Forum

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The Economics of Honey Bee (Hymenoptera: Apidae) Management and Overwintering Strategies for Colonies Used to Pollinate Almonds

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Abstract

Commercial honey bee (*Apis mellifera* L.) colonies significantly contribute to agricultural productivity through crop pollination. Almond production requires the most colonies because there are more than a million acres of orchards that require cross-pollination for nut set. With the rising costs of managing and transporting colonies to almond orchards combined with the high colony losses beekeepers routinely experience, we asked if renting colonies for almond pollination was profitable. We conducted a longitudinal study on 190 colonies from their establishment in April until they were placed in almond orchards 10 mo later. In the fall, equal numbers of colonies were placed either in cold storage (CS) facilities or in outdoor apiaries for the winter. We found that the cost of overwintering colonies in CS was lower than in apiaries, but CS did not reduce overwintering losses. A key finding from our study is that there is little or no profit in renting colonies for almond pollination once summer management and overwintering costs are considered. Our only profitable venture was honey production in the summer. We propose alternative management strategies to lower costs and make almond pollination profitable. We also developed a decision tool for selecting colonies to overwinter in CS and reduce expenditures on those that will not reach sufficient size for almond pollination. Our study exposes the unsustainable financial burden experienced by migratory beekeepers that is not included in estimates of yearly colony losses, and underscores the urgent need for forage plantings to generate revenue from honey and improve overwinter survival.

Key words: Varroa, nutrition, cold storage, colony loss, forage planting

Commercial honey bee colonies are an integral part of agricultural production in the United States. Each year, hives are moved across the country to pollinate crops that generate billions of dollars to the agricultural economy. The economic dependence of agricultural sectors on pollination services is significant (US$14.2–23.8 billion), but the higher-order economic dependence of industrial sectors fueled by crop production also is substantial (US$10.3–21.1 billion) (Chopra et al. 2015). The value of crops produced by honey bee pollination cascade through multiple socioeconomic sectors, generating jobs and revenue to small towns and rural areas and to numerous industrial sectors through equipment and machinery manufacturers, agrochemical companies, food processing, shipping, and transportation, to name just a few. Honey bee pollinated crops also create export markets that help balance trade deficits (https://www.jec.senate.gov/public/_cache/files/266a0bf3-5142-4545-b806-ef9fd78b9c2f/jec-agriculture-report.pdf). From a perspective of human nutrition, honey bee pollinated crops such as berries, almonds, pome, and stone fruits and various seeds are essential to human health and are cornerstones to cancer prevention and heart-healthy diets (Seeram 2008, Ros et al. 2010).

Perhaps no crop is more reliant on honey bees than almonds. Acreages of almonds have been expanding for decades in the Central Valley of California, and by 1973, the pollination needs exceeded what could be serviced by colonies kept in California. Additional colonies from Oregon and Washington were brought into almond orchards, but by 1977 were not sufficient to pollinate all the almond acreage (Rucker et al. 2012). Currently, more than a million hives from throughout the United States are moved into the almond growing regions of California to pollinate the nearly 1 million acres (4,000 km²) of bearing trees (CDFA 2018). The almond crop is worth $2.2 billion and adds an estimated $21.5 billion to the California economy and 104,000 jobs in production, processing, manufacturing, and marketing (Sumner et al. 2016).

Though the multibillion-dollar almond crop depends on honey bee pollination, the supply of colonies is unstable. For more than a decade, colony losses have been in excess of 30% (vanEngelsdorp et al. 2007, 2011; Steinhauer et al. 2014; Kulhanek et al. 2017). Reasons for losses include poor nutrition, diseases, parasitism by *Varroa destructor* Anderson and Trueman (Mesostigmata: Varroidae), queen loss, and pesticide exposure (Döke et al. 2015). Most colonies are lost from combinations of these factors, and many are lost over the winter (Highfield et al. 2009, Guzman-Novoa et al. 2010). Poor overwintering has a particularly strong impact on beekeepers and almond growers, because almonds bloom in February when colonies are at their lowest populations and just beginning to build. Weak colonies cannot rear enough brood to reach sufficient sizes for almond pollination. Colonies that are lost cannot be replaced by splitting stronger ones because in February there are no drones to mate with queens. Therefore, the number of colonies that survive until February are the number available to rent and to pollinate almonds.

In temperate climates, brood rearing declines in the fall with shortening day length, so that by winter there is little or no brood in the colony (Winston 1987). The bees overwinter in a tight thermoregulated cluster surrounding the queen (Winston 1987). Alternatively, colonies can be moved to warmer climates in the southern states or California to overwinter. In these areas, bees forage and rear brood throughout the winter. Many colonies used to pollinate almonds are moved to California in late fall to overwinter.

There are challenges with placing colonies in areas where bees can rear brood and forage during the winter. Often floral resources are insufficient to keep colonies supplied with nectar and pollen. To prevent colony loss from starvation, beekeepers feed protein supplements and sucrose solutions or high fructose corn syrup (HFCS). Though protein supplements can meet some of the nutritional requirements of honey bees, if pollen is unavailable, colonies will show signs of malnutrition. Populations will decline and there will be increased incidence of disease (DeGrandi-Hoffman et al. 2010, DeGrandi-Hoffman et al. 2016a). HFCS also can present health risks to bees (Wheeler and Robinson 2014). Varroa mites can exacerbate effects of nutritional stress. Varroa parasitizes developing bees by crawling into brood cells just before they are sealed and feeding on larvae and pupae. Adult bees parasitized during development will have reduced longevity particularly if they are infected with the viruses Varroa transmit (Genersch et al. 2010, Francis et al. 2013). Varroa population growth due to reproduction occurs slowly especially in colonies that begin with low mite numbers. However, Varroa can migrate into colonies on foragers particularly in the fall and significantly increase mite populations even in colonies that were previously treated with miticides (Sakofski et al. 1990, Greatti et al. 1992, Goodwin et al. 2006, Frey and Rosenkranz 2014, DeGrandi-Hoffman 2016b). Colonies that are infested with mites in the fall have little chance of survival overwinter (Genersch et al. 2010).

An alternative overwintering method is to put colonies into cold storage (CS) facilities in the fall. There are advantages to this management strategy. Colonies put into CS after a fall miticide treatment avoid being reinfested with Varroa that can enter colonies on foragers. Bees clustered inside the hive rather than foraging have greater longevity and require fewer resources. The cost of overwintering bees in CS also might be lower than in areas with warm winters if resources are limited and bees need supplemental feeding.

With the increasing costs of managing and transporting honey bee colonies for pollination, combined with the colony losses beekeepers routinely experience, we asked if renting colonies for almond pollination was a profitable venture, and if the overwintering strategy (CS vs outdoors) affected profit margins. Each year the percentage of colonies that are lost is reported, but the economic implications are not included. To provide a more complete picture of the expenses of migratory beekeeping and the cost of managing bees for almond pollination, we conducted a longitudinal study on 190 commercial honey bee colonies. The study began in April and ended the following year just prior to almond bloom. We calculated all expenditures incurred by a commercial beekeeper including salaries, transportation, and cost of materials. In the fall, we divided the hives into groups that overwintered either in apiaries or in CS facilities. When both groups of colonies were moved from their overwintering sites to almond orchards, we compared the cost of each overwintering strategy. We calculated profit margins for almond pollination based on the size and percentage of surviving colonies overwintered either in apiaries or in CS, cost of the overwintering strategy, and the per colony pollination rental fee. We found that the costs of maintaining colonies and overwintering them exceeded rental fees regardless of how the colonies were overwintered. Our only profitable activity was honey production during the summer. Our study underscores the challenges faced by migratory beekeepers, and their untenable economic position especially if the availability of nectar and pollen sources continue to decline. We conclude with recommendations and possible solutions for maintaining a profitable and sustainable commercial beekeeping industry.

Materials and Methods

An overview of the migratory route of the study, and the management procedures that occurred is shown in Fig. 1. The study began in April, 2016 in Danbury, TX where 95 colonies returning from pollinating almonds in California were split into 190 colonies. A laying European queen purchased from Olivarez Honey Bees Inc. (Orland, CA) was introduced in a self-releasing cage to each of the 190 colonies 48 h after making the split. We purchased commercially produced mated queens because the hives were in Texas at the time when they were established. Texas has a resident feral Africanized honey bee population (Pinto et al. 2004), and if we allowed the colonies to rear their own queen, they would have mated with African drones and the colonies would be Africanized.

Colony and Mite Population Measurements

Frames of bees were recorded when colonies were established, and again in June, September, and October as an estimate of colony size. Frames of open and sealed brood were measured when colonies were established and again in September. Areas on frames with brood and bees were estimated using methods for colony measurement described in Delaplane et al. (2013) and DeGrandi-Hoffman et al. (2014). Mite populations were estimated using an alcohol wash of adult bees or a mite drop count on a sticky board when outside temperatures were too low to open hives and sample bees from frames. For the alcohol wash method, approximately 300 adult worker bees were brushed from frames with brood into jars containing approximately 50 ml of 70% ethanol (Dietemann et al. 2013). The jars were refrigerated until the bees and mites were counted. We counted mites by vigorously shaking the jar for 20 s and then pouring the entire contents into a strainer positioned over a pan. We counted the mites that went through the strainer and were now in the pan. We examined the bees in the strainer for mites, and then counted all the bees, so we could estimate the percentage of bees with mites.

We included data from hives owned by a second beekeeper in an analysis of factors affecting the size of colonies prior to almond

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                        ┌──────────────────────┐
              ┌────────►│   Bees in California  │◄────────┐
              │         └──────────┬───────────┘          │
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              │         │    Move bees to Texas │          │
              │         └──────────┬───────────┘          │
              │                    ▼                       │
              │         ┌──────────────────────┐          │
              │         │   Split 95 colonies to│          │
              │         │  make 190 cost - $7443│          │
              │         └──────────┬───────────┘          │
              │                    ▼                       │
              │         ┌──────────────────────┐          │
              │         │ Move colonies to      │          │
              │         │ North Dakota          │          │
              │         │ cost - $2327          │          │
              │         └──────────┬───────────┘          │
   ┌──────────────┐     ▼     ┌──────────────┐            │
   │Miticide      │──►  ◄──────│Add honey supers│         │
   │treatment     │           │cost - $813     │          │
   │cost- $1753   │           └──────────────┘            │
   └──────────────┘     ▼                                 │
              │ ┌──────────────────────┐                  │
              │ │ Harvest honey -       │                  │
              │ │ cost - $2895          │                  │
              │ │ Value of honey -      │                  │
              │ │ $20,307               │                  │
              │ └──────────┬───────────┘                  │
   ┌──────────────┐        ▼                               │
   │Miticide      │──►                                     │
   │treatment     │                                        │
   │cost- $1142   │                                        │
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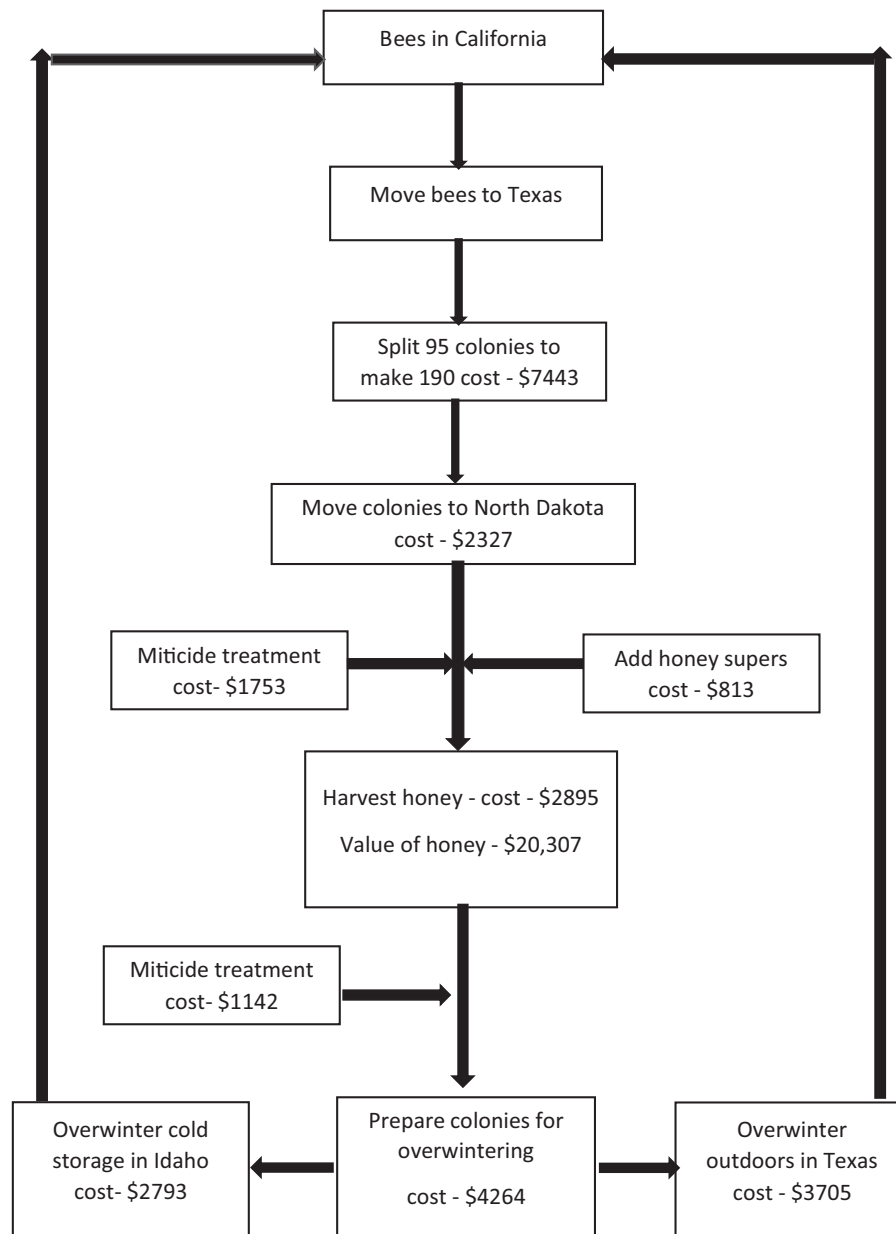
Fig. 1. Overview of a longitudinal study with commercial honey bee colonies. The hives were moved after almond bloom from California to Texas where they were split, and later moved to North Dakota. Colonies were overwintered either in cold storage in Idaho or in an outdoor apiary in Texas. Costs of all management practices are included.

pollination. The colonies were placed into the same CS facility along with our experimental hives. The additional data were needed to expand our range of colony sizes and mite numbers for our analyses. Frames of bees were measured in September and prior to almond bloom by visual inspection of each frame according to procedures described in Delaplane et al. (2013). Mites were counted in those colonies in September using powdered sugar instead of alcohol to dislodge the mites (Dietemann et al. 2013). We collected approximately 300 bees from brood frames and placed them in a jar with a mesh lid. Approximately 7 g of powdered sugar was poured over the bees in the jar, and then the jar was rolled until all bees were covered with sugar. We placed the jar in the shade for 10 min, followed by 10 s of vigorous shaking into a bowl of water. We counted the number of mites floating in the water and divided

it by the approximate number of bees (300) to estimate the percentage of bees with mites.

The effectiveness of our mite treatments was evaluated using sticky boards (Great Lakes IPM, Inc., Vestaburg, MI) placed on the bottom boards of all experimental hives for 48 h before and after the miticide treatment. Since Varroa numbers could be high in the colonies, we used the methods of Ostiguy and Sammataro (2000) to approximate total mite drop.

Colony Feeding

Colonies were fed carbohydrate supplement after the hives were split in April, and protein and carbohydrate supplements in the fall to prepare the bees for overwintering. We used the same supplements as

the commercial beekeeper collaborating with us on this project. The carbohydrate supplement was Pro-Sweet Liquid Feed (Mann Lake Ltd, Hackensack, MN), and the protein supplement was made by the beekeeper and composed of 24.7% pollen, 24.7% brewer's yeast, 0.5% vegetable oil, 0.5% lemon Juice, and 49.4% Pro Sweet Liquid Feed. Pro Sweet Liquid Feed contains 22.0% fructose, 27.0% dextrose, 50% sucrose, 0.5% maltose, and 0.5% higher saccharides and will not ferment like sugar syrup.

Management Actions and Costs—Spring – Fall

The cost of splitting 95 hives to create 190 new colonies including the cost of the queens, labor, transportation from Harvest Honey Headquarters to the apiary, and feeding 3.8 liters (1 gallon) of sugar syrup per colony was $6,651 (Table 1). An additional sugar syrup feeding 2 wk later (3.8 liters per colony) cost $792. In mid-June, the colonies were inspected and 158 were still viable. After inspection, the hives were moved from Danbury, TX to Baldwin, ND. The total cost of labor and transportation to move the colonies from Texas and unload them in North Dakota for the honey flow was $2,327. In July, the colonies were treated with a miticide (HopGuard II - BetaTec Hop Products, Washington, DC). HopGuard II was used because it can be applied during a honey flow. Two strips per 10 frames (four strips per colony) were used as stated on the label instructions. The cost of the labor, transportation, and material for treating 158 hives was $1,752 ($11 per colony).

From July through August, the colonies grew, and collected surplus honey so additional hive bodies with frames were added (i.e., hives were 'supered'). The 158 hives were supered three times at a total cost of $813 (labor and transportation). In August, honey was removed at a total cost of $2,432. The 158 colonies produced 12,160 lbs of honey (77 lbs per hive). The year of the study, extracted

unprocessed Dakota honeys sold for $1.67/lb (USDA-AMS Specialty Crops Program Market News Division, December 23, 2016), so the value of the honey crop was $20,307. Between the time when the colonies were established in April and the honey was removed in August, we invested $15,483 in colony management and honey extraction. The profit from the honey collected from 158 hives was $3,734 or about $23 per hive.

Between August and September, an additional 18 colonies were lost so that we had 140 remaining. We applied a miticide treatment (HopGuard II) at a total cost $1,342. The colonies also were fed 3.8 liters of sugar syrup with Fumagilin to control *Nosema*. The total cost of feeding was $697. An additional 20 colonies were lost between September and October, so that 120 colonies remained from the 190 we established. In preparation for overwintering, the colonies were fed 0.91 kg (2 lbs) of protein diet and 3.8 liters of sugar syrup with Fumagilin (as described above) per colony at a cost of $1,047. The colonies were fed protein diet one more time during October (cost = $507), and then moved to holding yards (cost = $220). The colonies were treated with Apivar according to label instructions (two strips per 6–10 frames of bees, four strips per colony) for Varroa control (cost = $1,397) in preparation for transport to either an apiary in Texas or CS in Idaho.

We spent $20,836 between April when 190 colonies were established, and October when 120 remained for overwintering. Our expenditures were offset by the honey harvested from the hives in August that generated $20,307. Prior to overwintering, expenditures exceeded income by $530.

Overwintering Management and Costs

In October, equal numbers of colonies were prepared for overwintering in either Texas apiaries or CS in Idaho. We added

Table 1. Expenditures for colonies started in April until preparation for overwintering

Date	Action	Labor - hours × ($16/hour)	Transport - miles × 0.88/mile	Materials	Cost of action	Total cost
SPRING						
11–12 April	Remove queens and split colonies	$768	$56		$824	$824
13-April	Install new queens, feed sugar syrup	$384	$28	$5,415	$5,827	$6,651
13-June	Sugar syrup feedings	$384	$28	$380	$792	$7,443
14-June	Inspect and prepare colonies for move to ND	$240	$28		$268	$7,711
17-June	Load and ship colonies on trucks	$223	$28	$1,580*	$1,831	$9,542
SUMMER June 21–26	Unload hives from truck in ND	$149	$79		$228	$9,770
15-July	Miticide treatment and add supers	$384	$79	$1,290	$1,753	$11,523
1-Aug.	Add supers	$192	$79		$271	$11,794
15-Aug.	Add supers	$192	$79		$271	$12,065
29-Aug.	Add supers	$192	$79		$271	$12,336
6-Sep.	Remove honey	$384	$79		$463	$12,799
	Honey extraction fee				$2,432	$15,231
9-Sep.	Miticide treatment	$121	$79	$1,142	$1,342	$16,573
FALL						
1-Oct.	Feed sugar syrup + Fumagillan	$128	$79	$490	$697	$17,270
12-Oct.	Feed sugar, protein + Fumagillan	$128	$79	$840	$1,047	$18,317
17-Oct.	Feed protein	$128	$79	$300	$507	$18,824
21-Oct.	Move colonies to holding yards	$113	$107		$220	$19,044
24-Oct.	Miticide treatment	$121	$28	$1,248	$1,397	$20,441
	Sugar syrup feeding	$128	$28	$240	$396	$20,837
	Total expenditure					$20,837
	Total income (honey – expenditures) ($20,307–20,837)					–$530

*Shipping cost by independent carrier.

24 colonies to increase our sample sizes, and divided these evenly between the two overwintering groups (CS and apiaries, *n* = 72 per group). The additional colonies belonged to our collaborating beekeeper, were positioned in the same apiaries in North Dakota, had the same queen sources, and were managed throughout the year (i.e., supplemental feeding and miticide applications) using the same procedures as our experimental colonies. All the additional colonies had 16 frames of bees.

CS colonies were fed sugar syrup 1 wk prior to shipment (cost—$236) (Table 2). On November 15, colonies were loaded on to trucks and taken to the CS facility in Idaho (cost—$466). The fee for CS was $8 per hive ($8 × 72 colonies = $576 total). Colonies remained in CS until February 1 when they were loaded on to trucks and taken to California for almond pollination (cost—$1,515). The total cost of overwintering 72 colonies in CS was $2,793.

A second set of 72 hives was shipped from North Dakota to Texas to overwinter in apiaries. The cost for shipping the hives was $725. When the hives arrived in the apiaries, they were fed protein supplement and sugar syrup (cost—$356). The feeding was repeated monthly until February (four feedings × $356 = $1,424) when the hives were loaded on the trucks and taken to California for almond pollination. Transportation to California and loading/unloading fees cost an additional $1,784. The total cost for overwintering 72 colonies in apiaries was $4,901 or about $1,300 more than in CS.

Statistical Analysis

Colony size in February was compared between those overwintered in CS and outdoor apiaries using a *t*-test. We tested for a relationship between colony size in February and frames of bees and brood and mite levels in September and October using multifactorial linear regression (MLR). Based on significant parameters from the MLR analysis, a multifactorial logistic regression was conducted using Python's *statsmodels* module to generate the probability of a colony having ≥ 6 frames of bees in February. All comparison tests were conducted using Minitab (Minitab Inc., State College, PA). MLR was conducted using JMP (SAS Institute, Cary, NC).

Results

Colony Size, Mite Numbers, and Survival

The study began in April with 190 hives that averaged 7.0 ± 0.1 frames of bees, 4.0 ± frames of brood and 1.0 ± 0.09 mites per 100 bees. By June, there were 158 colonies remaining, and these averaged 15.1 ± 0.6 frames of bees. Later in June, the colonies were moved to apiaries in North Dakota for honey production. There were 1.3 ± 0.1 mites per 100 bees in alcohol wash samples before application of HopGuard II, and 0.18 ± 0.03 mites per 100 bees 48 h later. In September, there were 140 colonies remaining. The colonies averaged 15.5 ± 0.1 frames of bees, 8.2 ± 0.14 frames of brood, 4.6 ± 0.3 mites per 100 bees, and 74.4 ± 8.4 mites on sticky boards prior to the miticide treatment. Forty-eight hours after treatment, colonies averaged 1.4 ± 0.14 mites per 100 bees and 529 ± 29 mites on sticky boards. Twenty-more colonies were lost between September and October (37% summer colony mortality). Specifically, the colonies with high mite numbers in September (i.e., ≥ 8.0 mites per 100 bees) either were dead by October or severely weakened so that they would not survive overwintering. The surviving colonies averaged 14.4 ± 0.2 frames of bees. Ambient temperatures were too low to open hives and measure brood frames or collect adult bees from the brood area for alcohol wash samples. Only mite drop from sticky boards is reported. Prior to miticide treatment, an average of 10.8 ± 0.7 mites dropped on to sticky boards; 48 h after the treatment, there were 61.7 ± 3.7 mites per sticky board.

Comparing Overwintering Methods

Of the 72 colonies put into CS, 54 (75%) survived overwinter, and 33 (61%) of these were large enough for almond pollination (≥ 6 frames of bees). The hives rented for almond pollination averaged

Table 2. Overwintering costs for placing 72 colonies in either cold storage or outdoors in apiaries

Date	Action	Labor hours* $16/hour	Transportation (0.88/mile)	Materials	Cost of action	Total cost
Overwintering in cold storage						
8 Nov.	Feed I gal. of sugar syrup per colony	$64	$28	$144	**$236**	$236
15–16 Nov.	Colony loading and cold storage fee ($8/colony)	$34	$432*	$576 (72 × $8)	**$1,042**	$1,278
3–5 Feb.	Move colonies to California and unload in orchards				**$1,515***	$2,793
Overwintering in apiaries						
25 Oct.	Load colonies for shipping to Texas	$34	$28			$62
27 Oct.	Ship colonies to Texas				**$725***	$787
29 Oct.	Place colonies in apiaries	$68	$28		**$96**	$883
12 Nov.	Check colonies, feed protein patties and sugar syrup	$96	$26	$234	**$356**	$1,239
28 Nov.	Check colonies, feed protein patties and sugar syrup	$96	$26	$234	**$356**	$1,595
22 Dec.	Check colonies, feed protein patties and sugar syrup	$96	$26	$234	**$356**	$1,951
14 Jan.	Check colonies, feed protein patties and sugar syrup	$96	$26	$234	**$356**	$2,307
1 Feb.	Load truck for shipment to California	$29	$28		**$57**	$2,364
2–5 Feb.	Ship colonies to California and unload in orchards				**$1,727***	$4,091

*Shipping fee from private contractor.

8.3 ± 0.55 frames of bees, 1.7 ± 0.15 frames of brood, and 0.04 ± 0.04 mites per 100 bees. Of the 72 hives that overwintered outdoors in Texas, 86% survived (i.e., 62 colonies) and all were of suitable size for almond pollination. Colonies averaged 9.1 ± 0.4 frames of bees, 2.6 ± 0.1 frames of brood, and 0.15 ± 0.05 mites per 100 bees. Colonies that overwintered in the Texas apiaries did not differ in frames of bees (t_{61} = 1.13, P = 0.26) or mite populations (t_{82} = 1.79, P = 0.08) compared with those that overwintered in CS, but those overwintered in apiaries had significantly more frames of brood (t_{63} = 4.78, P < 0.0001; Table 3).

Total expenditures per colony from September after the honey harvest until colonies were put in almond orchards in February was $205 for colonies overwintered in CS and $223 for those overwintered in Texas apiaries. The rental fee was $165 per colony, so there was a loss of $40 per hive for those overwintered in CS and $58 per colony for those overwintered in apiaries. The value of the colonies that were rented for almond pollination was $5,445 (33 hives × $165/colony) for those overwintered in CS and $10,230 (62 colonies × $165) for those overwintered in apiaries. Based on the cost of managing colonies from September to February, rental fees and colony losses, we absorbed a loss of $9,315 for the 72 colonies overwintered in CS and rented for almond pollination, and $5,826 for those overwintered in apiaries (profit = number of colonies rented × $165 − 72 × overwinter costs).

Costs of Colony Loss

The cost of losing colonies increased as the season progressed due to the additive investments of labor, transportation, and material (Fig. 2). In April, we invested $7,410 to create the 190 colonies, or $39 per colony. The loss of 32 colonies in June was $1,248 ($39 × 32). Between August and September, another 18 colonies were lost. By this point, we invested $81 per colony, so the cost of losing 18 colonies in late summer was $1,458 ($81 × 18). An additional 20 colonies were lost between September and October. We invested $136 per colony by October, so the loss of the 20 colonies was $2,720 ($136 × 20). Not all of the 72 colonies that overwintered in either CS or in the Texas apiary were sufficient in size to rent for almond pollination. Per colony losses for those that died or were too small to rent were $205 for those in CS and $223 for those overwintered in the Texas apiary. If the loss of rental fee is added, we estimated the loss of a colony overwintered in CS as $370 ($205 + $165 rental fee) and in apiaries as $388 ($223 + $165 rental fee).

Identifying Colonies to Overwinter

We invested $702 between September and October to prepare 72 colonies per treatment for overwintering (i.e., supplemental feedings, miticide, and Fumagillin applications) either in CS or in apiaries. Considering only those colonies overwintered in CS, additional costs

Table 3. Comparison of colony sizes and mite numbers in Feb. when colonies were overwintered in either apiaries or cold storage

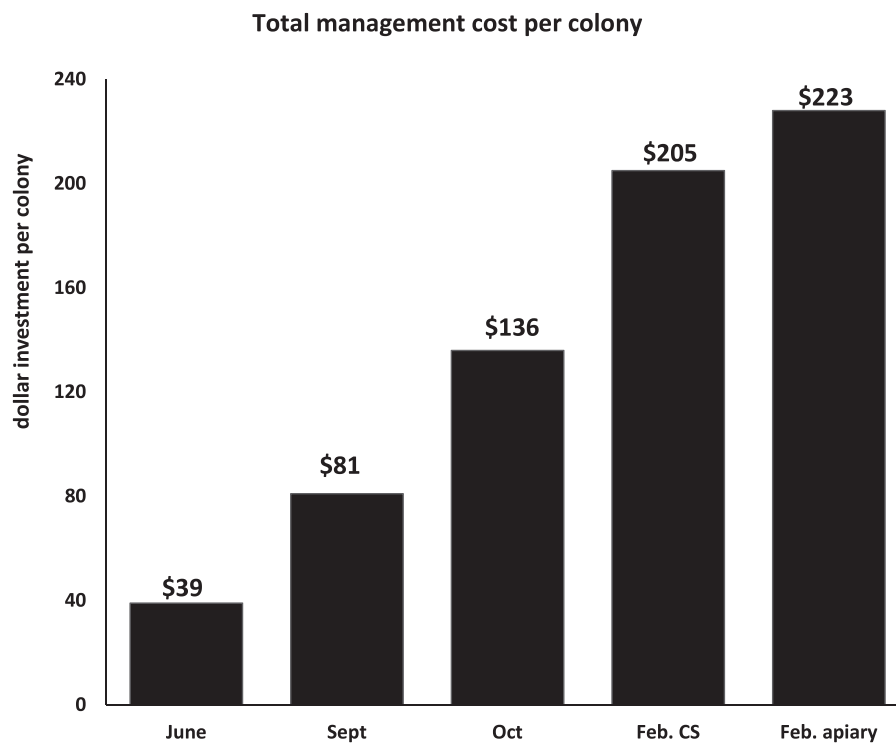| Measurement	Overwintering site		t	df	P
	Outdoor apiary	Cold storage			
Frames of bees	9.1 ± 0.4	8.3 ± 0.5	1.13	61	0.26
Frames of brood	2.6 ± 0.1	1.7 ± 0.1	4.78	63	<0.0001
Mites per 100 bees	0.15 ± 0.05	0.04 ± 0.04	1.79	82	0.08

Fig. 2. The dollar investment per honey bee colony from establishment (April) until rented in February for almond pollination. Colonies were overwintered either in a cold storage facility (February CS) or outdoors in an apiary.

Table 4. Relationships between frames of bees and mites per 100 adult bees in September and frames of bees the following February after colonies were overwintered in cold storage in Idaho or in outdoor apiaries in Texas

Winter management	Parameter	F	df	P
Cold storage	Regression	194.4	2	<0.0001
r^2 = 74.1	Sept. frames of brood	334.8	1	<0.0001
	Sept. mites/100 bees	44.71	1	<0.0001
	Error		133	
Texas apiary	Regression	114.11	2	0.53
r^2 = 2.3				
	Sept. frames of brood	90.94	1	0.39
	Sept. mites/100 bees	1.11	1	0.35
	Error		57	

were incurred for travel to the CS facility and then to California, and for CS occupancy (TOTAL = $2,793 or $39 per hive). We put all the colonies into CS, but only 45% were large enough in February for almond pollination rental (≥ 6 frames of adult bees). Ideally, we should have put only those colonies with a high probability of achieving populations suitable for almond pollination in CS. With this in mind, an analysis was conducted to create a decision-making tool to select hives to overwinter in CS. The analysis began with a multifactorial regression analysis using data on colony measurements and mite population sizes. The analysis revealed that colony size and mite numbers from alcohol washes in September were significantly correlated with colony size in February for hives overwintered in CS (Table 4). This analysis included data from hives owned by a second beekeeper (BK-2) whose colonies were overwintered with ours in CS treatment group. The additional colonies were needed to increase the sample size and provide greater ranges in colony sizes and mite numbers than in our original data set. Colonies belonging to BK-2 averaged 11.6 frames of bees and 0.13 mites per 100 bees in September (n = 92 colonies), 93% survived overwinter, and 93% were suitable for almond pollination rental (≥ 6 frames of adult bees).

Based on the results of the regression analysis, we next conducted a multifactorial logistic regression (MLR) on September and February colony sizes and September mite numbers from both beekeepers. This analysis generated probabilities of colonies being of suitable size for almond pollination rental. In the analysis, we used ≥ 6 frames of bees in February as a successfully overwintered colony. The logit function was used without a bias term and successfully converged to an optimal parametrization. Both September frames of bees and mites per 100 bees were significant based on Wald χ^2 values (frames of bees Wald χ^2 = 10.2, P = 0.0014; mites per 100 bees: Wald χ^2 = 5.84, P = 0.016). Unit odds ratios for frames of bees were 1.06 and 0.85 for mites per 100 bees, respectively. An array of coordinate pairs corresponding to the range of frames of bees and mites per 100 bees in the data set was run through the trained logistic regression model to produce an array of prediction values. The array was used to create a decision matrix within the Python module *seaborn* (Table 5). The matrix indicates that probabilities of meeting the minimum of 6 frames of bees are greatly influenced by September mite numbers. Even large colonies with more than 12 frames of bees (about 30,000 bees) have a less than 0.5 probability of being suitable for almond pollination if they have 5 or more mites per 100 bees in September. The analysis also indicates that mite numbers need to be controlled in August so that colonies have low mite numbers in September.
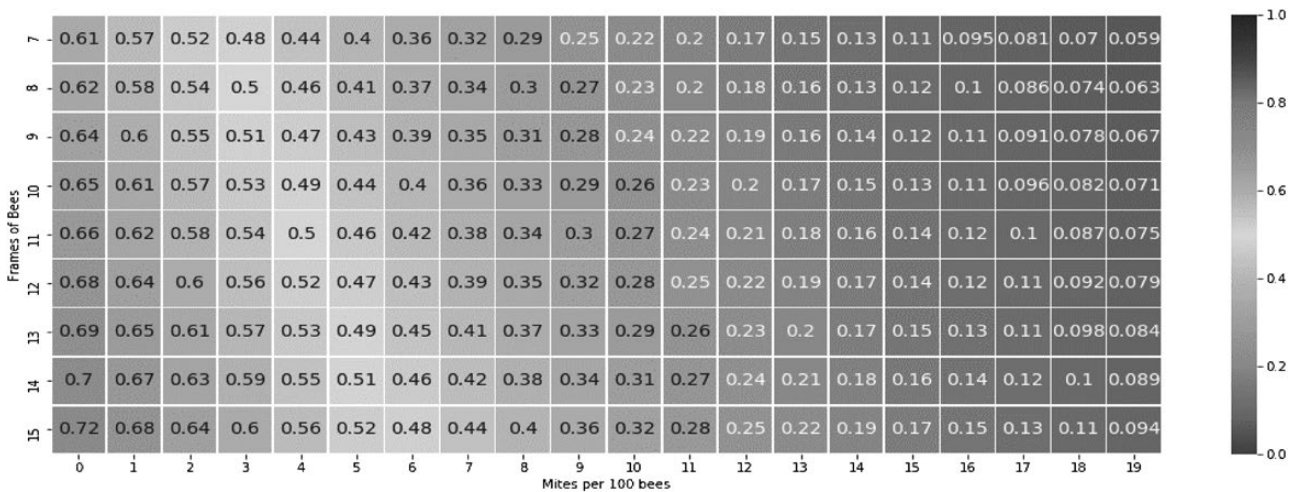
A similar analysis as described above was conducted to create a decision-making tool for colonies overwintered in apiaries. A multifactorial regression analysis indicated colony size or mite numbers in September were not significantly related to colony size in February (Table 4). A second analysis was conducted that included frames of bees and mite populations in October. Mite populations were estimated in October using mite drop on to sticky boards. While the

sampling technique differs from alcohol washes, the two techniques are similar in that they are estimates of phoretic mites. Analyses that included September and October data from mite drops and colony size also did not indicate a significant relationship between colony size and mite numbers in the fall and colony size the following February.

Discussion

For this study, we managed 190 colonies and recorded all costs from the time of establishment in April until they were placed in almond orchards for pollination the following February. We expended considerable resources for feeding and parasite/pathogen control, but still lost more than 30% of our colonies by the fall. Some colonies failed within 2 mo after they were established perhaps due to queen failure since colonies had adequate resources, low mite numbers, and were not exposed to pesticides. The acceptance and retention of introduced queens depends on their health and mating success (i.e., number of spermatozoa in the spermatheca) (Delaney et al. 2011, Pettis et al. 2016). About 14%–19.0% of commercially produced queens are not fully mated (Delaney et al. 2011). We lost 17% of the colonies we requeened, well within the range of poorly mated commercially reared queens. Varroa probably also caused some of our colony losses especially in the fall. Though we treated for Varroa in the summer, some colonies had high numbers of mites in September. These colonies were dead by October or if overwintered in CS had populations that were too small for almond pollination rental. Absorbed costs from losing hives increased throughout the year as more labor and resources were expended to keep the bees alive. Losing a colony over the winter cost five to six times more than in June particularly if lost pollination fees are included. A surprising finding from our study was that almond pollination was not profitable because the cost of managing colonies from September (after honey harvest) to February exceeded colony rental fees. Overwintering in CS cost less than in apiaries, but did not assure lower losses or more colonies of suitable size for almond pollination. Selecting colonies to overwinter in CS should be based on the adult bee and Varroa populations in September since these variables significantly affect the size of colonies in February. The relationship between September and February colony and mite populations did not occur in those overwintered in apiaries perhaps because additional feedings and other management practices stimulated colony growth during the winter. Almond pollination fees however, did not cover the cost of the additional management, so per colony deficits for those overwintered in apiaries were higher than CS. Our only profitable venture was honey production, underscoring the importance of available forage to the economic viability of the beekeeping industry.

The costliest management action we performed after colony establishment was treating for Varroa. We used HopGuard II during

Table 5. Probabilities of colonies consisting of six or more frames of bees in February based on frames of bees and mites per 100 bees in September

Frames of Bees	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
7	0.61	0.57	0.52	0.48	0.44	0.4	0.36	0.32	0.29	0.25	0.22	0.2	0.17	0.15	0.13	0.11	0.095	0.081	0.07	0.059
8	0.62	0.58	0.54	0.5	0.46	0.41	0.37	0.34	0.3	0.27	0.23	0.2	0.18	0.16	0.13	0.12	0.1	0.086	0.074	0.063
9	0.64	0.6	0.55	0.51	0.47	0.43	0.39	0.35	0.31	0.28	0.24	0.22	0.19	0.16	0.14	0.12	0.11	0.091	0.078	0.067
10	0.65	0.61	0.57	0.53	0.49	0.44	0.4	0.36	0.33	0.29	0.26	0.23	0.2	0.17	0.15	0.13	0.11	0.096	0.082	0.071
11	0.66	0.62	0.58	0.54	0.5	0.46	0.42	0.38	0.34	0.3	0.27	0.24	0.21	0.18	0.16	0.14	0.12	0.1	0.087	0.075
12	0.68	0.64	0.6	0.56	0.52	0.47	0.43	0.39	0.35	0.32	0.28	0.25	0.22	0.19	0.17	0.14	0.12	0.11	0.092	0.079
13	0.69	0.65	0.61	0.57	0.53	0.49	0.45	0.41	0.37	0.33	0.29	0.26	0.23	0.2	0.17	0.15	0.13	0.11	0.098	0.084
14	0.7	0.67	0.63	0.59	0.55	0.51	0.46	0.42	0.38	0.34	0.31	0.27	0.24	0.21	0.18	0.16	0.14	0.12	0.1	0.089
15	0.72	0.68	0.64	0.6	0.56	0.52	0.48	0.44	0.4	0.36	0.32	0.28	0.25	0.22	0.19	0.17	0.15	0.13	0.11	0.094

Mites per 100 bees

Predictions are based on a multifactorial logistic equation- Wald χ^2 values: frames of bees, χ^2 = 10.2, P = 0.0014; mites per 100 bees: χ^2 = 5.84, P = 0.016. Unit odds ratios for frames of bees were 1.06 and 0.85 for mites per 100 bees.

the honey flow at a cost of about $8 per colony in material, and Apivar in the fall at about $10 per colony. We could have reduced our costs by using other mite treatments such as formic acid or thymol (e.g., $4–5 in material per application). If labor to apply formic acid or thymol was similar to our treatments, we could have saved $3–5 per colony or a total of about $1,100 for our July and September treatments. The cool weather in October would have prevented us from using formic acid since the manufacturer advises using the product when temperatures are between 10 and 30°C. Though we applied miticides at regular intervals, we saw rapid growth of mite populations between spring and fall. Some of the population growth may have been because mites that were under sealed cells were not exposed to our HopGuard II treatment. A longer-lasting miticide treatment may have provided better control. However, most of the mite population increase occurred in the late summer and fall and may have been from the migration of mites into hives on foragers (Sakofski et al. 1990, Greatti et al. 1992, Goodwin et al. 2006, Frey and Rosenkranz 2014, DeGrandi-Hoffman et al. 2016b). Mites can enter hives when foragers rob weak colonies that are heavily infested with Varroa. Foragers with mites also can drift into hives when returning from a foraging flight. Our study site (a commercial apiary) had hundreds of colonies that could have been sources of mites. The weakening and loss of colonies from Varroa in the fall and overwinter are well documented, but because management costs were recorded in our study, we could quantify the financial burden caused by this pest. Colony losses in the fall and overwinter are the costliest to beekeepers because of the dollars invested throughout the year and the loss of rental fees in February. Since losses from Varroa most often occur in the fall and winter, the mite is financially devastating to beekeepers and a great threat to the solvency of their operations.

One way to reduce financial losses from Varroa is to select colonies to overwinter in CS based on their size and Varroa populations in September since these are correlated to colony size in February. We constructed a decision matrix containing probabilities of colonies reaching sufficient sizes for almond pollination given their size and mite numbers in September. Beekeepers can use the decision matrix to select colonies to overwinter in September, and reduce financial losses associated with preparing, transporting, and overwintering hives that are unlikely to reach sizes needed for almond pollination.

A limitation to the decision matrix is that it was generated from an analysis using the ranges of colony sizes and mite numbers in our data set. The predictions could be improved by adding data with broader ranges of colony and mite populations. Additional data also are needed for model validation in the form of a receiver operating characteristic curve and the area under the curve value to evaluate the accuracy of correct versus incorrect choices of colonies to overwinter. We will continue to refine the probability predictions with additional data sets, to improve the decision tool we created for beekeepers.

Though colony size and mite numbers in September were related to February colony size when hives were overwintered in CS, this was not the case for those overwintered in apiaries. We attribute this to a basic difference between the two overwintering methods. In CS, the colony size in February is determined by the population size and longevity of workers in the colony when it entered CS. When colonies are overwintered in apiaries, small colonies can be fed to stimulate brood rearing and frames of bees and brood can be added to improve population size and demographics. The added variability due to management practices and colony responses may have caused relationships between September colony conditions and February colony sizes to be difficult to evaluate.

The only profits we realized were from honey production when our colonies were in North Dakota during the summer. Our summer apiaries were in a region that is part of the Northern Great Plains. About 30–40% of the registered colonies in the United States spend the summer in this region because the vast expanses of rangeland and pastures, and large acreages of blooming alfalfa and oilseed crops provide abundant forage for the bees (Gallant et al. 2014, Otto et al. 2016). The Great Plains serves as both a respite for colonies stressed by crop pollination practices, and a source of revenue for beekeepers through honey production. In our study, the profits from honey sales provided the funds for late summer and fall colony management in preparation for overwintering. Based on our honey yields though, the costs for overwintering preparations exceeded the honey profits so we had a net loss. The loss could have been avoided by higher per colony honey yields. However, areas with abundant forage that could generate large honey crops are dwindling in the Great Plains (Otto et al. 2016). Acreages of crops such as corn and soybean are increasing, and these not only have limited forage value to honey

bees, but also may be contaminated with pesticides that compromise the health of colonies (Henry et al. 2012, Rundlöf et al. 2015). The effects of diminishing access to forage reverberate through both the beekeeping and almond industries, as colonies surrounded by agricultural crops are smaller in the fall and for almond pollination than those in grasslands with natural forage (Smart et al. 2018).

Our economic analysis is based on one management scheme for colonies used in almond pollination. Alternative schemes can be devised where per colony expenditures are based on colony rental fees and a desired per colony profit margin of $10–20. Since overwintering in CS costs less, and has the potential for lower overwintering losses (Desai and Currie 2016), we chose this as our overwintering strategy. If the hives were put into CS in early October rather than November and the final miticide application was not made, the savings per hive would be $9.60. If sufficient natural forage was available so that fewer fall feedings were needed, up to $21.00 per hive could be saved. Summing the savings from putting hives into CS in October, and adding $3 per colony to the CS cost for the extra month, the total savings would be $28 per hive. This would put the cost of managing hives from September to February at $167. If the only colonies put into CS were those that would be large enough in February to obtain close to $200 per hive, the profit margins for almond pollination could reach $20–30 per hive. The costs we state here are subject to inflation however, and should be calculated yearly. To avoid renting colonies at a loss, beekeepers should estimate their costs for managing and transporting colonies to almond orchards each year and set rental prices accordingly.

The economics of beekeeping and pollination services have been examined by others, and there are similarities between our findings and those of previous analyses with respect to factors affecting the profitability and sustainability of beekeeping. A bioeconomic model that integrated economic and biological factors to project colony dynamics and honey production predicted that the economic problems of beekeeping center on the availability of suitable forage (Champetier et al. 2015). Our study also points to the importance of forage for both growing colonies and providing income from a honey crop. In fact, an argument for hive rental in almond orchards and the slim to nonexistent profit margins that are realized could be that almond bloom provides substantial pollen and nectar to build overwintered colonies. After almond bloom, colonies can be split to make up winter losses, and increase the number of hives available for honey production in the summer. From this perspective, there is a reciprocal relationship between almond pollination and honey production that relies on available forage to sustain both the beekeeping and almond industries.

A model describing the economic linkages between pollination services and almond production included the relationship between colony losses and increases in colony rental fees (Lee et al. 2019). Though rental fees have increased steadily, the model revealed that they are not close to covering the costs from colony losses (Rucker et al. 2012, Lee et al. 2018). Our study supports these findings, and indicates that even with our proposed changes in management practices to reduce both costs and overwintering losses; profit margins for almond pollination remain narrow. Under an assumption of stable transportation and labor costs, additional miticide treatments and supplemental feeding when forage is unavailable would undermine our strategies, and require minimum rental fees of $190 or more for almond pollination to be profitable to commercial beekeepers.

Our study began as an economic analysis comparing outcomes of two overwintering strategies. What came to the fore is that reducing colony losses and stabilizing the economics of beekeeping will be difficult, and require cooperation among beekeepers, land managers, growers and federal agencies. A multifaceted approach is required because the challenges beekeepers face arise from a convergence of factors staged in ecosystems that have been altered more rapidly and extensively in the second half of the 20th century than in any comparable period in human history (Alcamo et al. 2003). Pollination ecosystem services in general and honey bees and beekeepers in particular have been critically exposed to ecosystem alteration. Acreage of pollen and nectar resources are shrinking, and warmer temperatures have altered bloom patterns (Barnes 2018), and reduced the nutritional values of pollens (Ziska et al. 2016). In combination with severe stress from pathogens and parasites, and fewer locations protected from pesticide exposure, beekeepers that pollinate almonds and perhaps other crops are experiencing a financial burden not explicitly captured in reports of yearly colony losses. This burden threatens the sustainability of commercial beekeeping and has the potential to impact food production and consumers across institutional scales (Chopra et al. 2015).

What can be done to improve the economics of migratory beekeeping? From our analysis, CS costs less per colony than overwintering in apiaries and could potentially expand profit margins for colonies used in almond pollination. However, best management practices for CS need to be developed that improve overwinter survival. Those methods should include decision-support tools to improve selection of colonies to overwinter. The optimal timing for placing colonies in CS and the amount of resources required for overwintering also need to be determined. Establishing and enhancing pollinator habitat in the summer and fall also are part of the solution because colony growth and honey yields are linked to the economic viability of commercial beekeeping. Furthermore, overwintering losses could be reduced with greater forage availability as fat body mass and vitellogenin levels critical for successful overwintering are enhanced when bees have access to fall pollens (Alaux et al. 2017). The wide-angle view of an economic perspective should generate a sense of urgency to address the challenges faced by the beekeeping industry, so this vital sector of the agricultural economy can remain profitable and sustainable.

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References Cited

Alaux, C., F. Allier, A. Decourtye, J. F. Odoux, T. Tamic, M. Chabirand, E. Delestra, F. Decugis, Y. Le Conte, and M. Henry. 2017. A 'Landscape physiology' approach for assessing bee health highlights the benefits of floral landscape enrichment and semi-natural habitats. Sci. Rep. 7: 40568.

Alcamo, J., N. J. Ash, C. D. Butler, J. B. Callicott, D. Capistrano, S. R. Carpenter, J. C. Castilla, R. Chambers, K. Chopra, *et al.* 2003. Millennium Ecosystem Assessment: Ecosystems and Human Well-Being. Island Press: Washington, DC, 2005; Vol. 5.

Barnes, C. S. 2018. Impact of climate change on pollen and respiratory disease. Current Allergy and Asthma Report, 19: 59. https://www.nccs.gov.sg/climate-change-and-singapore/national-circumstances/impact-climate-change-singapore.

California Department of Food and Agriculture (CDFA). **2018**. 2017 California Almond Acreage Report. http://www.almonds.com/sites/default/files/content/attachments/2017AlmondAcreageReport_0.pdf.

Champetier, A., D. A. Sumner, and J. E. Wilen. **2015**. The bioeconomics of honey bees and pollination. Environ. and Res. Econ. 60: 143–164.

Chopra, S. S., B. R. Bakshi, and V. Khanna. **2015**. Economic dependence of U.S. industrial sectors on animal-mediated pollination service. Environ. Sci. Technol. 49: 14441–14451.

DeGrandi-Hoffman, G., Y. Chen, E. Huang, and M. H. Huang. **2010**. The effect of diet on protein concentration, hypopharyngeal gland development and virus load in worker honey bees (*Apis mellifera* L.). J. Insect Physiol. 56: 1184–1191.

DeGrandi-Hoffman, G., F. Ahumada, R. Curry, G. Probasco, and L. Schantz. **2014**. Population growth of Varroa destructor (Acari: Varroidae) in commercial honey bee colonies treated with beta plant acids. Exp. Appl. Acarol. 64: 171–186.

DeGrandi-Hoffman, G. Y. Chen, R. Rivera, M. Carroll, M. Chambers, G. Hidalgo, W. Watkins deJong **2016a**. Honey bee colonies provided with natural forage have lower pathogen loads and higher overwinter survival than those fed protein supplements. Apidologie. 47: 186–196.

DeGrandi-Hoffman, G., F. Ahumada, V. Zazueta, M. Chambers, G. Hidalgo, and E. W. deJong. **2016b**. Population growth of Varroa destructor (Acari: Varroidae) in honey bee colonies is affected by the number of foragers with mites. Exp. Appl. Acarol 69: 21–34.

Delaney, D., J. J. Keller, J. R. Caren, and D. R. Tarpy. **2011**. The physical, insemination, and reproductive quality of honey bee queens (*Apis mellifera* L.). Apidologie. 42:1–13.

Delaplane, K. S., J. van der Steen, and E. Guzman-Novoa. **2013**. Standard methods for estimating strength parameters of *Apis mellifera* colonies. *In* V. Dietemann, J. D. Ellis, P. Neumann (eds.), The Coloss Beebook, Volume I. Standard methods for *Apis mellifera* research. J. Apic. Res. 52: 1–12. doi: 10.3896/IBRA.1.52.1.03

Desai, S. D., and R. W. Currie. **2016**. Effects of wintering environment and parasite-pathogen interactions on honey bee colony loss in north temperate regions. PLoS One 11: e0159615.

Dietemann, V., F. Nazzi, S. J. Martin, D. L. Anderson, B. Locke, K. S. Delaplane, Q. Wauquiez, C. Tannahill, E. Frey, *et al*. **2013**. Standard methods for varroa research. J. Apic. Res. 52: 1–54.

Döke, M. A., M. Frazier, and C. M. Grozinger. **2015**. Overwintering honey bees: biology and management. Curr. Opin. Insect Sci. 10: 185–193.

Francis, R. M., S. L. Nielsen, and P. Kryger. **2013**. Varroa-virus interaction in collapsing honey bee colonies. PLoS One 8: e57540.

Frey, E., and P. Rosenkranz. **2014**. Autumn invasion rates of *Varroa destructor* (Mesostigmata: Varroidae) into honey bee (Hymenoptera: Apidae) colonies and the resulting increase in mite populations. J. Econ. Entomol. 107: 508–515.

Gallant, A. L., N. H., Euliss, and Z. Browning. **2014**. Mapping large-area landscape suitability for honey bees to assess the influence of land-use change on sustainability of national pollination services. PLoS One. 9(6): e99268.

Genersch, E., W. Von Der Ohe, H. Kaatz, A. Schroeder, C. Otten, R. Buchler, S. Berg, W. Ritter, W. Muehlen, S. Gisder, *et al*. **2010**. The German bee monitoring project: a long term study to understand periodically high winter losses of honey bee colonies. Apidologie. 41: 332–352.

Goodwin, R. M., M. A. Taylor, H. M. Mcbrydie, and H. M. Cox. **2006**. Drift of *Varroa destructor* -infested worker honey bees to neighbouring colonies. J. Apic. Res. 45: 155–156.

Greatti, M., N. Milani, and F. Nazzi. **1992**. Reinfestation of an acaricide-treated apiary by *Varroa jacobsoni* Oud. Exper. and Appl. Acarol. 16: 279–286.

Guzman-Novoa, E., L. Eccles, Y. Calvete, J. McGowan, P. G. Kelly, and A. Correa-Benitez. **2010**. *Varroa destructor* is the main culprit for the death and reduced populations of overwintered honey bee (*Apis mellifera*) colonies in Ontario, Canada. Apidologie. 41: 443–450.

Henry, M, M. Béguin, F. Requier, O. Rollin, J. -F. Odoux, P. Aupinel, J. Aptel, S. Tchamitchian, and A. Decourtye. **2012**. A common pesticide decreases foraging success and survival in honey bees. Science. 336: 348–350

Highfield, A. C., A. El Nagar, L. C. M. Mackinder, L. M. L. J. Noel, M. J. Hall, S. J. Martin, and D. C. Schroeder. **2009**. Deformed Wing Virus implicated in overwintering honeybee colony losses. Appl. Environ. Microbiol. 75: 7212–7220.

Kulhanek, K., N. Steinhauer, K. Rennich, D. M. Caron, R. R. Sagili, J. S. Pettis, J. D. Ellis, M. E. Wilson, J. T. Wilkes, *et al*. **2017**. A national survey of managed honey bee 2015–2016 annual colony losses in the USA. J. Apicul. Res. 56: 328–340.

Lee, H., Hyunok, D. A. Sumner, and A. Champtier. **2019**. Pollination markets and the coupled futures of almonds and honey bees: simulating impacts of shifts in demands and costs. Amer. J. of Agric Econ. 101: 230–249.

Ostiguy, N., and D. Sammataro. **2000**. A simplified technique for counting *Varroa jacobsoni* Oud. on sticky boards. Apidologie. 31: 707–716.

Otto, C. R. V., C. L. Roth, B. L. Carlson, and M. D. Smart. **2016**. Land-use change reduces habitat suitability for supporting managed honey bee colonies in the Northern Great Plains. *Proc. Nat. Acad. Sci. USA*. 113: 10430–10435.

Pettis, J. S., N. Rice, K. Joselow, D. vanEngelsdorp, and V. Chaimanee. **2016**. Correction: colony failure linked to low sperm viability in honey bee (*Apis mellifera*) queens and an exploration of potential causative factors. PLoS One 11: e0155833.

Pinto, M. A., W. L. Rubink, R. N. Coulson, J. C. Patton, and J. S. Johnston. **2004**. Temporal pattern of Africanization in a feral honeybee population from Texas inferred from mitochondrial DNA. Evolution. 58: 1047–1055.

Ros, E., L. C. Tapsell, and J. Sabaté. **2010**. Nuts and berries for heart health. Curr. Atheroscler. Rep. 12: 397–406.

Rucker, R. R., W. N. Thurman, and M. Burgett. **2012**. Honey bee pollination markets and the internalization of reciprocal benefits. Amer. J. of Agric. Econ. 94: 956–977.

Rundlöf M, G. K. Andersson, R. Bommarco, I. Fries, V. Hederström, L. Herbertsson, O. Jonsson, B. K. Klatt, T. R. Pedersen, *et al*. **2015**. Seed coating with a neonicotinoid insecticide negatively affects wild bees. Nature 521(7550):77–80.

Sakofski, F., N. Koeniger, and S. Fuchs. **1990**. Seasonality of honey bee colony invasion by *Varroa jacobsoni* Oud. Apidologie. 21: 547–550.

Seeram, N. P. **2008**. Berry fruits for cancer prevention: current status and future prospects. J. Agric. Food Chem. 56: 630–635.

Smart, M. D., C. R. V. Otto, B. L. Carlson, and C. L. Roth. **2018**. The influence of spatiotemporally decoupled land use on honey bee colony health and pollination service delivery. Environ. Res. Lett. 13: 084016.

Steinhauer, N. A., K. Rennich, M. E. Wilson, D. M. Caron, E. J. Lengerich, J. S. Pettis, R. Rose, J. A. Skinner, D. R. Tarpy, *et al*. **2014**. A national survey of managed honey bee 2012–2013 annual colony losses in the USA: results from the Bee Informed Partnership. J. Apicul. Res. 53: 1–18.

Sumner, D. A., W. A. Matthews, J. Medellin-Azuara, and A. Bradley. **2016**. The economic impacts of the California Almond Industry. University of California Agricultural Issues Center. http://aic.ucdavis.edu/almonds/Economic%20Impacts%20of%20California%20Almond%20Industry_Full%20Report_FinalPDF_v2.pdf

vanEngelsdorp, D., J. Hayes, R. M. Underwood, D. Caron, and J. Pettis. **2011**. A survey of managed honey bee colony losses in the USA, fall 2009 to winter 2010. J. Apicul. Res. 50: 1–10.

vanEnglesdorp, D., R. Underwood, D. Caron, and J. Hayes. **2007**. An estimate of managed colony losses in the winter of 2006–2007: a report commissioned by the Apiary Inspectors of America. Amer. Bee J. 147: 599–603.

Wheeler, M. M., and G. E. Robinson. **2014**. Diet-dependent gene expression in honey bees: honey vs. sucrose or high fructose corn syrup. Sci. Rep. 4: 5726.

Winston, M. L. **1987**. The biology of the honey bee. Harvard University Press, Cambridge, MA.

Ziska, L. H., J. S. Pettis, J. Edwards, J. E. Hancock, M. B. Tomecek, A. Clark, J. S. Dukes, I. Loladze, and H. W. Polley. **2016**. Rising atmospheric CO_2 is reducing the protein concentration of a floral pollen source essential for north American bees. Proc. R. Soc. B. 283: 20160414.