on the importance of resistance against *V. destructor,* all groups had overall high mean values between 3.9 and 4.8, with the only exception of group 2 with a mean value of only 2.4.

Utility of resistance breeding

In order to estimate the willingness-to-pay for a selection strategy involving the resistance against *V. destructor*

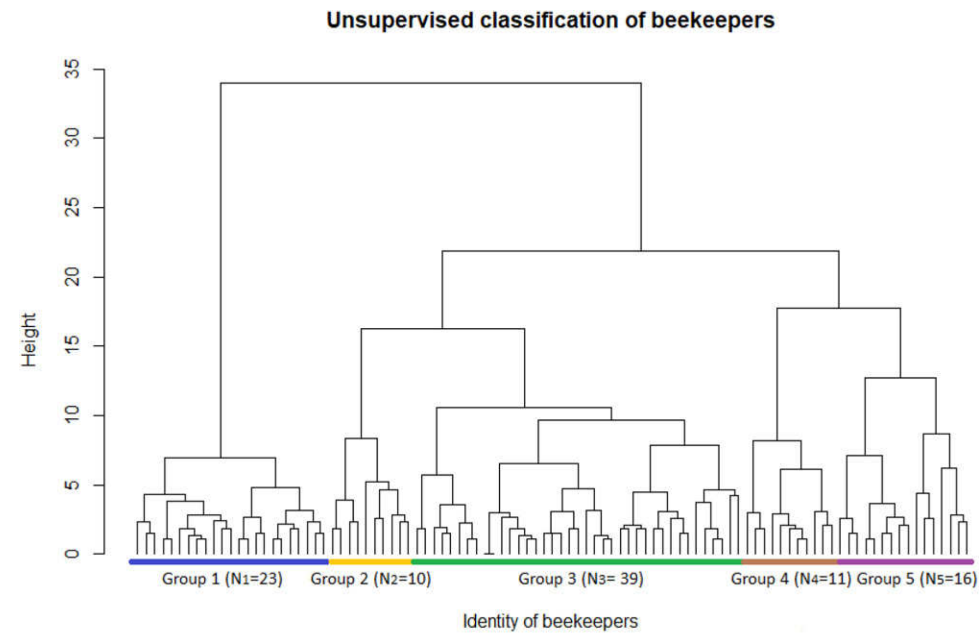

Figure 2. Unsupervised classification of beekeepers (ward. D2 method, Euclidean distances). Height of branches indicates dissimilarities between the beekeepers (located at the end of the branches). Five groups were identified, gathering respectively 23 (group 1), 10 (group 2), 39 (group 3), 11 (group 4) and 16 (group 5) beekeepers.

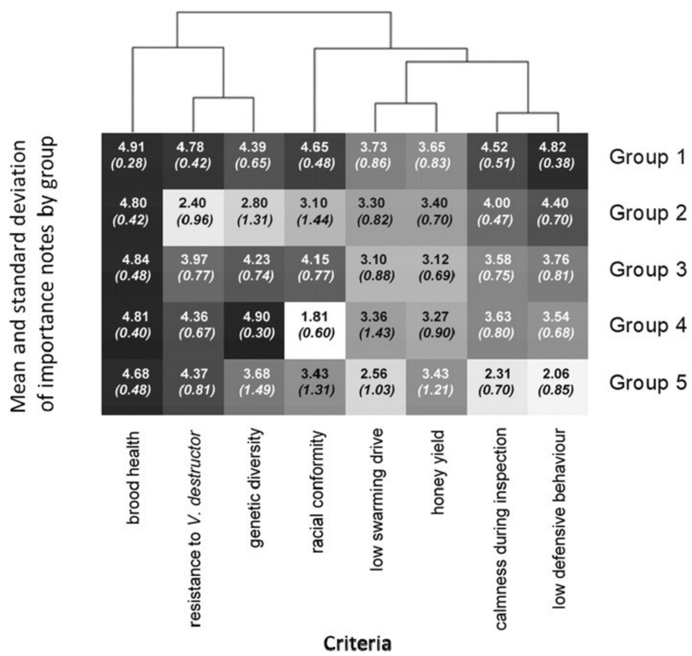

Figure 3. Heatmap of mean importance of the breeding-related criteria by group of beekeepers. Distances were calculated by the Euclidean method. Groups were defined from the clustering of beekeepers in Figure 2. Standard deviations for each criteria per group are indicated in italic between brackets.

among beekeepers by a choice-based conjoint analysis, they were first asked to which extent they would accept unfavourable colony performances or honey bees of foreign origins in exchange of resistance against *V. destructor*. The following different scenarios were proposed.

In a first scenario, lineages of *A. m. mellifera* resistant to *V. destructor* have been identified in Switzerland. Beekeepers were asked to what extend they would use them even if they had lower beekeeping aptitudes. Sixteen beekeepers replied they would continue to use their own honey bees in any case. Seventeen beekeepers would only use the resistant *A. m. mellifera* if they show a better performance compared to the current honey bees. Forty-one beekeepers were willing to switch to the resistant lineages even though they would produce about 25% less honey compared to their current honey bees, 20 if they would only produce half the honey of their current honey bees and 5 even if they would produce almost no honey.

Similarly, 33 beekeepers were in favour of resistant but more aggressive honey bees, and 48 were in favour of resistant honey bees with a higher swarming drive. Beekeepers belonging to the aforementioned group 4 (56% of them) were significantly more interested in having a resistant but more aggressive *A. m. mellifera* on their apiary than beekeepers belonging to group 1 (13%) (Wilcoxon test, $P = 0.048$, p adjust method BH).

In a second scenario, lineages resistant to *V. destructor* have been identified in Switzerland but they are not pure *A. m. mellifera*. These resistant honey bees might originate from other breeds (e.g., *A. m. carnica*) or are hybridised *A. m. mellifera*. 45 beekeepers replied they would continue using their own but not resistant *A. m. mellifera*, 28 were willing to switch to the resistant lineages, and 26 would have wanted to try cross breeding to incorporate resistance in their own *A. m. mellifera*. Beekeepers from groups 3 (70% of them) and 5 (63%) were significantly more interested in using Swiss honey bees resistant to *V. destructor* even if they were not pure *A. m. mellifera* when compared to the other groups 1 (21.7%) and 2 (10.26%) (Wilcoxon tests, *P*: 1 vs. $3 = 0.03$, 1 vs. $5 = 0.05$, 2 vs. $3 = 7.10^{-4}$, 2 vs. $5 = 1.10^{-3}$, *p* adjust method BH).

In a third scenario, lineages of *A. m. mellifera* resistant to *V. destructor* have been identified in a foreign European country. Forty-eight beekeepers replied they would continue using their own but not resistant *A. m. mellifera.* Twenty-three beekeepers were interested in working with the imported resistant lineages of *A. m. mellifera,* and 28 were interested in performing crosses to incorporate resistance in their own *A. m. mellifera*.

When comparing the proportions of beekeepers choosing the resistant honey bees in the second and third scenarios, despite an absence of significance, beekeepers preferred to choose a local non-native resistant honey bee than a resistant *A. m. mellifera* honey bee originating from abroad (two-sample test for equality of proportions, chi-squared $= 0.42$, $P = 0.26$). This point may need a detailed survey.

Implementing resistance breeding in the selection strategy

In the survey, several questions study how the beekeepers would imagine including resistance against *V. destructor* in the selection program if they wanted to select efficiently for it. Detailed results are presented in Table 2.

First, beekeepers expressed on possibilities to select resistance against *V. destructor* in the Swiss population of *A. m. mellifera* (Table 2, 2.1). Among the studied sample, the majority of beekeepers considered that selection for resistance could result in a genetic progress. Some other beekeepers had a similar opinion but expressed concerns about possible losses of genetic diversity linked to the intensive selection. Some respondents assumed that infestation is mainly not regulated by genetic factors of the host. Finally, a minority considered the infestation to be effectively manageable by the currently recommended treatments, with no need to develop selection strategies.

The beekeepers were asked how such a selection program could be established in terms of selection criteria, selection methods and selection intensity. Imagining they would one day own 500 colonies to select for resistance towards *V. destructor* (Table 2, 2.2), the majority of beekeepers stated they would proceed by re-queening rather than letting the population evolve only by natural selection. It could also be noticed that a minority was opposed to the idea of any artificial selection. When considering human mediated selection, beekeepers favoured a selection with a relatively low selection intensity (50% best queens used to produce next generation) (Table 2, 2.3). In the same time, a high proportion of the beekeepers was in favour of a 50% weighting of the *V. destructor* criteria in the selection index, preferentially to the current weighting for this criteria (20%) (Table 2, 2.4).

About three quarters of the beekeepers were in favour of using a genotyping service, if available in the future, to identify potentially resistant colonies on the basis of genetic markers (Table 2, 2.5). Beekeepers in favour mentioned a potential time gain in selection, the importance of an additional criterion to better estimate the value of single colonies and a means to possibly decrease treatment frequencies and improve the health state. Beekeepers against the application of genotyping mentioned a general mistrust in genetic techniques, possible negative outcomes in terms of genetic diversity, the fact that the service may not be affordable for hobby beekeepers and that they assumed their own beekeeping experience suffices to identify colonies with low infestations.

Discussion

The aim of this study was to develop a method to assess the desirability of resistance breeding against *V. destructor* among beekeepers, with a special interest for beekeepers performing selection in small closed populations in order to develop better or optimise existing breeding scheme. With our study in the case of the Swiss *A. m. mellifera* we suggest that desirability can be highlighted and the utility for beekeepers identified. Our results show that such approaches could be taken into account in studies planning to design breeding schemes or proposing new phenotypes. Indeed, research results could successfully be implemented in field actor's

Table 2. Beekeeper responses to multiple-choice questions on the implementation strategy of honey bee resistance against *V. destructor* in the selection program.

2.1: Varroa and selection: Do you think selection of the honey bee is a way to find a solution to the Varroa problem?			
Yes, I am convinced that *selection offers ways* to enable the bee to survive, despite Varroa.	**Yes,** but as long as it does *not reduce the genetic diversity* of bees	**No**, I think that *other factors* (environment, beekeeping practice …) are mainly implicated	**No,** I can fight Varroa effectively with other means; I *do not have to breed* against it.
52 replies	31 replies	11 replies	6 replies
2.2: Imagine that you have 500 dark bee colonies. You have started a selection for Varroa resistance in your own bees. How do you proceed?			
Only through natural selection: the colonies are not treated, only those who survive are used for breeding (BOND test)	The colonies with a lot of Varroa before treatment are *requeened* with queens from lines with little Varroa		Opposed to any selection
23 replies	**76 replies**		4 replies
2.3: Imagine, in Switzerland, a breeding program with the main focus on Varroa resistance in the dark bee started. What should be the percentage of selected queens? (Proportion of queens to be used for breeding)?			
breeding should be done from the *50% best queens* for Varroa resistance (*rather low selection intensity*)	breeding should be done from the *10% best queens* for Varroa resistance	breeding should be done from the *1% best queens* for Varroa resistance (*high selection intensity*)	Opposed to any selection
50 replies	35 replies	10 replies	4 replies
2.4: What should be the part of Varroa resistance in the overall breeding value?			
100% Varroa *resistance*	*50%* Varroa *resistance*, 50% other characters	*20%* Varroa *resistance*, 80% other characters (current)	Opposed to any selection
13 replies	**57 replies**	25 replies	4 replies
2.5: Imagine it has been proven that some genes in the dark bee enable Varroa resistance. There is a possibility to have your bees tested for these genes (genotyping). So you might know from which colonies you should continue to breed for Varroa resistance without taking phenotypic measurements.			
You *have* your bees genotyped			You do *not have* your bees genotyped.
73 replies			26 replies

networks if their goals and resources are taken into account.

In the Swiss *A. m. mellifera* beekeepers who replied to our survey, resistance to *V. destructor* generally belonged to the most important criterion. This was also highlighted by the fact that brood health in general was mentioned as the most important criteria, *V. destructor* being, together with bacteria, viruses and fungi, part of the threats to developing honey bees. In Switzerland, the severe and frequent European foulbrood infections (von Büren, Oehen, Kuhn, & Erler, 2019) may contribute to the high interest for good brood health.

Nevertheless, the general interest for resistant honey bees had to be observed in more detail in order to distinguish variability among beekeepers. The cluster analysis of the beekeepers allowed us to separate them in five groups (Figure 2) based upon their expectations regarding the phenotypic (beekeeping abilities) and genetic quality (correspondence to racial standards and genetic diversity) of their honey bees, reflecting thereby diverse profiles which are discussed below.

Group 1 gathered beekeepers in quest for the Perfect bee *(P-Bee)*, with high values for all the measured/proposed criteria. These high expectations may be difficult to reach, even by a selection on an index, since phenotypes may not all be positively correlated (Boigenzahn & Willam, 1999; Hoffmann, 1996). Group 2 gathered beekeepers who seemed to look for an Easy-to-manage honey bee *(E-Bee)* which allows beekeeping as a recreational activity; expectations were high to reduce defensive behaviour and swarming drive while improving calmness during inspection, which are criteria allowing simpler colony inspections. In contrast, resistance to *V. destructor* was of lower importance for them. Beekeepers from group 3 showed a similar trend to group 1 but with generally lower values and can be considered as beekeepers who want to raise Good bees *(G-Bee)* but were more realistic about the possible limits. Beekeepers from group 4 combined very low values for racial conformity and the highest values for genetic diversity, which can be interpreted as the desire to breed healthy and genetically Diverse honey bees *(D-Bee)* independently of their racial origin. Finally, in group 5, beekeepers showed low interest for calmness during inspection, low defensive behaviour and low swarming drive. They seemed to expect their colonies to express their Wild behaviour *(W-Bee)* with minimal beekeeping intervention.

Clustering beekeepers according to their breeding goals may be important to identify the diversity of beekeeping aims and thereby breeding goals for one single honey bee population. This knowledge could be useful to rear different lines corresponding to the different beekeeper's profiles.

Focusing more precisely on *V. destructor*, we noticed that beekeepers looking for E-Bees (group 2) seemed to be less interested in the resistance issue. This may indicate that they were using efficient management techniques and did not consider *V. destructor* as a serious threat for their beekeeping activity. They might nonetheless be interested in resistance stock if available one day as a supplementary part of their Integrated Pest Management strategy (Imdorf, 2009; Imdorf, Charrière, Kilchenmann, Bogdanov, & Fluri, 2003).

Once *V. destructor* had been identified as an important issue within the group of beekeepers, it appeared interesting to pursue conditions in which resistant stock would be useful for them. The choice-based conjoint analysis approach showed that beekeepers were generally ready to have lower honey yield or bees that were more aggressive in exchange of more resistance against *V. destructor*. This estimation method of a willingness-to-pay could also be used with a monetary evaluation in further populations reared by a majority of professional beekeepers. Beekeepers were also more susceptible to adopt honey bees resistant to *V. destructor* if they originated from the same subspecies as their own honey bees and were selected locally in Switzerland. Nonetheless, if a native resistant honey bee was not available, beekeepers would have preferred a local (but not pure *A. m. mellifera*) resistant honey bee to a foreign resistant *A. m. mellifera* honey bee. Crosses between already resistant and local susceptible lines could have also been accepted by a part of the beekeepers to acquire resistance-providing genes, but, as resistance mechanisms are often variable among resistant populations (Locke, 2016), additional information should be provided on their suitability in the case of Swiss *A. m. mellifera*. Beekeepers seemed to consider that the local dimension is more susceptible to confer adaptation than the belonging to the subspecies itself, which appeared to be a finding of a European research project (Büchler et al., 2014). This assessment would need further investigation in field conditions for the situation in Switzerland.

Since the breeding goal and the conditions of the beekeepers were identified, the design of the corresponding breeding scheme could be studied. Aspects related to the general structure of the approach were of main interest.

According to the situation in Switzerland, beekeepers favoured a selection approach using human-mediated selection to an approach relying on natural selection only. A reason could be that they may not have been convinced that such a method would necessarily deliver the desired outcome, and were therefore maybe not willing to submit their stock to transitory high colony losses (Fries, Imdorf, & Rosenkranz, 2006; Kefuss, Vanpoucke, Bolt, & Kefuss, 2016). Economic and psychologic reasons may have also been involved, as well as the lack of successful examples in beekeeping contexts which could help to estimate the probability of success and the selection progress of such a program. Some European examples of surviving populations in which only natural mating among susceptible colonies occur (Kefuss et al., 2016; Le Conte et al., 2007) may have also casted doubt on the origin of this survival, as dilution of the genetic material is likely to occur over generations.

Previously identified resistant populations were also often described as having less favourable characteristics for beekeeping, with frequent swarming, small populations and low honey yield (Fries & Bommarco, 2007; Le Conte et al., 2007). Even if beekeepers declared that they would be willing to rear less productive or gentle honey bees, there may be differences between the stated and the actual willingness-to-pay (Bhatia & Fox-Rushby, 2003; Carlsson & Martinsson, 2001), and so maybe different real acceptances for honey bees with less valuable aptitudes for beekeeping than compared to the results of the survey. Statements may have also be influenced by advices or opinions exchanged in the frame of the association, and not only reflected the own expertise of the beekeepers, thereby creating social desirability biases which are difficult to identify.

In their approach, beekeepers would have favoured a selection with a low intensity, perhaps to limit inbreeding problems in their small population, but with a high part of the breeding index dedicated to selection for resistance against *V. destructor,* higher than the 20% currently implemented. This can be interpreted as being in agreement with the importance of genetic diversity appearing in the first part of our analysis. Having a broad selection combined to a high focus on resistance in the index may allow to generate a breeding progress minimizing the loss of genetic diversity.

It can be concluded from our study that Swiss beekeepers rearing *A. m. mellifera* who replied to our survey were aware of the threat posed by *V. destructor* and that desirability for resistant stock exists. Nonetheless, for a generalisation at the level of the whole population of Swiss *A. m. mellifera* beekeepers, further market analysis would be necessary to better identify potential sampling biases, as beekeepers already interested by *V. destructor* or selection issues might have responded more to the survey than uninterested beekeepers. The majority of the respondents assumed that selection could provide adequate solutions, now they would need more information to estimate its feasibility and the results they could expect. The diversity of the beekeeper's profiles and needs could also require specific responses, for instance by breeding different lines with particular abilities. Although this diversity of goals can be seen as an additive complexity, it may also be the best guarantee for the maintenance of genetic diversity.

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Supplementary material

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