Journal of Invertebrate Pathology 103 (2010) S80–S95

Contents lists available at ScienceDirect

Journal of Invertebrate Pathology

journal homepage: www.elsevier.com/locate/jip

A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them

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ARTICLE INFO

Article history:
Received 8 June 2009
Accepted 30 June 2009
Available online 11 November 2009

Keywords:
Honey bee
Colony
Population dynamics
Abiotic
Biotic

ABSTRACT

Honey bees are a highly valued resource around the world. They are prized for their honey and wax production and depended upon for pollination of many important crops. While globally honey bee populations have been increasing, the rate of increase is not keeping pace with demand. Further, honey bee populations have not been increasing in all parts of the world, and have declined in many nations in Europe and in North America. Managed honey bee populations are influenced by many factors including diseases, parasites, pesticides, the environment, and socio-economic factors. These factors can act alone or in combination with each other. This review highlights the present day value of honey bees, followed by a detailed description of some of the historical and present day factors that influence honey bee populations, with particular emphasis on colony populations in Europe and the United States.

1. Introduction – the value of honey bees

The European honey bee, *Apis mellifera* L., is the most commonly managed bee in the world. A highly adaptable species, it has a native range that stretched from the southern parts of Scandinavia to Central Asia and throughout Africa (Seeley, 1985; Ruttner, 1988; Sheppard and Meixner, 2003). Since the 1600s, however, *A. mellifera's* range has expanded to nearly all habitable corners of the globe. Most of the European honey bee's range expansion has been the result of deliberate human transport (Crane, 1999). "Like the dog, the honeybee (*sic*) had accompanied man on most of his major migrations, and some of the early settlers in each part of the New World took hives of bees with them" (Crane, 1975). Unlike dogs however, honey bees were imported by settlers for their ability to make honey and bees wax. Honey was the only sweetener available to early African, Middle Eastern and European civilizations, and demand for the product no doubt lead to the domestication of bees by the Ancient Egyptians sometime before 2600 BCE. The practice of keeping bees was passed to the ancient Greeks by 650 BCE, who in turn passed the art to the Romans (by 150 BCE) who spread the art throughout what would become medieval Europe. It was the descendants of medieval European beekeepers who eventually spread both the practice of beekeeping and the bees themselves around the world (Ransome, 1937).

1.1. Honey

Honey was the only readily available sweetener to the peoples of Europe until methods were developed for refinement of sugar from sugar beets and sugar cane (Voorhies et al., 1933). Honey remains an important international commodity with global production estimated at 1.07 million metric ton in 2007, a 58% increase in production since 1961 (FAO, 2009). Using the average 2006 US price for honey, \$1168 metric ton, the global value of honey production in 2007 had an estimated worth of US\$1.25 billion.

1.2. Pollination

By far the most important contribution honey bees make to modern agriculture is the pollination services that they provide. Fifty-two of the 115 leading global food commodities depend on honey bee pollination for either fruit or seed set (Klein et al., 2007). Some (five) honey bee-dependant commodities would have $\geqslant$90% yield reduction without honey bees (Klein et al., 2007). In addition, yields in terms of fruit size, quality, or quantity would be greatly reduced (90–40%) in 16 commodities, modestly reduced (10–40%) in a further 19 commodities, and slightly reduced (<10%) in a further 13 commodities (Klein et al., 2007). In total, 22.6% of all agricultural production in the developing world, and 14.7% of agricultural production in the developed world is directly reliant on animal pollination to some extent (Aizen et al., 2008). However, when foods that indirectly benefit from pollination are included, 35% of the human diet is thought to benefit from pollination (Klein et al., 2007). Globally, the value of insect pollination has been esti-

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0022-2011/\$ - see front matter © 2009 Elsevier Inc. All rights reserved.
doi:10.1016/j.jip.2009.06.011

mated at US$ 212 billion (€153 billion), which represents about 9.5% of the total value of agricultural production. The value of insect pollination to agriculture is approximately the same for EU25 €14.2 billion (US$19.8 billion) and North American (excluding Mexico) nations (€14.4 billion; US$20.1 billion; (Gallai et al., 2009)).

Not all animal-dependent pollination is provided by honey bees, nor are honey bees the most efficient pollinators of most crops (NRC, 2006). However, they remain the most important pollinator for most crop monocultures worldwide (McGregor, 1976; Delaplane and Mayer, 2000). Managed honey bees are ideally suited for the pollination of large monocrop plantings for several reasons. Colonies of bees have a relatively large year round work force of 10,000–40,000 individuals, approximately one-third of which are foragers (Seeley, 1985). Beekeepers can stimulate the growth of these populations in preparation of a pollination event by feeding artificial diets of sucrose or high fructose corn syrup and artificial protein diets. Further, managed colonies are maintained in standardized equipment which facilitates the transport of colonies over large distances to pollination sites.

The biology of honey bees also makes them well suited as commercial pollinators. Honey bees are generalists, visiting a wide range of flower types, even those they are not well suited to pollinate, such as blueberries and alfalfa. Traveling an average of 4.5 km to forage (Seeley, 1985), honey bees are able to pollinate crops over an area of 6360 ha, allowing colonies to be placed in groups in the center of large orchards without affecting pollination in the orchards' periphery. Further, a bee's ability to communicate the location of floral resources to her nest mates makes honey bees particularly efficient pollinators (Seeley, 1985).

Crops not-dependent on animals for pollination represent the majority of caloric intake in human diets (Klein et al., 2007). While the total land area under cultivation has increased globally over the last 46 years, the proportion of land dedicated to the production of non-pollinator-dependent crops has shrunk when compared to land used to cultivate pollinator-dependent crops (Aizen et al., 2008). In part, this shift in land use is motivated by the fact that pollinator-dependent crops tend to have higher value than non-pollinator-dependent crops (Gallai et al., 2009). Between 1961 and 2006, agriculture industry's dependence on pollinators has increased by 50% and 62% in the developed and developing world, respectively (Aizen et al., 2009). This rate of increase surpasses that of global increases in the number of managed honey bee colonies, suggesting that pollinators may limit production of pollinator-dependent crops in the future (Aizen and Harder, in press).

The loss of all pollinators would reduce agricultural production by an estimated 8%. However, because many crops are not 100% reliant on insect pollination, some reduced production could be compensated for by increasing cultivated acreages. The loss of animal pollinators would require the developed and developing world to increase land cultivated in pollinator-dependent crops by 15% and 42%, respectively, to make up production deficits (Aizen et al., 2009). Pollinator declines and/or failure of pollinator populations to increase at the rate of pollinator-dependent crop expansion could have serious effects on world food security, just as the recent increased demand for corn for ethanol production has had significant effects on food prices (Elobeid, 2007).

2. Populations of managed honey bees

2.1. Worldwide

The total number of managed honey bee colonies worldwide was estimated at 72.6 million in 2007 (FAO, 2009). This represents a 64% increase in the total number of colonies managed since 1961 (Fig. 1). This crude approximation overestimates the change in managed bee populations because it does not account for changes in the number of nation states reporting colony numbers over the period. Aizen and Harder (in press) estimated that global stocks have increased by ~45%, after excluding all states that did not report colony numbers for the entire time series between 1961 and 2007.

While it is clear that global stocks of honey bees have increased over the last five decades, not all regions have experienced gains. Notably, in the period between 1961 and 2007, managed colonies decreased in both Europe (−26.5%) and North America (−49.5%), while large increases were recorded for Asia (426%), Africa (130%), South America (86%), and Oceania (39%) (FAO, 2009). Even within regions there was considerable variability in the honey bee colony population trends. For example, in North America, both the US and Mexico saw declines over the 46 year period, while Canada saw increases in colony numbers. In Europe, similar discrepancies in trends were apparent (Fig. 2: FAO, 2009).

2.2. United States

The number of honey-producing colonies in the US dropped 61% from their high of 5.9 million managed in 1947 to the low of 2.3 million reported in 2008 (Fig. 3). The number of honey-producing colonies has been tabulated by the USDA National Agricultural Statistics Service (NASS) for almost all years since 1943. Between 1982 and 1985 NASS discontinued its survey and colony numbers for those years were estimated by the Agricultural Stabilization and Conservation Service (Rodenberg, 1992) (Fig. 3). The annual census was designed to capture the number of honey-producing colonies in each state. As a result, the survey counts colonies that produce honey in more than one state multiple times, potentially inflating national figures (NRC, 2006). In addition, after 1985, NASS no longer counted beekeepers with five or fewer hives, potentially explaining some of the steep decline in colony numbers recorded between 1985 and 1986 (Fig. 3) (Rodenberg, 1992).

NASS also counts honey bee colonies as part of its agricultural census, an effort it conducted once every 5 years since 1982 (Fig. 3). The agricultural census (Ag Census) effort is meant to provide comprehensive information about US farms, including those with apicultural enterprises. It specifically inventories the number of honey bee colonies owned on farms on December 31 of survey years. This may underestimate the number of "production" colonies in the country as beekeepers may reduce colony numbers going into winter to avoid overwintering costs (Daberkow et al., 2009). The census survey also excludes beekeepers who do not produce or sell $1000 worth of produce per year (Hoppe et al., 2007). Total colonies inventoried by the Ag Census show a period of decline in managed colonies similar to that recorded by the Honey report between 1987 and 2002 (17% vs. 22% respectively), however, between 2002 and 2007 the number of colonies recorded by AG Census dramatically increased.

Standardized periodic surveys that quantify colony numbers provide a measure of total losses and/or gains over a period, but do not necessarily capture actual losses over that period. Beekeepers can quickly replace large losses (i.e. winter losses) by splitting surviving colonies and/or by purchasing and installing packages of bees (vanEngelsdorp et al., 2007). It is, therefore, possible for inventories of colonies reported by a given periodic survey to remain stable or even increase when substantial losses occurred between survey dates (Daberkow et al., 2009). This appears to have been the case in 2007 and 2008. After an estimated overwintering loss of 32% and 36% in the winters of 2006–2007 and 2007–2008, respectively (vanEngelsdorp et al., 2007, 2008), the total number of colonies recorded by the Honey report increased by 5% between

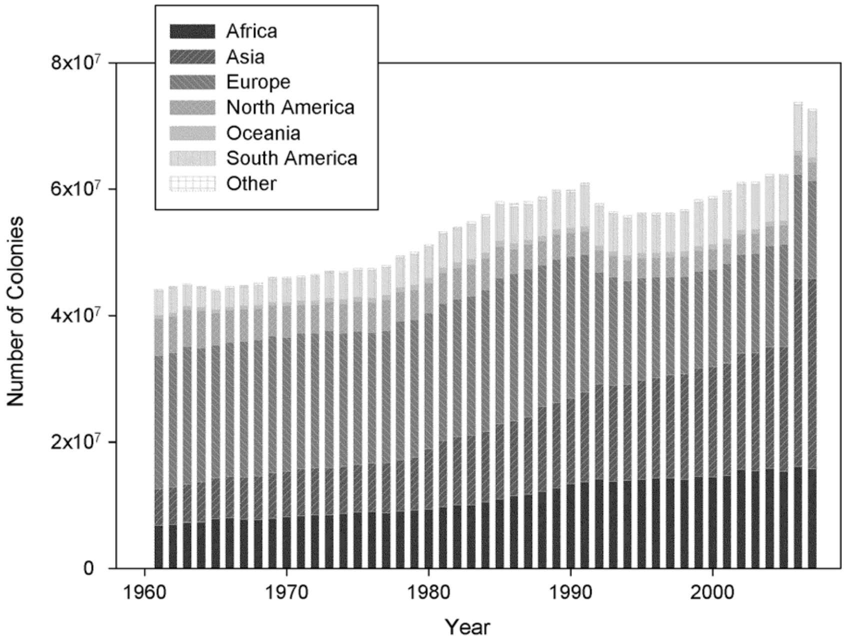

Fig. 1. Total global number of managed honey bee colonies between 1961 and 2007 (FAO, 2009). The large increase in Asian bee populations between 2005–2006 primarily results from countries reporting managed colonies to the FAO for the first time in 2006.

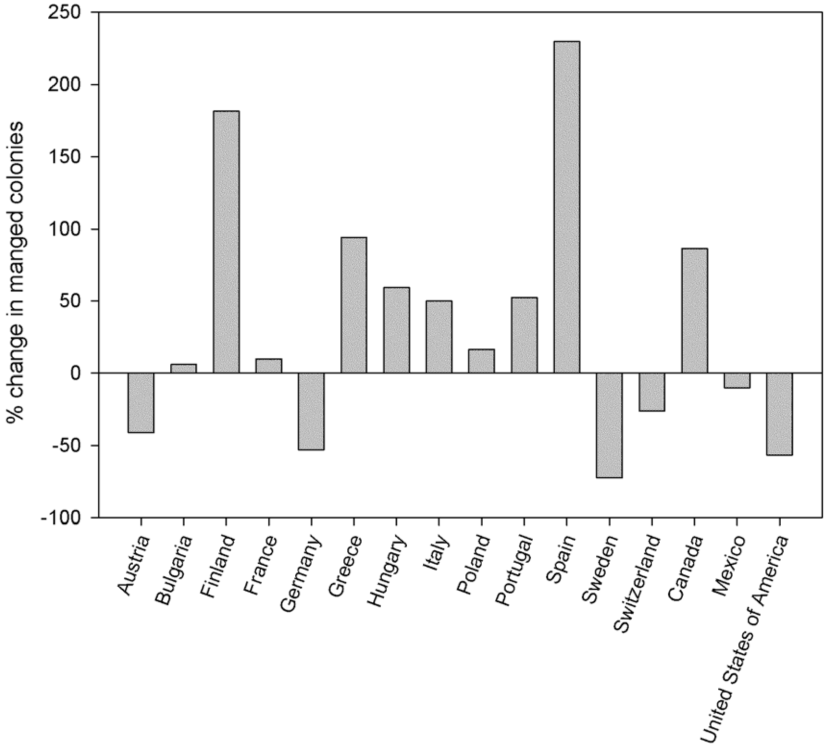

Fig. 2. Percent change in number of managed bee colonies between 1961 and 2006 in selected countries in Europe and North America (FAO, 2009).

2006 and 2007, and decreased by 14% between 2007 and 2008 (USDA-NASS, 2009a,b).

2.3. Europe

Colony numbers in Europe decreased from over 21 million in 1970 to about 15.5 million in 2007 (FAO, 2009). While this decrease was slow and gradual before 1990, a much steeper decline was observed thereafter. As there is no Europe-wide central annual census, comparable to the National Agricultural Statistics Service in the US, estimations of colony numbers and fluctuations over years are much harder to compile. Colony numbers for most countries are reflected in the FAO figures, but for several countries colony number data are either incomplete or do not exist at all. In addition, in some cases the FAO numbers are estimates made by the FAO or the reporting country.

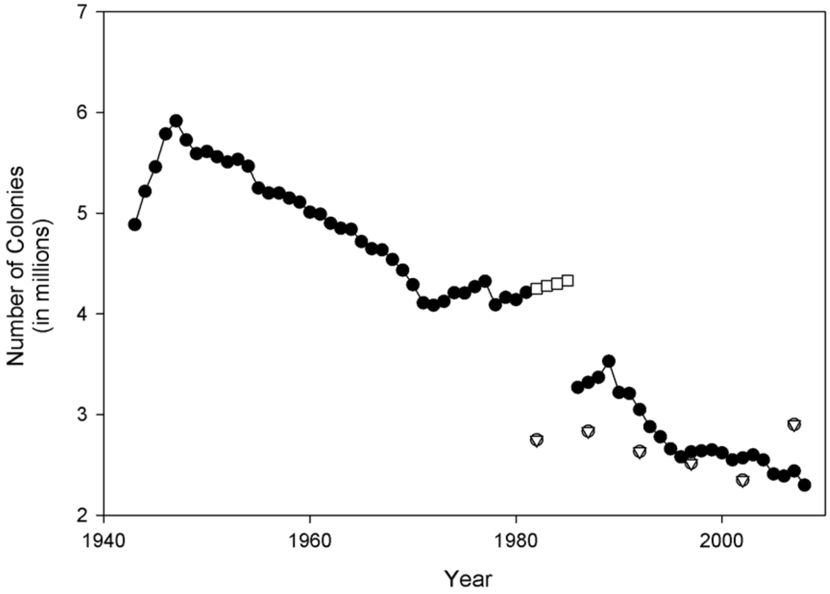

Fig. 3. Numbers of managed honey bee colonies in the United States of America 1944–2008. Annual estimates of the number of honey-producing colonies (solid circles) were obtained from the annual Honey reports with the expectation of the years 1982–1985 when the survey was discontinued. During these years estimates are provided by the USDA Agricultural Stabilization and Conservation Service (hollow squares). Estimates of the total number of colonies as inventoried by AG census are also provided (hollow triangles) (USDA-BAE, 1949; USDA-AMS, 1955; USDA-NASS, 1967, 1972, 1978, 1981; Rodenberg, 1992; USDA-NASS, 1999, 2004a,b, 2009a,b).

Over the last 48 years the change in the number of honey bee colonies managed in individual European states has been extremely variable (Fig. 2). Since 1961, colony numbers in several countries have increased; remarkably Finland and Spain have seen managed colonies increase by more than 50%. These numbers should, however, be viewed with caution as early data were based on FAO estimates. In contrast, Austria and Germany saw a decline in the number of managed bee colonies over the same period, while Sweden saw a drop of approximately 75%.

The changes in populations experienced by different nation states did not occur consistently over time. For instance, colony numbers in Germany have been increasing slowly since 2000, despite experiencing an absolute loss of more than 50% when compared to 1961 populations. In contrast, while the number of colonies managed in France is greater today when compared to 1961 populations, colony numbers have consistently decreased after reaching a peak in 2000.

2.4. Factors to consider when comparing variations in winter mortality between nations: Survey effort and reporting

Overwintering mortality can be extremely variable within a region, for instance in the US in the winter of 2007–2008 the average winter mortality in the US was 35.8%; however, the total loss in individual states ranged from 7.3% to 56.2% (vanEngelsdorp et al., 2008). Overwintering losses in Europe over the winter of 2008–2009 also showed similar variation (Fig. 4). Some caution, however, is required when comparing overwintering losses in different nations, as survey efforts from different countries are not the same. For instance, some results reported in Fig. 4 come from survey efforts that were conducted by beekeeper groups (e.g. Finland), others by regulatory and research officials (e.g. Canada and the US), and others by monitoring specific colonies (e.g. Germany). Typically, beekeepers responding to these surveys are not randomly selected potentially biasing results; for instance, if only beekeepers attending national meetings fill out surveys, non-attending beekeepers' losses, which could be quite different, are not tabulated. In other cases, such as France, only a randomly selected portion of the nation's largest beekeepers were surveyed. Equally variable is the presentation of survey results. In all cases total colony losses were reported, but this number is biased by larger operations, whose losses may differ from smaller operations. As increased attention is given to annual winter losses, uniform survey and reporting methods would be beneficial (see Fig. 4).

3. Factors affecting managed honey bee populations

Many factors may account for the declines of honey bees in the US and Europe. In all likelihood, no one factor on its own can account for all losses or gains over a given time period. Many factors can occur simultaneously and some influence one another. The remainder of this article is a general review of some important factors thought to impact colony numbers and a discussion of their likely impact on honey bee populations.

With few exceptions it is nearly impossible to determine the cause of a honey bee colony death after the fact. If a colony dies during winter, a considerable amount of time may pass before it is noticed by the beekeeper, and clues to the cause are usually lost. To definitively determine the cause or causes of mortality in colonies *a priori* sampling and analysis of a representative portion of colonies is needed. Such longitudinal studies enable causes of mortality to be inferred and the relative risk of risk factors (on their own or in combination) to be calculated.

Several national colony monitoring programs have been initiated. One of the first and most comprehensive of these programs was the German Honey Bee Monitoring Program (http://www.ag-bienenforschung.de), where about 1200 colonies are continuously followed over a period of several years. Colony strength and health status are regularly assessed, and samples are taken and checked for disease and parasite loads. Although laborious and cost-intensive, this project has proven useful, because it generates reliable data enabling relationships between risk factors and colony death to be determined.

3.1. Diseases and parasites

There are many honey bee diseases (bacterial, fungal, viral, microsporidial), parasites (mites), predators (bears, birds, humans),

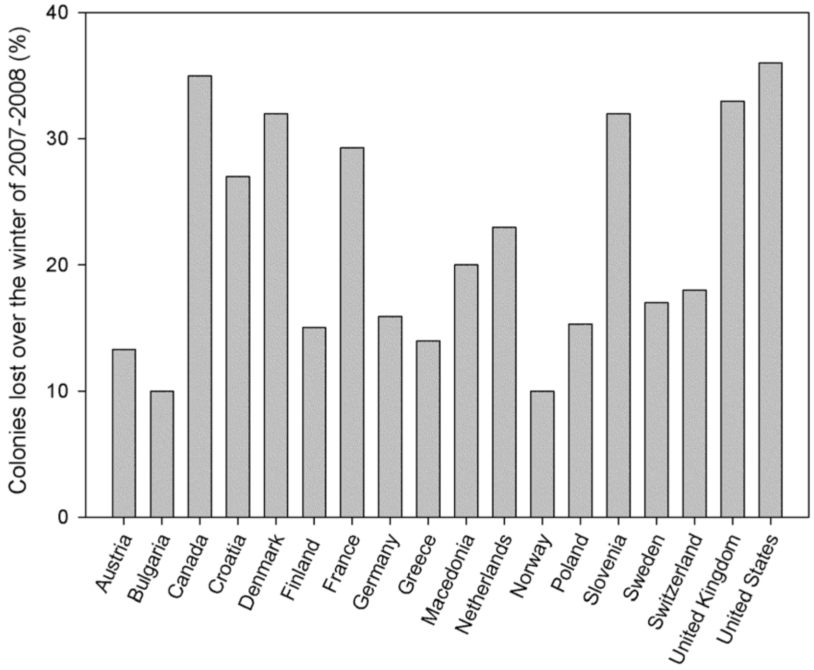

Fig. 4. Percentage of colony winter losses in 2007/2008 in several countries (Anonymous, 2008; Pernal, 2008; Coloss, 2009).

and pests (beetles, moths) that can adversely affect managed honey bee productivity and survival (Morse and Flottum, 1997). A comprehensive discussion of the most important diseases and parasites of bees is provided in subsequent chapters of this issue. Here, we provide a brief discussion of a few of the most significant diseases and parasites, specifically those that may have and/or continue to play a significant role in changing honey bee populations.

3.1.1. *Varroa destructor*

The parasitic mite, *V. destructor* (Anderson and Trueman, 2000; formerly known as *Varroa jacobsoni*), is the most detrimental honey bee parasite in the world today (Rosenkranz et al., 2010). This mite moved from its original host, the Asian bee *Apis cerana*, to *A. mellifera* colonies imported to Asia. On their new host, varroa mites have spread to nearly all continents where *A. mellifera* are kept. Today, it can safely be assumed that all honey bee colonies within the mite's range harbor varroa mites. As a consequence of mite infestation, dramatic colony losses have repeatedly occurred in affected countries (Finley et al., 1996; Martin et al., 1998; vanEngelsdorp et al., 2007).

Female varroa mites feed on adult bees, but depend on bee brood for reproduction. Both the adult female and her offspring feed on pupae, where they can cause damage by ingestion of hemolymph, resulting in severe nutritional deficits for the developing bee (Duay et al., 2003; Garedew et al., 2004). In addition, alteration of the bee's physiology and secondary infections contribute to the damage (Amdam et al., 2004).

The level of infestation of varroa mites that cause colony damage appears to have decreased over time. In the early 1980s, in Europe, a bee colony could harbor several thousand mites without dramatic symptoms (Boecking and Genersch, 2008). Today, however, a fall infestation rate of 10%, corresponding to about one thousand mites in a colony of 10,000 bees, is considered to be a critical threshold for winter survival of the colony (De Jong, 1997; Siede et al., 2008).

3.1.1.1. Interactions between viruses and mites. Colonies with varroa mite infestations that are not effectively controlled quickly develop disease symptoms and, if left untreated, inevitably will collapse. The damage is manifested by reduced colony development, the presence of malnourished, deformed, and underweight bees, or crawling bees that are unable to fly or have crippled wings (De Jong, 1997). Brood in infested colonies may also have a condition termed "parasitic mite syndrome (PMS)" (Shimanuki et al., 1994). Many of these symptoms are thought to be caused by viruses associated with varroa mite infestations (Hung et al., 1995, 1996). Varroa mites can vector several viruses, most of which were present in honey bees before varroa invasion (Bailey and Ball, 1991), but remained covert, symptomless infections (Bowen-Walker et al., 1999; Yue and Genersch, 2005).

For several of the about 18 known honey bee viruses (Chen and Siede, 2007) interactions with *V. destructor* are known, either through virus transmission by the mite, or through other means of action. For instance, pupae parasitized by varroa mites may suffer from an impaired immune system and seem to be more susceptible to virus infections (Yang and Cox-Foster, 2005). The distribution of many viruses appears to match the distribution of the varroa mite, but, for some viruses, there also appear to be regional differences (Ellis and Munn, 2005). Results from the German Bee Monitoring Program over 4 years indicate a clear and highly significant correlation between colony winter mortality, fall mite infestation rates, and both Deformed wing virus (DWV) and Acute bee paralysis virus (ABPV) loads. Colonies with a high mite load in October had both more viruses and a significantly higher risk of mortality in the winter (Anonymous, 2008).

Although DWV can be transmitted directly from bee to bee, expression of clinical symptoms, such as crippled wings or a shortened abdomen, only occurs after mite-to-pupa transmission of virus particles (Bowen-Walker et al., 1999; Yue and Genersch, 2005; Yue et al., 2006, 2007; Tentcheva et al., 2006). DWV has repeatedly been shown not only to be efficiently transmitted by the mite, but also to replicate in mite tissues (Bowen-Walker et al., 1999; Shen et al., 2005; Yue and Genersch, 2005; Tentcheva et al., 2006). Thus, the number of viral copies transmitted to the bee by the mite is dramatically increased, perhaps also accompanied by immunosuppression of the bee (Shen et al., 2005) or an increase in virulence of the virus (Gisder et al., 2009). The biology of DWV and in particular the interactions between DWV and *V. destructor* have recently been described in detail (de Miranda and Genersch, 2010).

Like DWV, ABPV was known as a honey bee virus before the arrival of varroa mites, although it usually did not cause clinical symptoms or lead to colony death (Bailey and Gibbs, 1964). Nevertheless, the prevalence of ABPV in Europe was shown to increase after the arrival of the mite (Allen and Ball, 1996), which had been identified as an efficient transmission vector (Ball, 1983). While there is currently no experimental evidence for viral replication of ABPV in varroa mites, it has been confirmed that infections with this virus are more deadly in combination with the mites. A recent study found a strong correlation between high fall mite loads, viral loads and increased winter mortality (Siede et al., 2008). In contrast, all colonies with viral infections, but without detectable mite levels in the fall, survived (Siede et al., 2008).

The highly virulent Kashmir bee virus (KBV) has been found to be present in countries (e.g. Australia) still free of varroa mites (Bailey et al., 1979); however, interactions between the virus and the mite have been established. KBV can be transmitted by varroa mites, but there is still no proof of viral replication in mite tissues (Chen et al., 2004; Shen et al., 2005). The presence of mites clearly elevates viral titers in infected bee pupae suggesting that increased viral replication in the bee is correlated with parasitization although the exact mechanism remains elusive (Shen et al., 2005). It has been hypothesized that immunosuppression of the bee by protein components of the mite saliva facilitates virus replication (Shen et al., 2005). KBV has been shown to be prevalent in the U.S, but is unevenly distributed in Europe. It was found in France, but appears to be mostly absent in Germany (Siede and Büchler, 2004).

The Israeli acute paralysis virus (IAPV) has received considerable scientific interest as a potential causative agent for Colony Collapse Disorder (CCD), because its presence was correlated to an increased risk for colony collapse (Cox-Foster et al., 2007). Because IAPV has been detected in samples that predate CCD (Chen and Evans, 2007), its role in CCD is likely secondary (Cox-Foster and vanEngelsdorp, 2009). An interaction between IAPV and varroa mites has not been demonstrated to date.

However, recent data suggest that ABPV, KBV, and IAPV may not represent clearly separated, different species, but rather form a complex of closely related species. Due to their close genetic relationship, especially KBV and IAPV sequences have been frequently misclassified in the literature and the public sequence databases (de Miranda et al., 2010). The similarity of these three viruses has to be considered when evaluating their impact on colony health.

3.1.1.2. Impact of varroa mites on US bee populations. The negative impact of varroa mite parasitism on individual colonies is clear (Rosenkranz et al., 2010). However, its overall impact on managed bee populations may be less pronounced. According to the USDA (USDA-NASS, 1999, 2004a, 2009b,c), the number of managed colonies in the US dropped some 26% since the mite was introduced in 1987, a decline often linked to varroa-mediated mortality (NRC, 2006). However, the rate of decline after 1987 (1.09% per year) is barely different from the rate of decline recorded between 1947 and 1987 (1.11% per year) suggesting that varroa mites did not have a direct effect on the rate of colony loss, which began more than six decades ago. This is not to say that the mite has had no impact on the US apicultural industry. A majority of beekeepers in the US (~70%) are relatively small, managing less than 25 colonies. Between 1987 and 2002, there was a ~40% decline in the number of these small apicultural farms, but these operations accounted for only a small portion of the colonies managed in the nation (<10%) (Daberkow et al., 2009). It seems likely that many of those small operations leaving the apicultural industry over the period did so as a result of an inability to control varroa mites. Concurrent with a decrease in the number of small beekeepers was a 66% increase in the number of colonies managed by the remaining beekeeping operations (Daberkow et al., 2009). These larger operations are presumably better able to control mite populations and may have increased operational sizes in anticipation of increased annual losses (Burgett, 2004).

A simple comparison of colony numbers from year to year may mask fluctuations in colony numbers that can occur between survey dates. Prior to the introduction of varroa and tracheal mites, overwintering losses of 10% were normal (Voorhies et al., 1933). More recently, beekeepers reporting "normal" losses had an average loss of 21% (vanEngelsdorp et al., 2008). Since the introduction of mites, severe overwintering losses have been recorded. Some of these losses are almost certainly linked to mite infestation (NRC, 2006). For instance, over the winter of 1995–1996 Pennsylvania beekeepers recorded an average loss of 53%. Those beekeepers that reported treating colonies with Apistan (for varroa mite control) in the fall of 1995 reduced their overwintering loss by an average of 26% (Finley et al., 1996). In a more recent survey of winter losses in the US, beekeepers considered varroa mites to be the third most important contributor to mortality following queen failure and starvation (vanEngelsdorp et al., 2008).

While overwintering losses do not seem to have had a pronounced effect on the overall rate of declines in managed honey bees enumerated in the United States, they have almost certainly had a pronounced effect on beekeepers' bottom line (Kemp, 2000). Managing varroa mite populations has directly increased operational costs because of the costs associated with purchasing and applying control products (NRC, 2006). The costs of mite control applications may have been passed onto producers renting bees for pollination by way of increased fees (Burgett, 2004). Mites have also indirectly affected beekeeper profitability as colonies made or purchased to replace mite-killed colonies are smaller than full sized overwintered colonies, and hence, tend to be less productive (NRC, 2006).

3.1.2. *Nosema* spp.

Although not always resulting in evident disease symptoms, infections with microsporidia of the genus *Nosema* are regarded among the diseases that are most economically important for beekeepers (Fries, 1993, 1997, 2010). Infections with *Nosema* spp. are known to be correlated with reduced lifespan of individual bees, reduced performance of colonies, and increased winter mortality (Fries et al., 1984). The honey bee is host to two different species, *Nosema apis*, which has been known for a long time as a bee pathogen (Zander, 1909), and the recently described *Nosema ceranae* (Fries et al., 1996). *Nosema* infections are transmitted horizontally among bees, by ingestion of spores from the environment. For example, housecleaning bees, on removing nosema-infected bee feces deposited in the hive, ingest nosema spores, which then germinate in the ventriculus, causing inflammation of and damage to the gut epithelial cells.

N. ceranae originates from Asia and was originally described as a pathogen of the Asian cavity nesting bee *A. cerana* (Fries et al., 1996). It was later found to occur in colonies of *A. mellifera* in Taiwan (Huang et al., 2007) and reported from Spain (Higes et al., 2006). It has been suggested that *N. ceranae* may be more virulent than *N. apis* when infecting *A. mellifera*, and it has been reported to cause severe colony losses, especially in southern Europe (Higes et al., 2007, 2008). *N. ceranae* has been present in the US since at least 1995 (Chen et al., 2007) and in Europe (Finland) since 1998 (Paxton et al., 2007). While the time of the *N. ceranae* jump to *A. mellifera*, and the date of its arrival in Europe and North America remain unknown, these are most likely recent events (Paxton et al., 2007).

3.1.3. Bacterial brood diseases

American foulbrood (AFB; *Paenibacillus larvae*) is the most serious bacterial disease of the honey bee (for a recent review see: Genersch, 2010). Early apiculturists did not distinguish this disease from European foulbrood (EFB; *Melissococcus plutonius*; for a recent review see: Forsgren, 2010), which is now mostly considered less virulent than AFB.

3.1.3.1. American foulbrood. American foulbrood is a bacterial disease of the bee brood, caused by the gram-positive bacterium *Paenibacillus larvae*. Due to its high contagiousness, easy and rapid spread within a colony, among colonies in an apiary, and between apiaries, American foulbrood is a notifiable disease in many countries where it is subject to strict regulations, enforced by veterinary authorities. Usually, colonies with active AFB have to be destroyed (burned) to prevent the disease from spreading further. While several countries, like the US, permit the prophylactic use of antibiotics to control AFB, many countries follow an opposite approach, interdicting any antibiotic treatment. Antibiotics are not effective in killing spores, and non-destructive control methods, such as the "shook swarm technique" (i.e., shaking bees onto new comb foundation and destroying the infected comb), are also available (Pernal, 2008). Common problems associated with antibiotic use are increased occurrence of resistant AFB strains and antibiotic residues in honey (Miyagi et al., 2000; Mussen, 2000; Kochansky et al., 2001a; Lodesani and Costa, 2005).

Several European countries are currently changing the focus of AFB control toward a more efficient prevention of clinical AFB outbreaks by prophylactic determination of *P. larvae* spores in honey samples. By recognizing infected although not yet diseased colonies, i.e. before clinical symptoms of the disease appear, sanitation measures can be taken at an early stage and outbreaks can be prevented.

3.1.3.2. European foulbrood. European foulbrood is a disease of bee larvae, caused by the gram-positive bacterium *Melissococcus plutonius* (formerly known as *Melissococcus pluton*) (Bailey and Ball, 1991; Shimanuki, 1997). In several countries, EFB is a notifiable disease and currently appears particularly prevalent and dramatically increasing in the UK (Wilkins et al., 2007; Tomkies et al., 2009) and Switzerland (Forsgren et al., 2005; Belloy et al., 2007; Roetschi et al., 2008).

3.1.3.3. Impact of American and European foulbrood on US managed honey bee populations. Of all diseases of the honey bee, AFB has had the greatest impact on the industry. In 2000, annual economic loss attributed to AFB infection in the US was estimated at US$5 million (Eischen et al., 2005). This estimate is likely only a fraction of the cost to the industry prior to the mid-1900s.

The earliest known documented shipment of bees to the Americas occurred from England in December of 1621 which likely arrived several months later (Oertel, 1976). By 1650 nearly all farms in New England are reported to have had a colony or two of bees. However, the number of bees managed by these colonists rapidly declined after 1670, presumably because of AFB (Pellett, 1938). Substantive documentation of AFB's presence in the new world, however, did not occur until more than a century later, by the late 1800s and early 1900s. Then, AFB and EFB were a "veritable scourge" in many parts of the country (Surface, 1916) resulting in the passage of many state bee laws and implementation of state apiary inspection programs (Phillips, 1920). These early apiary laws proposed to mitigate the spread of AFB by requiring the destruction of all infected colonies and the burning of infected bee equipment. This effort was not insignificant, for instance, in the state of Pennsylvania over 32,000 colonies were burned between 1930 and 1965, a number that is just shy of the total number of colonies in the state in 2007 according to the Ag Census (PA Dept of Ag, unpublished records; USDA-NASS, 2009c). Beekeepers that did not burn their colonies had their colonies burned by inspectors, and some particularly uncooperative individuals were fined $100 dollars (~US$1,173-2007 adjusted dollars) or jailed for non-compliance.

Early laws also required the mandatory transfer of colonies from box and gum hives (i.e. colonies established in crudely made boxes without frames, or in hollowed out tree trunks) into movable frame hives which permitted inspection of colonies for disease. The Rev. L. L. Langstroth's discovery of the bee space (that is the space of about 0.95 cm between hive components which bees will not fill with propolis nor fill with additional comb), and subsequent development of the movable frame hive in 1852 revolutionized the practice of keeping bees.

Pellett (1938) claims that prior to the widespread adoption of movable frame hives, honey bee diseases in America were not widely distributed. While he does not explicitly provide evidence for this claim, one can assume the basis of his claim relies on the fact that, except for wax moth, *Galleria mellonella*, there exists little discussion of disease in the robust bee literature of the time prior to the 1860s. Many factors, however, could have contributed to underreporting of disease. As Pellett himself states, before the adoption of the movable frame hive, little was known about the biology of the colony, and so diseases, if present, would have been permitted to run their course. Weakened colonies provide opportunity for wax moth larvae, which in the process of consuming pollen and cocoon castings in the comb, destroy them. Wax moth damage is distinct, and it is likely that many cases of colony death attributed to the moth were, in fact, caused by other factors such as a failing queen or a disease (Benton, 1899). As summarized by Miller (1901), blaming wax moth for colony death is the same as concluding that "maggots had killed a horse if (one) should find a horse filled with them a few weeks after it had been shoot."

Beekeeping practice prior to moveable frame hives may also have had an indirect role on disease mediation. Beekeepers killed both the heaviest and weakest fall hives to harvest honey The strongest colonies were chosen because they were heavy with honey, and the weakest were chosen because they were the most likely to die over the winter. The annual killing of weak (and possibly diseased) colonies and rendering their comb could have slowed the spread and multiplication of disease harbored in the comb similar to the way regular comb replacement reduces disease incidence (Fries, 1988).

Prior to 1943, US honey and bees wax production data were collected every 10 years by the National Census, however colony numbers were not consistently reported, and when they were reported were tabulated at different times of the year, making meaningful comparisons of colony numbers difficult. Thus, the impact of AFB/EFB on US colony numbers is difficult to assess. Using honey production figures as a rough estimate of colony numbers, Voorhies et al. (1933) noted a distinct increase in honey production between 1860 and 1890, followed by a two decade decline in production, and then an increase in production in 1920–1930. While many factors likely contributed to these gains and losses, including changing climate and forage availability (Voorhies et al., 1933), it is of note that decreased productivity between 1890 and 1910 was associated with notable outbreaks of both EFB and AFB (Surface, 1916; Voorhies et al., 1933). Increased production observed in the 1920s coincided with decreased disease incidents. The incidence of EFB, which reportedly killed many thousands of colonies, was dramatically reduced by changing the race of bees used. The EFB-susceptible German black bee (*A. mellifera mellifera*) was largely replaced with the EFB-resistant Italian bee (*A. mellifera ligustica*) in the second decade of the 1900s (Voorhies et al., 1933). Early State efforts certainly reduced AFB incidence, however the widespread use of antibiotics (Sulfathiazole in the 1940s and 1950s, Oxytetracycline from the 1950s until the 1990s, and more recently Tylosin tartrate: Haseman and Childers, 1944; Turell, 1974; Elzen et al., 2002) has significantly (and arguably more dramatically) reduced the incidence of bacterial diseases. However, while prophylactic use of antibiotics may prevent disease outbreak, discontinuation of regular antibiotic application often results in disease reoccurrence (Alippi et al., 1999).

3.1.4. Unexplained or unresolved bee epidemics

The beekeeping literature is ripe with incidents of bee epidemics, localized or regional events typified by mass mortality of honey bee colonies (Underwood and vanEngelsdorp, 2007). Many of these losses remain unexplained, or their cause remains disputed. Perhaps the most infamous honey bee epidemic occurred on the Isle of Wight during the early 1900s. In three events between 1905 and 1919, 90% of the island's bees was lost (Bailey, 1964; Adam, 1968). The cause of the affliction remains disputed, with some arguing that the protozoan fungus, *N. apis* was the cause (Fantham and Porter, 1912), while others believe the honey bee tracheal mite *Acarapis woodi* was to blame (Adam, 1968). Both diseases of adult bees are known to have a pronounced negative effect on colony overwintering ability. In a survey of Pennsylvania beekeepers conducted just as *A. woodi* was first spreading in the state, beekeepers who overwintered colonies with *A. woodi* infestations lost an average of 31% of their colonies as compared to the 11% loss suffered by their non-infested neighbors (Frazier et al., 1994). More recently, large losses of honey bees were experienced by Spanish beekeepers and blamed on *N. ceranae* (Higes et al., 2008).

Colony Collapse Disorder (CCD) is a condition of colonies that first came to light in the United States in the fall of 2006. The condition is defined by a clear set of symptoms that distinguishes it from most other conditions. These include the total lack of dead bees in the colony or apiary, evidence that the loss of adult bees from dead or dying colonies was rapid, and a lack of kleptoparasitism in dead hives despite the presence of surplus honey and pollen stores (Cox-Foster and vanEngelsdorp, 2009). Outbreaks of colony mortality similar to CCD have occurred in the US before (Underwood and vanEngelsdorp, 2007), although not to the extent documented in the winters of 2006–2008 (vanEngelsdorp et al., 2007, 2008).

The cause of CCD remains unknown (Cox-Foster and vanEngelsdorp, 2009). It is likely that several "stress factors", acting alone or in combination, contribute to weakening the bees and allowing opportunistic pathogens to infect and eventually kill colonies (Cox-Foster and vanEngelsdorp, 2009). Over the winter of 2007–2008 operations suspected of suffering from CCD lost more than two times the number of colonies lost by operations not suffering from the condition (vanEngelsdorp et al., 2008).

The effect of high overwintering losses on total managed bee populations is not clear. As previously discussed, high overwintering losses do not necessarily translate to an overall reduction in colonies managed by beekeepers in the summer (vanEngelsdorp et al., 2008). In fact, the high losses experienced over the winter of 2006–2007 may explain the increase in colonies enumerated in December of 2007 by the Ag Census (Fig. 3). Since 2004, an increasing number of US commercial beekeepers have begun moving colonies from across the continent to pollinate almonds, motivated largely by the increased demand for pollinating units, which caused colony rental prices to increase from US$54 a unit in 2004 to US$136 in 2006 (Sumner and Boriss, 2006). The large losses experienced by beekeepers in the winter of 2006–2007 left several operations without enough bees to meet their contractual obligations. As a result, many migratory beekeepers may have increased their stocks the following winter in anticipation or fear of higher losses. The greatest increases in colony inventories occurred in California and in states in which large numbers of colonies are wintered (Florida, Georgia, and Texas) before moving to California tacitly supporting this hypothesis (USDA-NASS, 2004a, 2009c).

3.2. Non-disease factors influencing managed honey bee populations

3.2.1. Pesticides

Modern agriculture increasingly depends on the use of chemical substances to control weeds, fungi and arthropod pests to ensure high yields. Honey bees may frequently become exposed to environmental chemicals as a consequence of their foraging activities, and traditionally, the focus of pesticide regulations was more on protection of bees against direct poisoning (Croft, 1990; Thompson, 2003; Desneux et al., 2007). However, since the substances that are being used have changed, damage from acute toxicity is not the only threat to bees. Instead, sub-lethal effects such as paralysis, disorientation or behavioral changes, both from short-term and long-term exposure, increasingly come into focus.

3.2.1.1. Direct effects – poisoning. In most countries, a legal framework is in place to protect honey bees and other pollinator insects from the negative effects of pesticides and other agrochemicals. The relevant decrees are the European Council Directive 91/414 in Europe, and the Federal Insecticide Fungicide and Rodenticide Act in the US. To determine the effects of pesticide exposure on bees, the standard methods used are the calculation of the LD50 (median lethal dose) or LC50 (median lethal concentration) of a given substance with respect to adult bees or larvae. Another common measure is the hazard quotient which is based on the LD50. Based on the results of these assays, substances are then classified into different categories of risk to bees (e.g. in Germany B1–B4), and conditions and restrictions for application of substances in each category are defined.

As a consequence of the protection by laws and decrees, direct poisoning of honey bees by pesticides in the field is now a comparatively infrequent event in most countries of Europe and North America. For instance, the absolute number of samples with damaged bees sent to the Julius-Kühn-Institut (JKI) in Germany (the central institution for analysis of damage by poison), decreased from more than 400 in the 1970s to 67 in 2004 (www.jki.bund.de). However, the hazards of agricultural pesticides to honey bees have been most dramatically illustrated by a recent accident in southern Germany, where in the spring of 2008, more than 11,000 honey bee colonies were severely damaged by direct poisoning. The colonies were poisoned by toxic dust containing neonicotinoid insecticides that had become loosened from dressed corn seed due to incomplete incrustation during the dressing process. When the corn seed was sowed using pneumatic sowing machines, the dust became windborne and drifted across the fields onto colonies and other plants visited by honey bees at the time. Unfortunately, major nectar and pollen sources, such as dandelion, oilseed rape and fruit trees were blooming at the time so that millions of foraging bees were poisoned by the dust (http://www.jki.bund.de/presse).

The seed dressing with the neonicotinoid insecticide Clothianidin had been made compulsory by decree for broad areas in southern Germany to prevent outbreaks of the corn root worm *Diabrotica virgifera*. As a consequence of the accident, the registration of Clothianidin in Germany has been withdrawn, and the ingredient may currently not be sold or used (http://www.bvl.bund.de). Among EU countries, the legal situation concerning neonicotinoid insecticides is currently quite variable. For example, they are banned in France, but seed dressing of corn is still a compulsory measure against corn root worm in some other countries, including Austria.

3.2.1.2. Sub-lethal effects. In contrast to direct poisoning of bees that is apparent and easily observable, sub-lethal effects of pesticides on honey bees and other pollinators are much more difficult to demonstrate. However, they have received growing scientific interest (recently reviewed by Desneux et al. (2007)). Sub-lethal negative side effects of pesticides often may become apparent only after prolonged exposure. They may affect various life stages and organizational levels of honey bees, ranging from cell physiology or the immune system of the individual bee to consequences affecting the colony as a whole, such as effects on learning, behavior and communication (Desneux et al., 2007).

While data on effects of pesticides on singular aspects of honey bee life are emerging, very few datasets exist that describe the pesticide load within honey bee colonies, or indicate possible correlations between pesticide exposure and colony losses. In a recent survey conducted in the US, a considerable number of pesticides were detected in samples of pollen (108 samples) and beeswax (88 samples) (Frazier et al., 2008). In association with elevated pesticide levels, a new, albeit rare, condition in bee bread recently was described from honey bee colonies, and named "entombed pollen" (vanEngelsdorp et al., 2009). Compared to normal pollen, samples of entombed pollen contained significantly higher levels of pesticides, most prominently among them the miticides coumaphos and fluvalinate, and the fungicide chlorothalonil. While experimental feeding with entombed pollen did not lead to increased mortality of larvae or adult bees, colonies containing such pollen had a higher risk of mortality in the field (vanEngelsdorp et al., 2009).

In a recent field study in France, residues of several pesticides, including neonicotinoid insecticides and their metabolites, were detected in honey bee colonies. Although no direct correlations between colony mortality and residues could be observed, synergistic effects of pesticides with other factors affecting colony health could not be precluded (Chauzat et al., 2009).

Within the German Honey Bee Monitoring Program, possible effects of pesticide exposure in relation to winter losses have also been investigated using a sensitive method allowing detection and quantification of a total of 258 relevant pesticides (Anonymous, 2008). No direct correlations between single substances and colony death were found, although the analysis focused on samples with poor overwintering scores. The most unexpected result of this survey was the considerable number of agricultural pesticides found in the bee bread. Most samples contained more than one pesticide and only 24% of the samples were free of residues. The total number of single residues found is compiled in Fig. 5, broken down by substance class, but irrespective of residue level. Fungicides were the most frequent pesticides detected, but the number of both herbicides and insecticides/acaricides increased in 2007 compared to previous years. Among all contaminants, the miticide coumaphos, applied by beekeepers to control varroa mites, was the most frequently detected single substance (46 detections in 2005/06, 33 in 2007).

The comparison of the results from Germany and the US reveals striking differences in the residue levels between pollen samples collected in these two countries, although this observation has to be interpreted with caution in light of the small and unequal sample sizes (vanEngelsdorp et al., 2009; Anonymous, 2008). For example, residues of chlorothalonil (a fungicide), with mean levels of over 1300 ppb in entombed pollen from the US, were not found in Germany. Samples of entombed or capped pollen in the US study had mean coumaphos residue levels of about 800 ppb, while the highest single coumaphos residue detected in German bee bread samples was about 130 ppb. Likewise, the highest residue of the acaricide tau-fluvalinate in Germany was about 20 ppb, compared to 600 ppb in the US study. This can be explained by the fact that tau-fluvalinate is not registered for the control of varroa mites in Germany, but is registered for this use in the US.

3.2.1.3. Residues of varroacides. Residues of varroacides, substances used to kill varroa mites, increasingly appear to be of major importance in the discussion of sub-lethal pesticide loads in honey bee colonies. Varroacides, such as coumaphos or fluvalinate, commonly used for varroa mite control and registered for use in many formulations in several countries, have been frequently found in the honey bee environment in significant concentrations. In recent surveys from France and the US, 100% of all tested wax samples were contaminated with both substances (Martel et al., 2007; Frazier et al., 2008). No recent data on wax are available from Germany, where

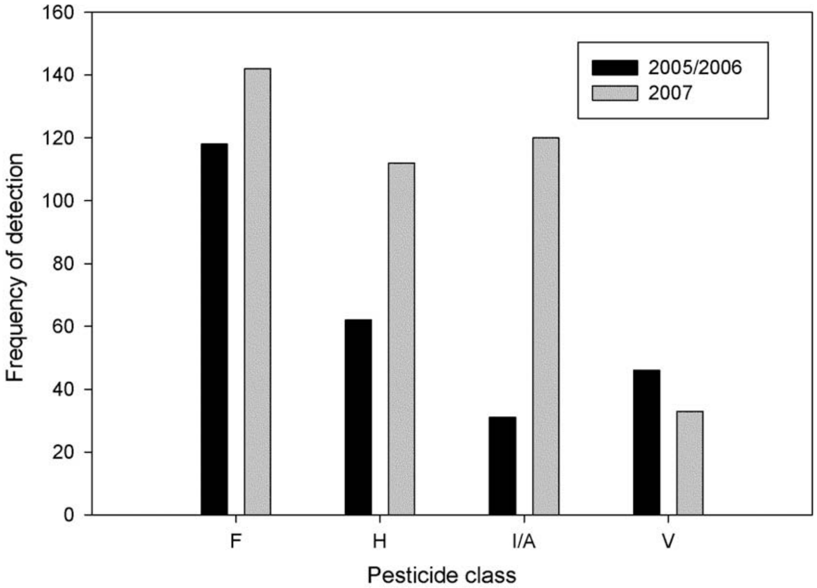

Fig. 5. Number of single pesticide residues in bee bread from Germany in the years 2005/06 (105 samples) and 2007 (110), broken down by substance class. *X*-axis: F = fungicides, H = herbicides, I/A = insecticides and acaricides, V = varroacides; *Y*-axis: number of times a substance from the respective classes was detected in the samples, irrespective of residue level. The figure also contains all instances where a substance was detected, but in concentrations too low to quantify (Anonymous, 2008).

in 1999 coumaphos was found in 28% of wax samples (Wallner, 1999). The situation is further exacerbated by the fact that mites have increasingly developed resistance against various treatments in different parts of the world (Milani, 1999; Pettis, 2004; Lodesani and Costa, 2005). In response to this problem, and driven by economic considerations, beekeepers may resort to the use of unauthorized products, often in excessive quantities (Martel et al., 2007; Chauzat et al., 2009).

While pesticide residues in honey, wax and other parts of the "bee environment" have been explored (Wallner, 1999; Kochansky et al., 2001b; Tremolada et al., 2004; Bogdanov, 2006), their effect on bee health is largely unknown (Martel et al., 2007; Frazier et al., 2008; Desneux et al., 2007). The consequences of long-term exposure to varroacide residues on larvae, pupae and adult bees remain unknown and, thus, future research is clearly needed.

3.2.2. Effect of pesticide poisoning on managed honey bee colony numbers

The adverse effect pesticide application has on colony numbers dates back to the early part of the 1900s, when arsenic spraying of fruit trees was listed as one of the top five reasons why colony numbers in California were declining (Voorhies et al., 1933). Agricultural sprays used widely in the 1960s and 1970s were particularly hard on bees, with a 48% drop in colony numbers experienced in Arizona between 1963 and 1977 that was blamed on pesticide-mediated bee kills. Between 1962 and 1972 California beekeepers were thought to have lost an average of 62,500 colonies a year ($\sim$11.5%) from pesticide poisoning. While many of these colonies were replaced, the cost of bee kills to the industry was not insignificant. A 1962 study of Washington beekeepers concluded that as a result of pesticide-mediated bee kills, they lost about 3.2% on their apicultural investments compared to an 11% gain they would have received in the absence of any such bee losses (Johansen and Mayer, 1990).

3.3. Genetically Modified Crops

Genetically Modified Organisms (GMOs) were developed, in part, to help prevent the potentially adverse effects of pesticides on pollinators (NRC, 2006). Initial concerns that GMO crops with insecticidal properties would have a negative, albeit sub-lethal, effect on bees (Malone and Pham-Delègue, 2001) have not been verified (Marvier et al., 2007; Duan et al., 2008). For example, worker bees and colonies fed pollen from genetically modified Bt corn did not have increased rates of mortality (Rose et al., 2007). Further, pollen from Bt corn did not affect the microflora in bee intestines (Babendreier et al., 2007) nor did it affect hypopharyngeal gland development (Malone et al., 2004). The Cry1Ab toxin expressed in Bt corn did not affect learning performance of the honey bee under natural conditions suggesting that consumption of Bt corn pollen expressing Cry1Ab is unlikely to have an effect on colony performance (Ramirez-Romero et al., 2008).

3.4. Genetic variability of honey bee colonies

The evolution of beekeeping as a cultural practice and as a profession (Crane, 1999) has resulted in the development and use of techniques that may ultimately reduce the vitality of honey bee colonies. Selective pressures on the bee population are routinely being influenced by management decisions like the regular use of medication to control parasites and diseases, the protection of hives against cold weather, and artificial feeding. Consequently, weak and susceptible colonies are kept alive and given a chance to participate in the reproductive process. Colonies that were treated against diseases or parasites may be selected over non-treated colonies that have been forced to cope with the pathogens, thereby lowering the natural resistance against diseases and other environmental selection factors in the honey bee population.

In addition, beekeeping has also favored the distribution of the preferred commercial subspecies outside of their native range, usually to the disadvantage of less productive subspecies or species of honey bees. Thus, genetic diversity can be lost rapidly as native populations are threatened by newly introduced parasites or replaced by imported stock. Large parts of the original *A. m. mellifera* areas in Western Europe are today occupied by introduced stock with more desirable apicultural traits.

As a consequence of professional beekeeping, specialists in queen breeding produce and distribute large numbers of progeny from few queen mothers, a process which inevitably reduces genetic variability in honey bee populations. To increase genetic diversity, several European countries, especially those with a tradition in the production of the commercially most desirable races (*A. m. ligustica* and *A. m. carnica*), have coordinated national breeding schemes. From these programs, thousands of queens are produced and exported across Europe and the world (Lodesani and Costa, 2003). In the US, honey bees are not native and were first imported in the 17th century (Sheppard, 1989a,b). Thus, the genetic variability of the US honey bee population is reduced compared to that of indigenous honey bee populations of Europe (Sheppard, 1988). In addition, it has been reported that as few as 500 breeder queens have been used to provide progeny for most of the commercial hives present in the US (Schiff and Sheppard, 1995, 1996; Delaney et al., 2009). Breeding, thus, can act as a bottleneck, significantly reducing genetic variability in honey bee populations. Genetic similarity among colonies in wide areas increases the chances of successful disease transmission, and therefore the risk of colony losses.

Sufficient genetic variability within the colony is also known to be important for disease resistance, homeostasis, thermoregulation and overall colony fitness (Tarpy, 2003; Jones et al., 2004; Graham et al., 2006; Mattila and Seeley, 2007). If genetic variability is important for immune response and defense against parasites, colonies with diminished genetic variability are left with a reduced capacity to ward off stressors.

3.5. Poor queens

Anecdotal reports of increased rates of queen failure, supersedure, and drone laying have persisted in the US since in the mid-1990s (Camazine et al., 1998). Over 4 years of monitoring, the Pennsylvania apiary inspection program found that, on average, 2.36% of all inspected colonies were queenless (PDA, unpublished data). US beekeepers ranked poor queens as the number one cause of winter mortality (vanEngelsdorp et al., 2008). The reason for poor queen quality is not understood, and could be related to several factors. *N. apis* and possibly other infections of queens may be responsible for increased rates of supersedure (Camazine et al., 1998; Loskotova et al., 1980). Rates of queen failure may be related to environmental factors such as placement under high power electrical lines (Greenberg et al., 1981). Colonies headed by queens that are being superseded are less productive, and there is a significant risk that supersedure will fail, leading to queenlessness (Camazine et al., 1998). Poor queens may also be the result of the presence of pesticides in wax comb. The use of synthetic miticides to control varroa mite populations is common in the US, and these lipophilic products can build up in the wax over time (Bogdanov, 2006). Coumaphos, a product almost universally found in wax from the brood nest (Frazier et al., 2008), is known to have a detrimental effect on queen rearing (Pettis et al., 2004). Thus, it is possible that colonies with high coumaphos loads in their wax are having difficulty replacing failing queens.

3.6. Bee forage

The availability of adequate bee pasture has impacts on both beekeeping profitability and bee health. The need for adequate forage was recognized early on by US beekeepers and motivated early migratory beekeeping (Anonymous, 1792). The amount and quality of bee pasture in the US has been declining consistently for over the last half a century, largely on account of changing agricultural practices. For example, the use of fertilizers has allowed for a reduction in the rotation of legumes into cropping systems and the extensive use of herbicides has reduced weeds both within crops and at crop edges (Bohan et al., 2005). In addition, reduced pasturing of cattle and the harvesting of alfalfa before bloom to maximize protein content, have all played a role in the reduction of available bee forage. The result has been a near stagnant colony productivity between 1945 and 1981 (19.4 and 20 kg/colony per year) (Ayers and Harman, 1992; Bohan et al., 2005).

Increased colony losses suffered by individual states between 1992 and 2003 have been linked with decreased ratios of open land to developed land. States with greater amounts of open space tended to have more productive colonies, presumably because they had more available forage (Naug, in press). Decreased productivity can have a dramatic effect on total colony numbers in several ways. Productive colonies are less likely to starve over the winter, and starvation has been identified as the second most important cause of winter mortality in the US (vanEngelsdorp et al., 2008). Malnourished colonies are more susceptible to disease outbreaks (Gilliam, 1986) and are less able to tolerate pesticide exposure (Wahl and Ulm, 1983). Finally, and perhaps most importantly, less productive colonies translate into decreased profitability for beekeepers. The near exponential increase in colony productivity that occurred in Canada between 1945 and 1982 has been linked to the increased acreages of superior nectar crops like canola, making beekeeping more profitable, which in turn played a role in the 70% increase in colony numbers during that period (Ayers and Harman, 1992).

Changing agricultural practices as well as increased urbanization and suburban sprawl have also decreased available apiary sites. The consequence of reduced apiary locations on total colony numbers is difficult to ascertain but is almost certainly detrimental. Reduction in apiary locations is of particular concern in areas where Africanized "killer" bees have become or are becoming established. Florida has recently been colonized with feral populations of Africanized honey bees. As a result, some private and public land owners, fearing litigation, have requested that colonies be removed from long-established apiary sites (Jerry Hayes, personal communication). Public concern over "killer" bees has also motivated the passage of local ordinances that forbid or restrict beekeeping – a practice that is counterproductive as the presence of managed European bees is thought to slow the establishment of Africanized bees (Jerry Hayes, personal communication). It should be noted that there is no evidence that Africanized honey bees have directly caused honey bee declines since their introduction into the United States in 1990 (NRC, 2006).

3.7. Weather and climate

Weather has a very real effect on colony welfare. Extended periods of cold, rainy, and hot weather have been blamed on severe, oft unexplained, colony mortality in the past (Anonymous, 1869; Kauffeld et al., 1976). Beekeepers identified severe winter weather as the fourth most important contributor to winter mortality in the US (vanEngelsdorp et al., 2008). Weather can have a direct effect on colony productivity. For example, higher ambient temperatures tend to increase colony productivity because of reduced metabolic demands on foragers (Harrison and Fewell, 2002), while long periods of rain and cool weather have a detrimental effect on productivity as bees remain in the hive.

Arguably, the more significant effects of weather on colony productivity, both positive and negative, are indirect. High temperatures and sufficient precipitation are both correlated to increased nectar production (Shuel, 1992), which in turn translates to increased colony productivity (Voorhies et al., 1933). Conversely, insufficient rain or rain at inopportune times can have a negative effect on colony productivity. Both prolonged summer drought and persistent fall rains have been blamed on poor overwintering in the northeastern US as they prevent fall plants, such as goldenrod and aster, from producing their usual amounts of pollen and nectar. Dwindling pollen reserves in the fall result in early cessation of brood rearing that triggers the premature development of long-lived winter bees (Mattila and Otis, 2007). Colonies containing winter bees that were reared early because of pollen scarcity are less likely to survive the winter than those colonies that rear winter bees later in the fall.

Weather can also have an effect on pathogen loads within colonies. For example, temperature and humidity have a direct effect on varroa mite population growth (Harris et al., 2003). Conversely, cool weather, especially when a colony's adult population is small (which is common in the spring), can result in chilled brood. While chilling can kill immature bees outright, brood chilling is required for some pathogens, such as chalkbrood, *Ascosphaera apis*, to become established (Bailey and Ball, 1991), and adult bees that were chilled when immature are more susceptible to *A. woodi* infestation (McMullan and Brown, 2005).

In tropical regions, where floral resources are available year round, brood rearing also occurs year round. As a consequence, populations of parasites that reproduce on immature bees, like the varroa mite, grow much more quickly than they would if brood rearing was interrupted (Calis et al., 1999).

3.8. Socio-political factors affecting managed colony populations

3.8.1. Trade

Over the last several decades the world has seen increased international trade. International trade agreements that facilitate trade liberalization provide ways for nations to prevent the import of bees or bee products if such imports pose a risk to domestic bee stocks (Matheson, 1995a). Risk assessments must be justified by sound technical evidence, such as the presence of a disease or parasite in the exporting country that is not present in the importing country. The recent relaxing of bans on importation of live bees from Australia to the US no doubt has helped offset some of the declines in bee populations over the last several years (Sumner and Boriss, 2006). Importation from Australia was facilitated by the fact that Australia harbored no bee pathogens or parasites not already established in the US. However, such risk assessments, as dictated by international law, do not account for possible introduction of different pathogen strains (Palacios et al., 2008) or parasite haplotypes (Solignac et al., 2005), and so, do not protect against the introduction of potentially more virulent varieties of established disease or parasites. By far the largest threat to the beekeeping industry, however, is the illegal importation of queens or bees. Bee smuggling is thought to be a major vehicle for the spread of bee diseases and parasites (Matheson, 1995b).

While liberalized trade can have both positive and negative impacts on managed populations, trade restrictions can also have an effect. The detection of *A. woodi* in Europe and its early linkage to the Isle of Wight disease resulted in the US federal government passing the Honeybee Act of 1922. This law initiated a long period of restricted bee imports into the US from all but a few countries. Considering that the law prevented the arrival of *A. woodi* for over 66 years, its passage seemed warranted, although the cost to beekeepers is unknown (Mussen, 2001). The closure of the Canadian border to US imports had a more measurable effect. In 1987, the detection of *A. woodi* in California queen breeder operations coincided with the first detections of varroa mites in the US, and exports of bees into Canada were banned (Mussen, 2001). California breeders supplied 250,000 packages of bees to Canadian provinces each year before the ban. The closure of the Canadian border therefore, explains both the dramatic decrease in colony sales recorded by the AG census (1987 sales ~600,000 colonies vs. 2002 sales ~76,000 colonies) (Daberkow et al., 2009) and the 22% drop in colonies managed in California (compared to a national drop of 16%) over the subsequent decade (USDA-NASS, 1995, 1999).

Increased world trade in non-bee products can also inadvertently introduce new bee pests and diseases. For example, the small hive beetle, *Aethina tumida*, was thought to have been imported to the US in a shipment of citrus from South Africa (Hood, 2000; Le Conte, 2008). Not all introduced "pests", however, are detrimental to beekeeping. At least 66 different plants or genera of plants that have been introduced into the US and Canada provide bee forage (Ayers and Harman, 1992). Some, like purple loosestrife (*Lythrum salicaria*) and Japanese knotweed (*Fallopia japonica*), are the principle honey source in some regions, and beekeepers often resist efforts to control these "noxious weeds".

3.8.2. Economics

The profitability of beekeeping operations likely has a major influence on managed colony populations (Sumner and Boriss, 2006). Colony declines in the US prior to mite introduction have been linked to stagnant honey production figures (honey produced per colony per year), while increased colony productivity (and, presumably, profitability) over the same period has been used to explain increasing numbers of managed colonies in Canada (Ayers and Harman, 1992). Annual records of the price of honey (Fig. 6) and colony numbers in the US (Fig. 3) provide data needed to crudely examine what, if any, effect the price of honey has on national colony numbers. The price (adjusted to 2008 US$) of honey in a given year and the percent change in national colony numbers between years are related ($F = 27.81$, df = 1, 58, $P < 0.0001$; Fig. 7). The resulting regression suggests that only when the price of honey exceeds US$ 1.45 per lb (2008 adjusted) do colony numbers increase nationally. This threshold has only been surpassed 16 times in the last 66 years (Fig. 6). Increased demand for honey, and thus, increased price during the First World War is cited as the underlying reason for the increase in the number of managed colonies during that period (Phillips, 1928).

In the US, beekeepers have derived income not only from hive products, but also from renting colonies for pollination. This practice is not new and dates back to the early 1900s (Voorhies et al., 1933). Colony rentals have become an important source of income for many beekeepers, especially to meet the demand created by the increasing number of almond bearing acres in California. Almond bearing acres have increased dramatically over the last decade, with some projections estimating that as many as 2 million colonies (some 86% of current US bee stock) will be needed by 2012 to meet demand (Sumner and Boriss, 2006). These estimates, however, do not take into account the current drought facing California, and the resulting water restriction that forced many almond producers to plow under mature groves in early 2009. The effect this drought will have on pollination demand remains to be determined. Nonetheless, the high price paid for colonies in California certainly has been an incentive for some operations to increase in size and, as previously discussed, may help to account for the increase in colony numbers recorded by the 2007 Ag Census.

Almonds, however, are not the only crop requiring pollination. East and west coast berry, stone, and pit fruits, and cucurbits all require pollination services. It is not uncommon for a beekeeper to travel 37,000–40,000 miles per year to pollinate four or more different crops (Rucker et al., 2001). The price received for rental of colonies varies by crop, with those crops that produce honey (e.g. apples) generally commanding a lower price than crops that do not produce honey (e.g. pumpkins) (NRC, 2006). Rental prices also tend to increase as honey prices increase (Rucker et al., 2001).

In Europe, a dramatic decline in the number of hives was observed during the early 1990s. It is safe to assume that this decline resulted from the political and economic disruption caused by the Soviet collapse, rather than from widespread ecological factors, because it largely disappeared when data for Soviet Bloc countries were excluded from statistical analysis (Aizen et al., 2009). The economic situation of beekeepers drastically changed with the

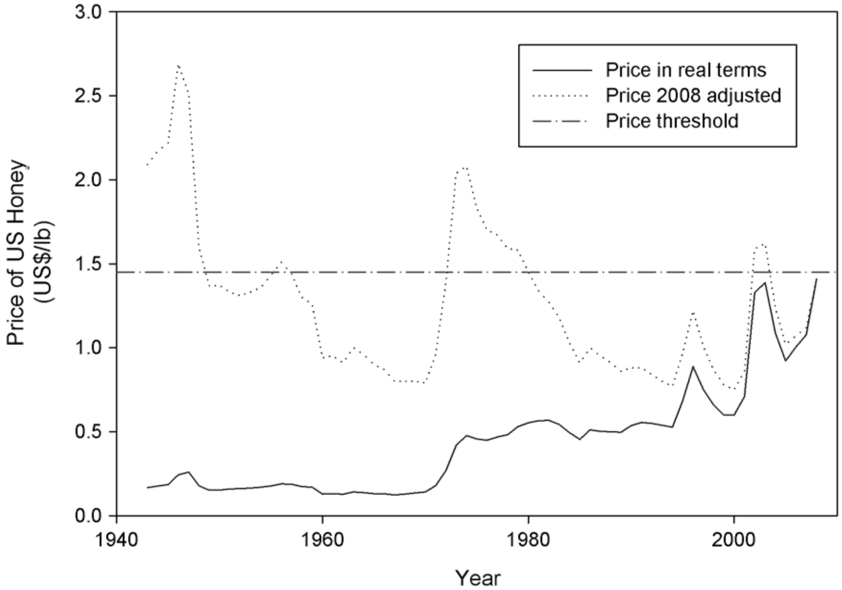

Fig. 6. Average price of honey ($/lb) in the US (Rodenberg, 1992), Prices are presented in actual (solid blue line) and dollars adjusted for inflation presented in US$2008 (dotted blue line) (Williamson, 2008). The horizontal red dashed line represents the theoretical threshold price: when prices exceed this threshold, colony numbers begin to increase in the United States (see text for details). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

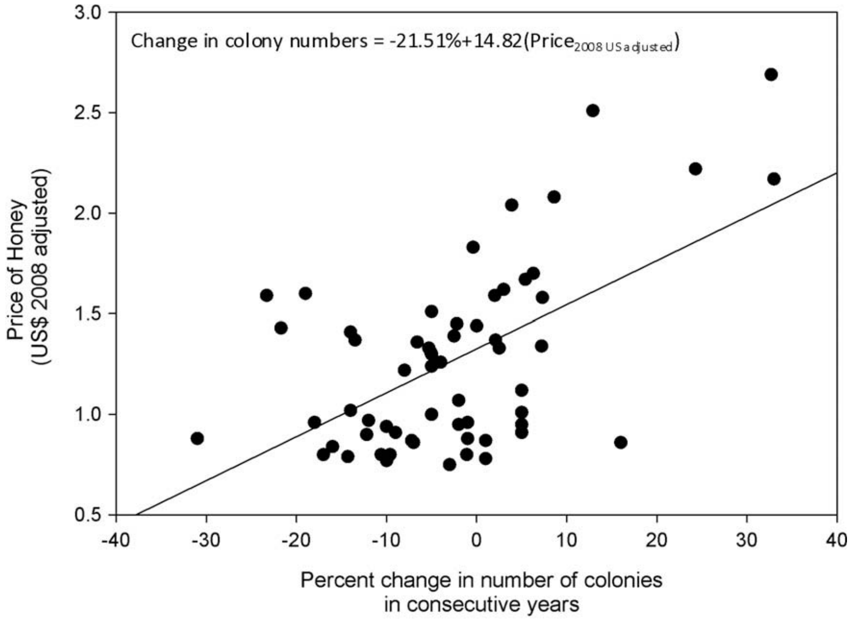

Fig. 7. The percent change in colony numbers in the US as compared to the average retail price of honey (in 2008 adjusted dollars/lb). A significant relationship occurs between the factors, with increases in colony numbers seen when the price of honey exceeds $1.43/lb (see text for details).

dissolution of the Soviet Union. Honey served as a second currency in many countries of the Soviet Bloc and, thus, many people were motivated to keep bees. Due to the political and economic upheaval in eastern Europe in the early 1990s, honey lost its relevance in those countries and the number of bee hives for instance in the former German Democratic Republic dropped by approximately 75% within a year's time (data from the German Bee Keeping Association), underlining the importance of economic factors in bee keeping.

4. Summary

Managed honey bees remain a critical resource for world agricultural and food security. While global honey bee populations have increased over the last 5 decades, this increase has not been universal. Notably, Europe and North America have suffered steep declines in managed populations. However, within these regions some nations have seen increases while others have seen decreases. Disease factors, such as the bacterial diseases AFB and EFB, have likely played an important role in honey bee colony declines in the US over a century ago; however, their role in current overall declines is likely minimal. Varroa mites, together with the virus complex associated with mite parasitism, are likely one of the major causes for considerable overwintering losses documented by many northern nations over the last several years. However, overwintering losses do not have a direct or measurable effect on total managed colony numbers as enumerated by national surveys in the US, likely because beekeepers are able to replace losses quickly. Pesticides, specifically those that directly affect colony health, had a pronounced effect on colony populations in the US. However, modern pesticides with reduced acute toxicity may have sub-lethal effects that are more difficult to quantify. Additional factors, such as reduced bee forage, climate, narrowing of the gene pool, poor queens, and socio-economic factors all have measurable effects on managed honey bee populations. Many of these factors influence the profitability of beekeeping which may have the most dramatic effect on managed populations of honey bees.

Conflicts of interest

There are no conflicts of interest to be declared.

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