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A national survey of managed honey bee colony losses in the USA: results from the Bee Informed Partnership for 2017–18, 2018–19, and 2019–20

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ABSTRACT
Beekeepers in the United States have experienced high losses of managed honey bee (*Apis mellifera*) colonies for more than a decade. Long-term, multi-year monitoring efforts are crucial to provide a temporal and spatial context to these losses. To document and explain these losses, the Bee Informed Partnership has conducted national surveys on managed honey bee colonies since spring 2011, continuing the work of surveys first commissioned by the Apiary Inspectors of America in spring 2007. Here we present survey results from three years – 2017–18, 2018–19, and 2019–20. Each year, colony loss rates were estimated and compared among three loss periods – summer, winter, and annual – and three beekeeping operation types based on their number of colonies managed – backyard (≤50 colonies), sideline (51-500 colonies), and commercial (>500 colonies). At the national level, we recorded the highest winter colony loss rates (37.7%) in 2018–2019, while 2019 marked the year with the highest summer losses (32.1%). As documented in past surveys, we observed that smaller scale backyard beekeepers experienced the highest winter loss rates when compared to the larger operation types. Similarly, commercial beekeepers experienced higher loss rates during the summer compared to the other operation types. Overall, our results highlight the temporal variability, specifically among loss periods and years, of colony loss rates in the United States, and suggest a strong effect of beekeeping operation size.

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Apis mellifera; colony losses; citizen science; survey; beekeeping; *Varroa destructor*; queen

Introduction

For more than a decade, Europe, Canada, and the United States have consistently experienced high losses of managed honey bee colonies as documented by their respective monitoring programs (Brodschneider & Gray, 2022; CAPA, 2007, 2022; Gray et al., 2020; Kulhanek et al., 2017; van der Zee et al., 2012; vanEngelsdorp et al., 2007; vanEngelsdorp, Tarpy, et al., 2012). Meanwhile, significant colony losses have not been reported in Africa, Australia, South America, and Asia over the same period; however, this could be an artifact of scarce monitoring efforts in these locations rather than realistic estimates (Antúnez et al., 2017; Hristov et al., 2020; Liu et al., 2016; Pirk et al., 2014; Requier et al., 2017, 2018). Regardless of the geographical location, honey bee colony losses strain the beekeeping industry that is responsible for the pollination of many agricultural crops (Calderone, 2012; Ferrier et al., 2018; Popovska Stojanov et al., 2021).

Colony losses are likely a result of a plethora of biotic and abiotic risk factors (Havard et al., 2019; Hristov et al., 2020; Neov et al., 2019; Steinhauer et al., 2018). Biotic risk factors include the availability of floral resources in natural and agricultural regions, poor quality queens, and introduced parasites like the *Varroa destructor* mite (hereafter Varroa) (Brodschneider & Crailsheim, 2010; Dainat et al., 2012; Dolezal & Toth, 2018; Tarpy et al., 2013; Traynor et al., 2020; vanEngelsdorp, Tarpy, et al., 2013). Similarly, diverse abiotic risk factors exist, including unfavorable extreme weather events and environmental contaminants such as fungicides and insecticides (Becsi et al., 2021; Kulhanek et al., 2021; Le Conte & Navajas, 2008; Traynor et al., 2016, 2021).

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DvE and KR conceptualized the original structure of the Loss Survey. All authors contributed to adjustments made to the survey design. NS and MW contributed to data collection; NS, MW, and SB curated and analyzed the data. The article was written by SB and reviewed by all other authors. All authors agreed on the final version. DvE and GRW acquired funding to conduct the work.

The pressure of such risk factors may vary seasonally; D'Alvise et al. (2019) for example showed that certain viruses like acute bee paralysis virus (ABPV) were more prevalent during summer, while others like deformed wing virus (DWV) were more abundant during winter. Furthermore, the effects of risk factors may not become evident immediately. Effects of exposure to sub-lethal concentrations of pesticides, for example, tend to appear after a time-lag (Grassl et al., 2018; Straub et al., 2019). Similarly, the consequences of winter bees raised under sub-optimal conditions may not become apparent until the colony collapses later in the season (Dainat et al., 2012). These empirical studies are further supported by anecdotal evidence from beekeepers—they commonly report Varroa, queen issues, and starvation, as important threats to their colonies (Gray et al., 2019; Kulhanek et al., 2017; Pirk et al., 2014). However, given the seasonal variability in risk factors and potential lag-effects, it is crucial to expand survey questions beyond winter hazards to also ask beekeepers about their summer experiences. This understanding could be instrumental in implementing regional and seasonal Best Management Practices (BMPs).

BMPs give beekeepers the option to apply management tailored to their specific needs while prioritizing colony health (Project Apis m, 2020). Some beekeepers maintain a handful of colonies in the area in which they reside for honey production for personal use, environmental stewardship, or leisure (Thoms et al., 2019; Underwood et al., 2019), whereas other beekeepers manage thousands of colonies as a business; in many cases, these commercially managed colonies are strategically moved across regions to provide migratory pollination services to a variety of economically important crops like almonds, and blueberries (Calderone, 2012; vanEngelsdorp, Tarpy, et al., 2013), or in search of high-intensity nectar flows for honey production (Whynott, 1991). This highlights that beekeeping practices are closely related to the number of colonies managed and goals and variations in practices can impact colony health (Haber et al., 2019; Steinhauer et al., 2021; Underwood et al., 2019). For example, beekeepers managing large numbers of colonies (i.e. sideline and commercial beekeepers managing 51-500 and more than 500 colonies, respectively) consistently employ synthetic in-hive chemicals to combat Varroa, which possibly reduces the risk of colony mortality in winter. On the other hand, backyard beekeepers managing 50 or fewer colonies are more likely to use non-synthetic chemicals or none at all, which could explain the greater loss experienced by this group of beekeepers, especially during winter (Haber et al., 2019).

The Bee Informed Partnership (BIP) is an American non-profit organization that has conducted an annual survey to assess national colony losses since 2011, continuing the annual survey first commissioned by the Apiary Inspectors of America in 2007 (Kulhanek et al., 2017; Lee, Steinhauer, Rennich, et al., 2015; Seitz et al., 2015; Steinhauer et al., 2014; VanEngelsdorp, Tarpy, et al., 2012; vanEngelsdorp et al., 2008; 2017). Instead of using the traditional definitions of a season, BIP has defined three specific loss periods: Winter, summer, and annual. Initially (prior to the 2010–2011 survey) only colony losses during the winter period were recorded because beekeepers historically reported high losses during this time of the year (Brodschneider et al., 2010; Ellis et al., 2010; Laurent et al., 2016; Pirk et al., 2014; Seeley & Visscher, 1985; Zee et al., 2014). Over the last ten years of surveys, winter colony loss rates fluctuated among years (winter colony loss rates ranged from 21.1% in 2016–17 to 35.7% in 2007–08), averaging 28%. This was 11 percentage points higher than the rates beekeepers reported to be acceptable (Kulhanek et al., 2017; Lee, Steinhauer, Rennich, et al., 2015; Seitz et al., 2015; Spleen et al., 2013; Steinhauer et al., 2014; vanEngelsdorp, Caron, et al. 2012; vanEngelsdorp et al., 2007, 2008, 2010, 2011). In 2011, BIP's loss monitoring efforts expanded to include the summer to document anecdotal reports of predominantly large-scale beekeepers losing colonies during the active honey bee brood-rearing season (Steinhauer et al., 2014). Since then, the survey has shown that colony losses do not only vary across years and operation sizes, but also among loss periods.

Here we present the results of BIP's national managed honey bee colony loss surveys conducted for three years – 2017-18, 2018-19, and 2019-20 (Bruckner, 2020). The primary objective of this work was to continue BIP's standardized survey of managed honey bee colony losses in the United States to document long-term industry trends. We compared colony loss rates between different states, operation sizes, operations that migrate and are stationary, as well as operations that pollinate almonds and ones that do not. Furthermore, we report on beekeeper-perceived acceptable colony loss rates during the winter period and beekeeper-perceived causes of colony losses. Past colony loss studies found that small-scale beekeeping operations experienced higher losses compared to large-scale ones, especially during the winter period, and that operation activity (i.e. migration or almond pollination) had no significant effect on colony loss rates (Brodschneider et al., 2018; Gray et al., 2019; Kulhanek et al., 2017; Seitz et al., 2015; Steinhauer et al., 2014). Thus, we expected to observe similar relationships regarding colony loss during the reported three years.

Materials and methods

Survey design

An online survey was created using Select Survey (https://10.selectsurvey.net) to collect information about managed honey bee colony losses across the United States beginning 1 April for each of the three survey years – 2017-18, 2018-19, and 2019-20. The surveys were designed to closely align with the previously published national colony loss surveys by BIP (Kulhanek et al., 2017; Lee, Steinhauer, Rennich, et al., 2015; Seitz et al., 2015; Spleen et al., 2013; Steinhauer et al., 2014; vanEngelsdorp, Caron, et al. 2012; vanEngelsdorp et al., 2007, 2008, 2010, 2011). Prior to the most recent survey year (2019-20), respondents had to complete the survey questionnaire in one sitting. Respondents were asked to create a login to the online platform in the survey year 2019-20, which allowed them to revisit their responses before their submission. The survey consisted of three sections - the "loss survey," the "management survey," and additional questions concerning socioeconomics. This work reports the results of the "loss survey" section.

Loss survey design

As in previous surveys, three colony loss periods were defined as 1 April 201X – 1 October 201X (summer), 1 October 201X – 1 April 201Y (winter), and 1 April 201X – 1 April 201Y (annual), whereby "X" and "Y" represent successive years. First, respondents were asked to provide the location of their operation at the state-level, followed by quantitative questions about the number of colonies in their operation at the start of each loss period, the number of increases made by splitting or purchasing, and the number of decreases made giving away or selling existing colonies. Additionally, respondents were asked to state the level of winter loss rate they deem acceptable and what they perceived as the most likely cause(s) for their colony losses. To address the latter, respondents chose from a selection of pre-defined "causes of winter loss" (Supplementary Tables S8–S10), but could also insert additional reasons using an open field text box. As in past efforts, this list included commonly reported risk factors; however, "Colony Collapse Disorder" (CCD) was removed from the pre-selected list in the 2018-19 survey year as the term has incorrectly evolved to encompass all unexplained losses despite its distinct set of characteristics (Cox-Foster et al., 2007; Williams et al., 2010). Therefore, its inclusion is considered no longer meaningful. In the survey year 2018-19, we also included "causes of summer loss" (Supplementary Tables S8–S10) for the first time to assess whether beekeeper-perceived causes of loss differ based on time of year.

All submitted data were cleaned by removing invalid responses and duplicated entries. Only colonies residing within the United States, as defined by her 50 states, the District of Columbia, and five territories were included. Three data subsets corresponding to the summer, winter, and annual loss periods were created; each included beekeeper respondents that maintained at least one colony at the start of the given loss period. This allowed for the inclusion of beekeepers that did not manage one or more colonies throughout an entire year. We differentiated between three different operation types based on the number of colonies managed on 1 October of each year - backyard beekeepers managed 50 or fewer colonies, sideline beekeepers managed 51-500, and commercial beekeepers managed 501 or more colonies (vanEngelsdorp et al., 2007). Finally, respondents categorized as sideline and commercial beekeepers were further subdivided based on two beekeeping activities – if they moved colonies across state lines (i.e. migratory beekeepers) or not (i.e. stationary beekeepers), or if they sent colonies to California for almond pollination or not. To evaluate whether these activities affected colony health, we compared winter colony loss rates between migratory and stationary beekeepers, as well as between beekeepers that provided almond pollination services and those that did not.

Survey distribution

The survey represents a non-random subsample of beekeepers in the United States and is convenience-based because respondents provided their answers voluntarily upon personal invitation, advertisement, or word of mouth (Lee, Steinhauer, Travis, et al., 2015). For example, the survey was advertised electronically to beekeepers via the BIP website, via email communication if an address was voluntarily provided in previous BIP colony loss surveys, and via the USDA Animal Plant Health Inspection Service National Honey Bee Disease Survey. Recipients were encouraged to forward the survey link to other beekeepers to increase the response rate. The survey was also promoted by two national beekeeping organizations (American Beekeeping Federation and American Honey Producer's Association), two national beekeeping journals (American Bee Journal and Bee Culture), and two subscriber email lists (Catch the Buzz and ABFAlert). Furthermore, we asked the Apiary Inspectors of America, state extension apiculturists, beekeeping industry leaders, and a number of regional beekeeping clubs to promote the survey among their stakeholders and members. Traditionally, backyard beekeepers account for the majority of the online survey responses. Likely, this is a result of them representing the majority of beekeepers in the country (USDA, 1993; USDA NASS, 2012). To collect more responses from commercial beekeepers that manage the majority of colonies in the United States, BIP staff conducted telephone interviews with beekeepers participating in its Technology Transfer activities. Furthermore, approximately 600 paper-versions of the survey were distributed each year to beekeepers participating in other associated BIP projects.

The online survey was live from 1-30 April each survey year, whereas paper versions were mailed to beekeepers during the last week of March (Online Resource 1 in the supplementary material); those returned by 30 May of each respective year were included in the study.

Statistical analyses

All calculations and statistical tests were performed using the statistical program R (R version 3.6.2) using a significance level of $\alpha = 0.05$. According to vanEngelsdorp, Lengerich, et al. (2013), weighted (total) and unweighted (average) colony losses were calculated for the three fixed loss periods (summer, winter, and annual) of each year using the R code presented in Steinhauer et al. (2014). For total loss, every colony was counted individually without considering operation size; this is more representative of respondents with larger operations like commercial beekeepers since they manage the majority of colonies in the United States (USDA NASS, 2018, 2019, 2020). Conversely, average loss counts each operation as one unit, which facilitates comparison among operation types and activities (e.g. migration and almond pollination). Ninety-five percent confidence intervals were calculated by employing a bootstrap sampling distribution. For that, the data set was resampled 1000 times while employing the N-out-of-N-method (Frost, 2020).

We identified differences in average colony loss rates among operation types (backyard, sideline, commercial), and between migration and California almond pollination statuses, using the Kruskal-Wallis rank sum test (KWrs). For multiple comparisons, KWrs was followed by the Tukey's honestly significant difference (HSD) test. State colony losses were reported by including colonies of multi-state beekeepers in each state in which they reported having colonies. To maintain respondents' anonymity, losses for states with ten or fewer respondents were not reported.

Results

Loss survey responses

Loss survey response rates declined each year, with 5599 nationally validated responses in 2017-18, 5510 in 2018-19, and 3773 in 2019-20, representing an estimated 4.7%, 4.6%, and 3.1% of the beekeepers in the U.S. (National Honey Board, 2016). However, the number of colonies managed by respondents increased overall, from 159258 in 2017-18, 318932 in 2018-19, and 262044 in 2019-20, despite lower participation rates. This represented 6.3%, 11.1%, and 8.7% of the total number of estimated honey producing colonies in the U.S. in 2017, 2018, and 2019, respectively (USDA NASS, 2018, 2019, 2020). The number of respondents and managed colonies per operation type was variable among both type and year (Supplementary Figure S1, Supplementary Table S1).

National total and average colony loss estimates

Over the three survey years, the national estimate for total summer loss was highest in the survey year 2019-20 (32.1%) and lowest in 2017-18 (17.9%). For total winter loss, the national estimate was highest during the survey year 2018-19 at 37.0% and lowest in 2019- 20 at 22.9%. Total annual loss ranged between 40.4% in the survey year 2018-19 to 44.0% in 2019-20 (Figure 1, Supplementary Table S2). Conversely, over the three survey years the national estimate for average summer loss was highest in the survey year 2019-20 at 21.5%, and lowest in 2018-19 at 14.6%. The highest average winter loss was 50.4% in the survey year 2017-18, whereas the lowest in 2019-20 at 35.7%. The average annual loss ranged between 46.1% in the survey year 2019-20 and 57.3% in 2017-18 (Supplementary Table S2).

State respondents, total and average colony loss estimates

To protect participants' privacy, we did not include states with less than 10 respondents in the state analyses. The number of valid state-specific respondents and colony loss estimates were highly variable among states, loss periods, and survey years (Supplementary Tables S3–S5). Similarly, colony loss estimates varied between states, loss periods, and survey years (Figures 2, S2 and S3, Supplementary Tables S3–S5).

National total and average loss estimates by operation type

For all three loss periods per year, total and average colony losses were estimated for each operation type (backyard, sideline, commercial). Commercial beekeepers experienced higher average summer loss compared to backyard and sideline

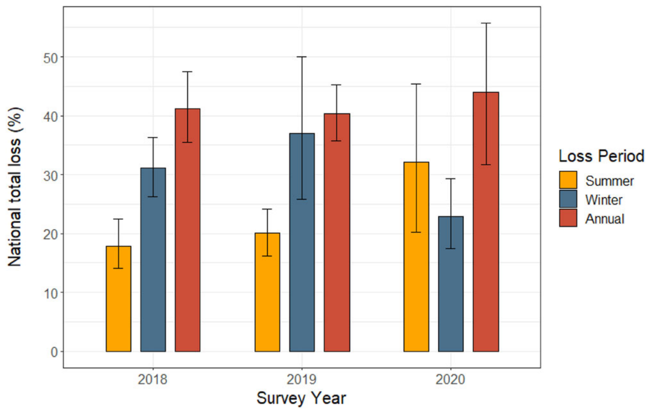

Figure 1. Managed Apis mellifera honey bee colony total loss estimates per loss period in the United States for three years of the Bee Informed Partnership's loss survey. The bar graphs indicate the national total loss estimates [%] for summer (1 April 201X – 1 October 201X), winter (1 October 201X – 1 April 201Y) and annual (1 April 201X – 1 April 201Y) loss periods, whereby "X" and "Y" represent successive years. Vertical black lines indicate the 95% CI.

Table 1. A summary of managed Apis mellifera honey bee average (unweighted) colony losses in the United States by operation type and loss period for three survey years of the Bee Informed Partnership's loss survey. Average (unweighted) colony loss estimates are listed for respondents (N) belonging to one of three operation types: Backyard, sideline, and commercial beekeepers who managed 50 or fewer, between 51 and 500, and more than 500 colonies, respectively. Different letters identify differences in average colony loss between operational types for each year's specific loss periods.

Survey Year	Period	Operation type	N	Average loss (% [95%CI])	χ2, p
2017-18	Summer	Backyard	3908	18.7[b] [17.9-19.5]	15.94, <0.01
		Sideline	127	14.7[b] [12.0-17.6]	
		Commercial	39	22.8[a] [18.2-27.7]	
	Winter	Backyard	4674	51.0[a] [49.8-52.0]	22.20, <0.01
		Sideline	15	37.4[b] [32.9-41.4]	
		Commercial	38	31.6[c] [24.2-39.2]	
	Annual	Backyard	3730	57.9[a] [56.8-58.9]	24.57, <0.01
		Sideline	125	45.9[b] [41.5-50.2]	
		Commercial	34	43.8[b] [36.4-50.7]	
2018-19	Summer	Backyard	3669	14.5[b] [13.8-15.3]	46.07, <0.01
		Sideline	91	14.1[c] [10.6-17.9]	
		Commercial	57	20.8[a] [17.2-24.9]	
	Winter	Backyard	4466	44.2[a] [43.1-45.4]	9.31, 0.01
		Sideline	108	33.3[ab] [28.5-37.8]	
		Commercial	58	26.2[b] [20.8-31.6]	
	Annual	Backyard	3514	49.8[a] [48.6-50.9]	10.67, <0.01
		Sideline	87	41.4[ab] [36.2-46.9]	
		Commercial	52	36.4[b] [31.9-41.3]	
2019-20	Summer	Backyard	2712	21.5[b] [20.5-22.5]	8.96, 0.01
		Sideline	81	17.5[b] [14.3-20.9]	
		Commercial	41	28.2[a] [21.3-35.4]	
	Winter	Backyard	3169	36.0[a] [34.8-37.3]	0.005, 0.99
		Sideline	91	28.9[a] [24.2-33.7]	
		Commercial	41	28.9[a] [22.6-35.9]	
	Annual	Backyard	2574	46.3[a] [45.0-47.6]	2.86, 0.24
		Sideline	78	38.8[a] [34.0-43.8]	
		Commercial	36	46.2[a] [39.4-53.0]	

beekeepers in all three survey years (all $p < 0.05$, Table 1, Supplementary Figure S4). In 2017-18 and 2018-19, Backyard beekeepers had higher average winter and annual colony losses compared to commercial beekeepers (all $p < 0.05$). While backyard beekeepers also had higher average winter and annual loss compared to sideline beekeepers in 2017-18 ($p < 0.05$), the losses suffered by both operation types did not differ in 2018-19. Finally, there were no differences among operation types for average winter and annual loss estimates in 2019-20 (Table 1, Supplementary Figure S4).

Average winter loss estimates for migratory beekeeping operations and those providing almond pollination

Since large-scale (sideline and commercial) beekeepers are more likely to move colonies across state lines and provide pollination services to almonds compared to small-scale (backyard) beekeepers, we only compared winter loss rates for beekeepers that manage more than 50 colonies. Average winter loss estimates for sideline and commercial beekeepers did not differ between migratory status within any of the three survey years (2017-18: $\chi^2=3.79$, $p=0.05$; 2018-19: $\chi^2=2.14$, $p=0.14$; 2019-20: $\chi^2=1.59$, $p=0.21$). Similarly, average winter loss estimates were not different for operations that sent colonies to California for almond pollination compared to ones that did not (2017-18: $\chi^2=3.61$, $p=0.06$; 2018-19: $\chi^2=1.29$, $p=0.26$; 2019-20: $\chi^2=0.39$, $p=0.53$) (Supplementary Table S6).

Self-reported acceptable winter colony loss

We asked respondents to report the level of loss they would have deemed acceptable in the preceding winter. More than 90% of all valid winter loss respondents answered this question (Supplementary Table S7). The average acceptable winter loss was 20.6% in the survey period 2017-18, 22.3% in 2018-19, and 21.2% in 2019-20, respectively. The three-year average of acceptable winter loss was 21.3%.

Self-reported causes of summer and winter loss

Self-reported causes of summer and winter loss were ranked according to the selection frequency of beekeepers. In the summer, "Queen issues" was ranked first for all operation types and survey years in which the question for this loss period was included (i.e. 2018-19 and 2019-20), followed by "Varroa mites and associated viruses" (Figure 3A, Supplementary Tables S8–S10). Ranked third among the cause of summer losses was "Don't know" for backyard beekeepers, while sideline beekeepers ranked "Nutritional stress (Pollen)" third in 2018-19 and "Pesticides and apicultural treatments" in 2019-20. Finally, "Pesticides and apicultural treatments" were ranked third by commercial beekeepers in both years.

The causes of winter loss rankings were less consistent (Figure 3B, Supplementary Table S8–S10). Backyard beekeepers ranked "Starvation" first in years 2017-18 and 2018-19, followed by "Varroa mites and associated viruses" in the second rank and "Don't know" in the third rank for both years. In 2019-20, backyard beekeepers ranked "Varroa mites and associated viruses" first, followed by "Don't know" and "Starvation." In contrast, sideline and commercial beekeepers consistently ranked "Varroa mites and associated viruses" first in all three years. Ranked second for sideline beekeeper was "Starvation" in 2017-18 and 2019-20 followed by "Queen issues," while the order was reversed in 2018-19. Commercial beekeepers consistently ranked "Queen issues" second in all three years. "Pesticides" were ranked third in years 2017-18 and 2019-20, while they ranked "Nutritional stress (Pollen)" third in 2018-19.

Discussion

Long-term monitoring of managed honey bee colony losses in the United States and elsewhere is critical given their economic, environmental, and societal importance (Lee, Steinhauer, Travis, et al., 2015; Lindenmayer et al., 2012). Consistent with surveys performed in previous years (Kulhanek et al., 2017; Lee, Steinhauer, Rennich, et al., 2015; Seitz et al., 2015; Steinhauer et al., 2014), we recorded national winter and summer loss rates of managed honey bee colonies in 2017, 2018 and 2019. Backyard beekeepers managing 50 or fewer colonies experienced the highest winter losses among all beekeeping operation types for two of the three surveyed years. Commercial beekeepers managing more than 500 colonies experienced the highest summer losses in all three survey years. According to our results, beekeepers consider "Varroa mites and associated viruses" to be a major cause for colony losses in winter, while "Queen issues" were stated to be an important problem in summer.

National total winter loss fluctuated around 30% for the first seven years of the Bee Informed Partnership (BIP) surveys (Steinhauer et al., 2014; vanEngelsdorp, Caron, et al. 2012; vanEngelsdorp et al., 2007, 2008, 2010, 2011), with the exception of Spleen et al. (2013, 23% total winter loss), while it trended downward in the following four years (Kulhanek et al., 2017; Lee, Steinhauer, Rennich, et al., 2015; Seitz et al., 2015; Steinhauer et al., 2017). However, here we show that national total winter loss rates were elevated yet again in 2017-18 (31%) and 2018-19 (38%), with the latter representing the highest loss rate estimate since the 2007-08 survey. These loss rates are considerably higher than historical winter losses of ~10% (Voorhies et al., 1933). Across the three reported survey years, an average of 21% winter loss was deemed acceptable by beekeepers. This is 4% above the ten-year average of 17% acceptable winter loss (Kulhanek et al., 2017; Lee, Steinhauer, Rennich, et al., 2015; Seitz et al., 2015; Spleen et al., 2013; Steinhauer et al., 2014; vanEngelsdorp, Caron, et al. 2012; vanEngelsdorp et al., 2007, 2008, 2010, 2011), and may indicate habituation by beekeepers to elevated losses. These results highlight a general trend and persistence of relatively high winter colony losses compared to what beekeepers deem acceptable.

Early honey bee colony loss surveys focused exclusively on winter loss since most losses were thought to occur during this period of the year (Neumann & Carreck, 2010; vanEngelsdorp et al., 2007, 2008; vanEngelsdorp & Meixner, 2010). Since the survey's winter loss period is defined as the time from 1 October to 1 April, it includes months in which high Varroa infestation levels dramatically

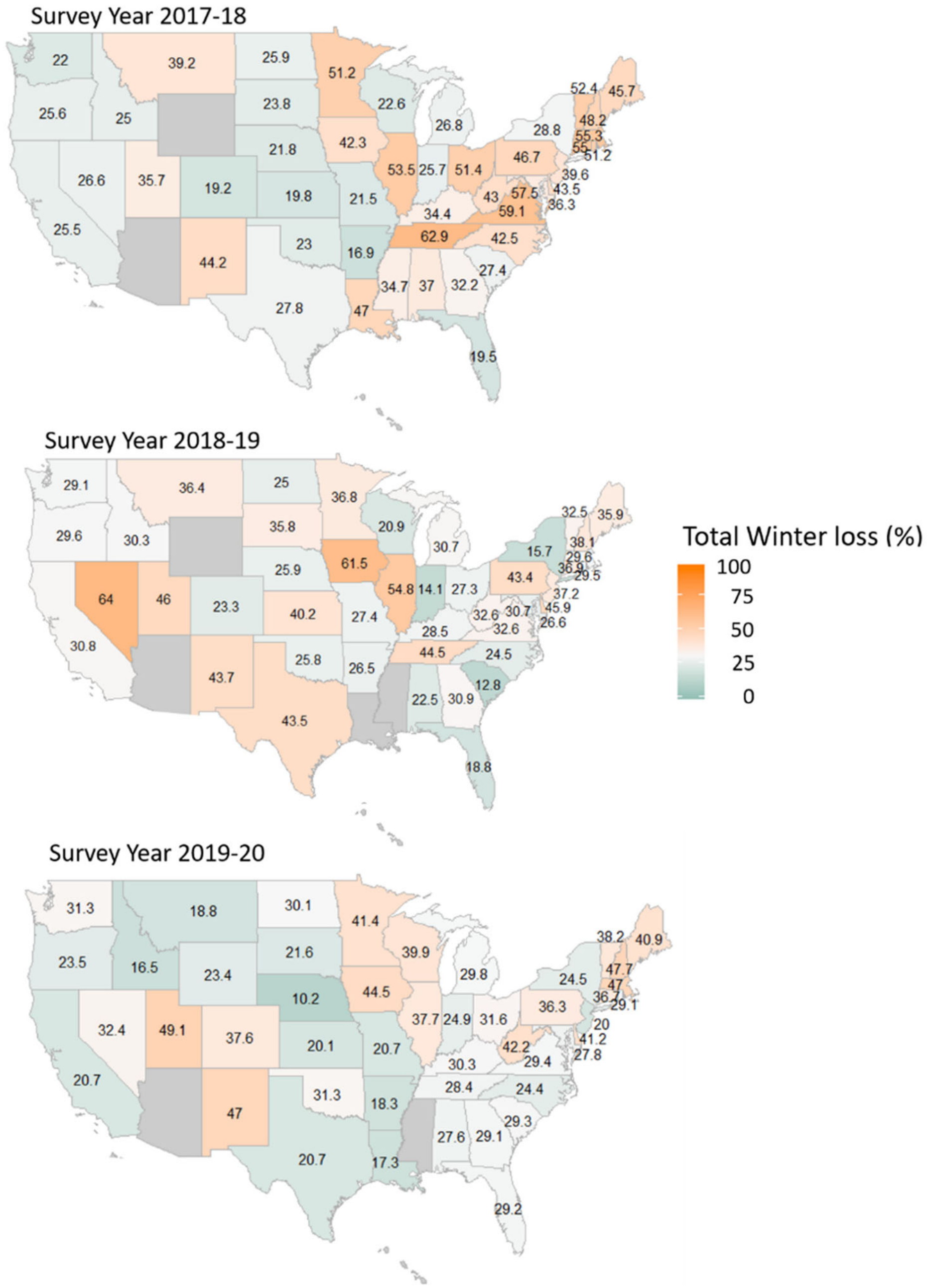

Figure 2. Managed Apis mellifera honey bee colony total winter loss estimates per state for three survey years of the Bee Informed Partnership's loss survey in the United States – 2017-18, 2018-19 and 2019-20. Maps represent state-specific total winter loss estimates [%] (winter: 1 October 201X – 1 April 201Y, whereby "X" and "Y" represent successive years). State-specific estimates, written within or near each state boundary, were only calculated if there were more than ten respondents. Coloration of the loss index is based on the ten-year national average for winter loss – states in blue are below and states in orange are above the national average of ~30%.

increase the risk for winter colony losses (Amdam et al., 2004; Dooremalen et al., 2012; Rosenkranz et al., 2010). Indeed, survey respondents across all three survey years and operation types reported "Varroa mites and associated viruses" as a main reason for their winter colony losses. Apart from Varroa, climatic conditions and resulting changes in forage availability turn winter into a challenging season for both honey bees and beekeepers (Döke et al., 2015). Cold temperatures in northern states are unfavorable for floral resources to persist; while extended periods of cold may not prevail in southern states, dwindling floral resources is a shared feature with the North (Feliciano-Cardona et al., 2020; Shehata et al., 1981). These factors greatly reduce or even pause foraging activity, forcing the colony to survive on food stores, and brood rearing ceases while adults continue to die (Avitabile, 1978; Johansson & Johansson, 1979; Mattila & Otis, 2007). In the three survey years, backyard and sideline beekeepers reported "Starvation" as a main reason for winter colony losses, while it was ranked lower for commercial beekeepers. Since supplemental feeding can alleviate some of the stress posed on colonies during scarce periods

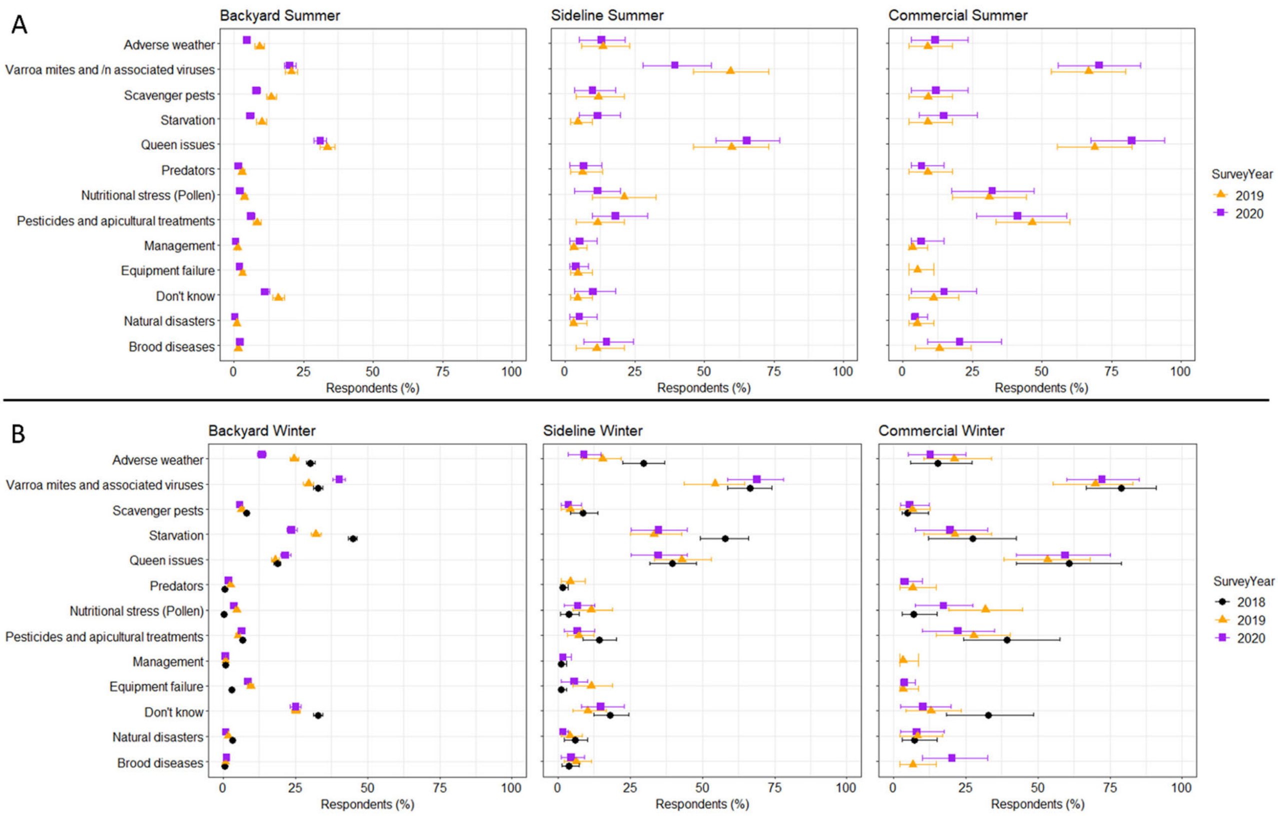

Figure 3. Beekeeper perceived causes of honey bee summer (A) and winter (B) colony losses in the United States by operation type for three years of the Bee Informed Partnership's loss survey 2017-18*, 2018-19 and 2019-20. Each panel represents the selections of each cause of summer or winter loss for three operation types: Backyard (managing fewer than 50 colonies), sideline (managing 51-500 colonies), and commercial (managing more than 500 colonies) beekeepers. Dots indicate the mean percentage of respondents that chose a specific cause of loss, while horizontal bars represent the 95% CI. (*Cause of summer loss was not yet included in this survey year).

(Brodschneider & Crailsheim, 2010; DeGrandi-Hoffman et al., 2008; Paiva et al., 2016), our results could indicate that commercial beekeepers consistently integrate supplemental feeding in their management practices, while it may be more infrequent for backyard and sideline beekeepers. Winter also provides limited opportunities to rectify problems that could result in colony loss such as the queen's death (Seeley & Visscher, 1985). Large-scale operations (i.e. sideline and commercial beekeepers) indeed reported "Queen issues" as a main reason for winter colony losses. Due to the absence of young brood, bees have no option to replace a dead queen (Butler, 1957; Graham et al., 1992), and supplementary mature, mated queens may not be readily available for purchase. Additionally, beekeepers in the North may not even notice a missing queen as colony inspections during cold temperatures are risky; they may disrupt the colony's thermoregulation causing considerable harm (ARS USDA, 1977). In summary, winter brings many unfavorable environmental conditions that can negatively affect honey bee colonies.

The survey's summer loss period is defined as the time from 1 April to 1 October, a time when honey bees have regular access to resources resulting in an abundance of food, and brood rearing is at its peak (Winston, 1991). Therefore, we would expect low colony mortality during that loss period. Yet, our results along with previous surveys indicate that summer is a period of substantial losses, particularly by large-scale beekeepers (Kulhanek et al., 2017; Lee, Steinhauer, Rennich, et al., 2015; Steinhauer et al., 2014). Since the first documentation of national summer colony loss in 2012 (Steinhauer et al., 2014), estimates have fluctuated around 20% (Kulhanek et al., 2017; Lee, Steinhauer, Rennich, et al., 2015; Seitz et al., 2015; Steinhauer et al., 2014). National summer loss estimates for 2017-18 (17. 9%) and 2018-19 (20.7%) fit this trend; however, 2019-20 marked the worst summer loss on record (32.1%). Interestingly, we documented record high national winter and summer colony loss in consecutive years, 2018-19 and 2019-20, respectively, which might indicate a spill-over effect. Beekeepers with high winter colony losses may have compensated for that in early spring by installing new or recently split colonies, thereby increasing the number of colonies at risk in summer (Delaplane, 2010, 2015; Steinhauer et al., 2021). Generally, summer affords beekeepers the flexibility to perform a range of management options such as queen replacement (Graham et al., 1992), and yet self-reported causes of summer loss are linked to management. Interestingly, all beekeeper operation types reported "Queen issues" as the main hazard in summer, followed by "Varroa mites and associated viruses." While several factors have been explored to explain "Queen issues" including local adaptability, genetic bottlenecks, and reproductive health (e.g. Delaney et al., 2011; Meixner et al., 2014; Pettis et al., 2016; Tarpy et al., 2012; Walsh & Rangel, 2016; Withrow et al., 2019), it remains unclear what exactly causes evidently good queens to fail. There is a common understanding that they are the result of various, interacting factors which should be foci for future research and extension efforts to mitigate loss during this period.

The number of colonies managed is closely connected to the goals of beekeepers, and strongly shapes their management philosophies (Thoms et al., 2019; Underwood et al., 2019). This could explain seasonal differences in colony losses experienced by different types of beekeepers. Similar to previous surveys here and abroad (Gray et al., 2019; Kulhanek et al., 2017; USDA NASS, 2020), backyard beekeepers experienced higher losses during winter compared to commercial beekeepers, except in 2019-20. Many commercial beekeepers rely on their colonies for income and need strong colonies at the beginning of the brood rearing season to provide adequate pollination services in spring (Goodrich & Goodhue, 2020). Those beekeepers are more likely to use chemical controls against the important biotic risk factor Varroa at important intervals (Haber et al., 2019). This possibly reduces the risk of winter mortality resulting from parasite pressure, as reflected in Steinhauer et al. (2021). Interestingly, Varroa was selected as the main beekeeper-perceived cause of winter loss across all three survey years, regardless of operation type. This suggests that backyard beekeepers are also aware of the risk of Varroa, but that their reluctance to use (synthetic) acaricides and inappropriate timing may affect the effectiveness of their management practices (Thoms et al., 2019). Conversely, commercial beekeepers lost significantly more colonies during summer compared to all other beekeeper operation types. Although they diligently manage their colonies in fall to ensure strong colonies in the spring (Goodrich & Goodhue, 2020; Underwood et al., 2019), the use of in-hive acaricides that could also result in resistant Varroa mites (Rinkevich, 2020), as well as exposure to agricultural chemicals could explain increased losses during summer (Traynor et al., 2016). Losses during the brood-rearing season are concerning and may be related to what beekeepers perceived as the most likely cause for summer losses—"Queen issues." A number of studies demonstrated that residues persisting from commonly used chemicals for Varroa control can negatively affect the reproductive health and behavior of queens, as well as their potential mates (Rangel & Fisher, 2019; Rangel & Tarpy, 2015). Large-scale operations also commonly pursue beekeeping activities that can impose considerable stress on honey bees like transportation over long distances to provide pollination services to important agricultural crops including almonds (Simone-Finstrom et al., 2016); however, our results support previous work that showed no significant negative association of these activities on winter colony loss rates (Kulhanek et al., 2017; Lee, Steinhauer, Rennich, et al., 2015; Seitz et al., 2015; Spleen et al., 2013; Steinhauer et al., 2014; vanEngelsdorp, Caron, et al. 2012; vanEngelsdorp et al., 2007, 2008, 2010, 2011). It could be that these activities do not impair the colony as a whole, or negative effects are mitigated through subsequent hive management practices of beekeepers. Moving forward, the relationship between beekeeper management activities and colony losses should be investigated to ultimately improve recommendations for Best Management Practices (BMPs).

It is noteworthy to mention that depending on their management philosophies, not all beekeepers readily adopt recommended BMPs (Thoms et al., 2019). Furthermore, beekeepers may face several barriers, including the environment and economics such as an increase in labor and cost associated with certain BMPs, which may be impossible to overcome (DeGrandi-Hoffman et al., 2019). Thus, while beekeepers have access to a variety of Varroa treatments, they are relatively costly, can cause resistance, require regular visits to the apiary and their effectiveness varies depending on common environmental factors (e.g. temperature) (Honey Bee Health Coalition, 2015; Rinkevich, 2020; Rosenkranz et al., 2010). Additionally, there is evidence that despite available learning opportunities, knowledge transfer and practical trainings do not necessarily result in the adoption of BMPs (Murray et al., 2021; Shouten & Lloyd, 2019).

Colony loss rates were highly variable among regions and states. One explanation could be that states employ different land use patterns such as the abundance of open versus developed land which can be used as a predictor for colony losses (Naug, 2009; Potts et al., 2010). Another factor involved in the observed variability could be the difference in climatic conditions. Calovi et al. (2021) found that growing degree days and precipitation during the preceding summer months were a predictor for colony survival. However, future studies, using spatial analysis tools like GIS, are required to identify potential connections between climatic conditions and colony loss rates. These studies are crucial given the projected change in climate and weather patterns that will pose various challenges for pollinators including honey bees (Le Conte & Navajas, 2008; Potts et al., 2010; Settele et al., 2016).

Despite persistent high colony losses reported in the United States (Kulhanek et al., 2017; Lee, Steinhauer, Rennich, et al., 2015; Seitz et al., 2015), the total number of managed honey bee colonies has increased from 2.39 million in 2006 to 2.67 million in 2020 (USDA NASS, 2007, 2020). This apparent contradiction can be explained by the compensation of colony losses by installing captured swarms or by splitting surviving colonies, whereby beekeepers divide one colony into two or more parts, which then can be brought on the beekeeping market as packaged bees and nucleus colonies (Rucker et al., 2019). While this could explain why colony losses do not necessarily translate into a decrease of the national colony stock, future studies should assess the potential for density-dependent effects on regional and national loss rates. Similarly, the number of managed colonies represented in the BIP survey increased since 2017 despite high losses. This can be explained by the higher number of colonies managed by participating beekeepers (especially commercials) each year, as both the proportion of respondents per operation type (backyard, sideline, and commercial) and the number of colonies managed by each remained stable across the reported survey years. Yet, the intensification and growth of pollinator dependent crop acreage far exceed global increases in colony numbers (Aizen & Harder, 2009). For example, as almond orchards expand, the demand for honey bee pollination exceeds the number of available colonies available to perform this task (Goodrich, 2020). Beekeepers frequently cite increased resources required to maintain colony numbers as a major threat to the long-term sustainability of the industry (Somerville, 2003).

The U.S. winter colony loss rates are on par with those in Canada (CAPA., 2018, 2019, 2020), but higher than the overall winter loss rates reported by European countries (Brodschneider et al., 2018; Gray et al., 2019, 2020). This difference may partially be explained by the vast variability in loss rates among European countries (Brodschneider & Gray, 2022). While it is important to consider the global pattern of colony losses, there are confounding factors that complicate a direct comparison of loss rates among different areas in the world. For one, the coverage of monitoring programs is unequal across continents (Brodschneider & Gray, 2022; Hristov et al., 2020; Requier et al., 2017, 2018). Furthermore, different surveys employ different data collection and reporting approaches which harbor their own advantages and disadvantages (Evans & Mathur, 2005); for example, while online questionnaires provide the benefit of a wide geographical reach, they disadvantage beekeepers without internet access (Bethlehem, 2010). Thus, to compare colony loss rates from different surveys and geographical locations, an in-depth meta-analysis is required.

Conclusions

Managed honey bee colonies in the United States are continuously threatened by simultaneous pressures from multiple, possibly interacting risk factors (Potts et al., 2010; Smith et al., 2013; Steinhauer et al., 2018). Our results highlight the variability in colony losses among states, loss periods, and years, but also by beekeeping operation type. Considering the importance of managed honey bee colonies across the globe, our long-term efforts provide crucial baseline information and valuable insight into relationships between honey bees and their beekeepers.

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