

Review

Pathogens, Pests, and Economics: Drivers of Honey Bee Colony Declines and Losses

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Abstract: The Western honey bee (*Apis mellifera*) is responsible for ecosystem services (pollination) worth US\$215 billion annually worldwide and the number of managed colonies has increased 45% since 1961. However, in Europe and the U.S., two distinct phenomena; long-term declines in colony numbers and increasing annual colony losses, have led to significant interest in their causes and environmental implications. The most important drivers of a long-term decline in colony numbers appear to be socioeconomic and political pressure on honey production. In contrast, annual colony losses seem to be driven mainly by the spread of introduced pathogens and pests, and management problems due to a long-term intensification of production and the transition from large numbers of small apiaries to fewer, larger operations. We conclude that, while other causal hypotheses have received substantial interest, the role of pests, pathogens, and management issues requires increased attention.

Keywords: honey bee, colony loss, *Varroa*, management, pollinator

SUMMARY

There has been significant concern over managed honey bee colony declines and losses given their role as crop pollinators and concurrent concern regarding perceived global pollinator declines. Political and socioeconomic factors have contributed to colony declines in Europe and the U.S. over the past half-century. Yet the overall global number of colonies has increased 45% since 1961. Although many environmental and anthropogenic factors remain under investigation for their role in annual honey bee colony losses, the introduction of pests and pathogens, and large-scale shifts in management practices may be

significant, under-researched drivers of colony losses in Europe and North America.

INTRODUCTION

There has been significant concern over managed honey bee colony declines and losses, coupled with a growing interest in the long-term fate of global pollinator populations. The Western or European honey bee (*Apis mellifera*) is a semi-free-ranging managed agricultural species (i.e., managed wildlife species) that pollinates US\$215 billion worth of crops worldwide (vanEngelsdorp et al. 2008; Gallai et al. 2009). While the number of colonies has increased 45% globally since 1961, the proportion of pollinator-dependent crops has risen by 300% (Aizen and Harder 2009). To perform the

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ecosystem service of pollinating agricultural crops honey bees are now managed intensively (particularly in the U.S.) as mobile pollinators, with millions moved annually by truck across the country (Sumner and Boriss 2006).

However, in recent decades both long-term (multi-year) declines and annual losses in honey bee colonies have occurred throughout Europe and the U.S. In this paper, we review the literature on patterns of bee declines and losses, their hypothesized causes, and the environmental, socioeconomic, and agricultural changes likely involved.

Long-Term Colony Declines

Long-term declines in honey bee colony numbers (i.e., the steady decrease in the overall number of colonies over time) in Europe and the U.S. appear to be associated with political and socioeconomic factors. They have involved more than a 25% decrease of European colonies since the mid-1980s and nearly a 60% decrease in the U.S. (Fig. 1) (Potts et al. 2010a). The collapse of the U.S.S.R. in the 1990s reduced governmental financing of beekeeping in former Soviet countries of eastern Europe, causing a 50% reduction in managed colony numbers there (Aizen and Harder 2009). In western Europe, higher production costs,

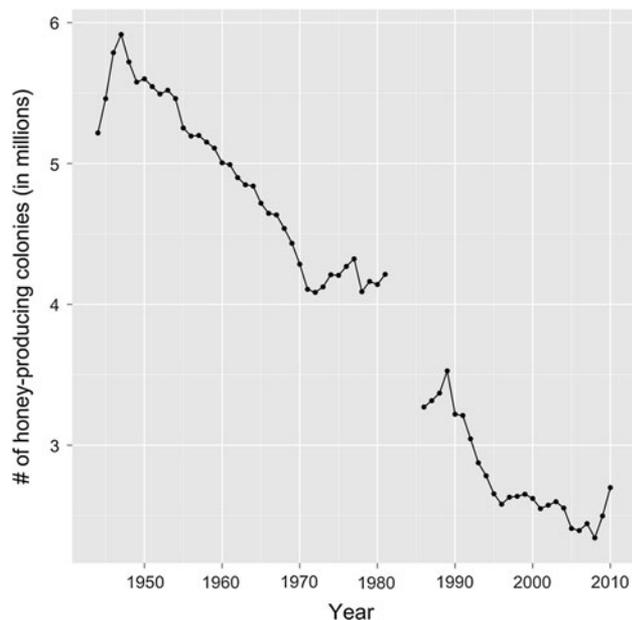


Fig. 1. Long-term declines in the number of honey-producing honey bee colonies (from 5.9 million in 1944 to 2.3 million in 2008), as reported by the USDA National Agricultural Statistical Service (NASS), and adapted from Potts et al. (2010a). Colony numbers reflect the highest year-to-year increases since 1944 between 2008 and 2010.

competition from cheaper imported honey, and increased affordability of sugar-based products have led to a 30% decrease in beekeepers and a 25% decrease in colony numbers since 1985 (Aizen and Harder 2009; Potts et al. 2010a). Honey demand and prices had already fallen in the U.S. at the end of WWII, making beekeeping less profitable. Declines were compounded by rapid expansion of honey importation from China, Argentina, and Vietnam during the 1960s leading to reduced demand for domestic honey (Daberkow et al. 2009; vanEngelsdorp and Meixner 2010). Other factors include suspension of federal support of honey prices in the U.S. in 1996 and the cessation of exports from the U.S. to Canada in 1987 which led to a loss of 250,000 colonies a year in California alone (vanEngelsdorp and Meixner 2010).

Additionally, long-term declines in the U.S. may be artificially heightened by the counting methods used by the USDA National Agricultural Statistics Service (NASS). A widely cited reduction by one million colonies during the 1980s (Fig. 1) coincides with NASS discontinuing the inclusion of colonies from operations with five or fewer hives (vanEngelsdorp and Meixner 2010). Thus, key political and socioeconomic factors including the process of data collection have played a primary role in the steady decline in honey bee colony numbers in Europe and the U.S.

Annual Colony Losses

In contrast to long-term colony declines, annual colony losses are designated as colonies that fail each year and (most frequently reported during the overwintering period) are often replenished by beekeepers “splitting” colonies. As colony losses are only officially counted once per year, they frequently do not include colonies lost during other seasons. This paucity of data on non-overwintering losses leads to a significant bias in the assessment of honey bee health. In the U.S. annual colony losses doubled from the average expected 15 to 30% in 2006–2007 and have remained elevated (vanEngelsdorp et al. 2007). A series of sudden and severe annual losses without evidence of dead bees or hive invaders, but the retention of brood and a queen, was reported with these elevated losses in 2006 and termed “colony collapse disorder” (CCD) (vanEngelsdorp et al. 2009b). The causes and significance of CCD remain unclear (Fig. 2). However, the number of U.S. operations reporting CCD declined in recent annual surveys (vanEngelsdorp et al. 2008, 2011), with no reports in neighboring Canada despite annual losses at a similar scale to the U.S.

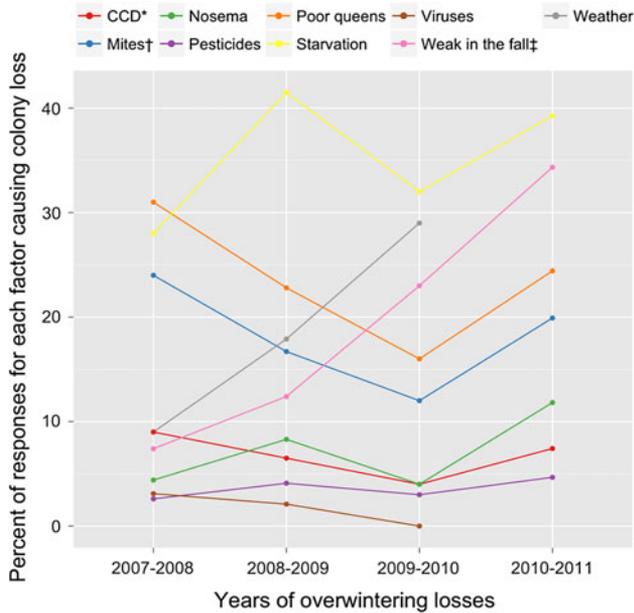


Fig. 2. The causes of U.S. honey bee overwintering losses from 2007 to 2011, self-reported by beekeepers through surveys conducted by the USDA, the Apiary Inspectors of America and online surveys through beekeeper associations, summarized by vanEngelsdorp et al. Respondents had the option to report multiple causes for colony loss each year; each cause is reported as percent of total responses given. *Double dagger* includes colonies reported to have been weak in the fall and usual overwintering losses. *Dagger* Primarily *V. destructor*; however, in some years reported as “invertebrate pests” including tracheal mites (*Acarapis woodi*) and the small hive beetle (*Aethina tumida*). *Asterisks* defined only by the loss of a colony with the absence of dead bees—and thus true cases of CCD are likely to be overestimated in all years.

since 2006 (Currie et al. 2010). CCD was reported by beekeepers as the eighth most important contributor to colony losses in 2009 (vanEngelsdorp et al. 2010; Williams et al. 2010). In 2010 and 2011, only 4 and 7% of beekeepers, respectively, listed CCD as a cause for their losses (vanEngelsdorp et al. 2011, 2012). Regardless of prevalence, some authors have questioned the validity of CCD as a clearly defined syndrome, especially when CCD is defined solely by colony loss with the absence of dead bees (the primary clinical sign investigated in the national beekeeper surveys) rather than the full accepted definition (vanEngelsdorp et al. 2007, 2008, 2010, 2011). However, in many cases adequate disease and health monitoring of an individual colony prior to its decline is absent. Many European countries have also reported elevated annual losses in recent years but similarly the lack of data standardization and the capacity of beekeepers to replenish colonies masks trends (Potts et al. 2010b; van der Zee et al. 2012).

HYPOTHESIZED CAUSES OF ANNUAL COLONY LOSSES

Pathogens and Pests

Pathogens and pests are known to cause annual colony losses and have been linked, hypothetically, to long-term declines in bee populations. Prior to the 1970s, diseases of bee larvae (brood diseases) were the most economically important threats, e.g., American Foulbrood (*Paenibacillus larvae*). These continue to cause significant losses and have global ranges (vanEngelsdorp and Meixner 2010). However in the 1970s and 1980s the parasitic mite *Varroa destructor* was introduced to honey bees in Europe and in North America respectively (Rosenkranz et al. 2010). This is now a pan-global pest with the exception of Australia, several isolated islands, and possibly some Central African countries (Potts et al. 2010a). This pest is a key factor in recently elevated colony losses in Canada (Currie et al. 2010; Guzman-Novoa et al. 2010) and much of Europe (Aston 2010; Chauzat et al. 2010; Gajger et al. 2010; Le Conte et al. 2010; Mutinelli et al. 2010; Neumann and Carreck 2010; Vejsnaes et al. 2010; Potts et al. 2010b), whereas regions in which *V. destructor* is not a significant problem have not experienced similar losses (Neumann and Carreck 2010).

The *V. destructor* mite transmits pathogenic viruses (Gisder et al. 2009) including deformed wing virus (DWV), which results in overt infection significantly correlated with colony loss (Genersch et al. 2010). Three other viruses, acute bee paralysis virus, Israeli acute paralysis virus, and Kashmir bee virus, also increase in virulence when transmitted by *V. destructor* and all are recognized as causes of colony loss in regions affected by the mite (Ribiere 2008; Highfield et al. 2009; Genersch and Aubert 2010). However, lack of standardized surveillance by beekeepers, inconsistency among studies, and the complexity of transmission dynamics hampers an assessment of their true significance. For example most studies report viral presence or absence, but do not collect sufficient clinical data over time to assess the relative contribution of a virus in a given colony loss event. Interactions between viruses, honey bee immunology, and strain variation may play a role in how an individual or colony responds to viral infection. Recent analysis of the emergence of *V. destructor* in the Hawaiian archipelago suggests that introduction of the mite leads to increased prevalence and intensity of infection by DWV, and the dominance of a single virulent strain (Martin et al. 2012). The rise of this virulent strain in Hawaii lagged the

introduction of the mite and may explain the lag in honey bee losses relative to the introduction of the vector elsewhere. This strongly suggests that the consequences of both *Varroa* introduction and the viruses it harbors are significant for global honey bee losses.

The microsporidian *Nosema apis* is the cause of bee dysentery. A close relative, *N. ceranae* from the Asian honey bee, has recently emerged in *A. mellifera* and may have replaced *N. apis* throughout much of its range (Klee et al. 2007, Chen et al. 2008). *N. ceranae* has been cited as the cause of significant colony losses in Spain (Higes et al. 2007, 2008), though such virulence has not been demonstrated elsewhere (Gisder et al. 2010). Further research is needed to understand the role of *N. ceranae* in honey bee losses and any possible additive or synergistic effects it may have with other stressors.

The recent, pan-global emergence of honey bee diseases correlates with broad trends in disease emergence (Daszak et al. 2000). These include a growing number of diseases spread by globalized trade and travel—a process termed “Pathogen Pollution” (Cunningham et al. 2003). The anthropogenic introduction of exotic pathogens and pests is the most common cause of disease emergence in crop plants (Anderson et al. 2004), and is responsible for the emergence of a wide range of diseases affecting livestock (e.g., H5N1 avian influenza, Rift Valley fever—Kilpatrick et al. 2006a; Al-Afaeq and Hussein 2011) and humans (e.g., West Nile virus—Kilpatrick et al. 2006a, b; Al-Afaeq and Hussein 2011). Honey bee pathogens have emerged and spread through trade in bees, bee products, and equipment [e.g., the introduction of tracheal mite (*Acarapis woodi*) and *V. destructor* to the Americas (Mutinelli 2011), and the spread of *V. destructor* and *N. ceranae* from the Asian honey bee (*A. ceranae*) to *A. mellifera*]. Recently, the World Organisation for Animal Health (or Office Internationale des Epizooties) has made a number of bee pathogens notifiable under regulations approved by country signatories of the World Trade Organization (Mutinelli 2011). This enables restriction of trade in bees and bee products from countries that have identified these pathogens in their bee populations.

Agrochemical Drivers

It has been hypothesized that the application of pesticides, in particular neonicotinoid insecticides, plays a significant role in honey bee colony losses. Neonicotinoids are extensively applied to some crops commercially pollinated by honey bees (Johnson et al. 2010). Neonicotinoids are

systemic insecticides that can be applied to seeds and absorbed into the growing plant tissue, making them highly effective, but allowing residues to be present in pollen and nectar (Thompson 2010; Creswell 2011). The application of pesticides directly to seed has environmental advantages over widespread spray treatments such as reduced run-off, less frequent non-target species toxicity (Thompson 2010), and reduction of pesticide use per hectare. Acute honey bee mortality events caused by the accidental drift of dust or spray from pesticide applications have occurred (Krupke et al. 2012). While drift reducing technologies have helped reduce the risk (Thompson 2010), a recent study revealed colony losses may still occur due to pesticide drift (Tapparo et al. 2012).

Exposure to pesticides may also result in sublethal effects on the health of individual honey bees that could lead to reduced survival. Recent studies suggest that low-level pesticide exposure can impair immune system functioning, learning ability, memory, foraging behavior, and odor discrimination in honey bees (Desneux et al. 2007; Yang et al. 2008; Alaux et al. 2010; Williamson and Wright 2013). Further, chronic exposure to pesticides that would otherwise have no harmful effects for healthy colonies may interact with pathogens to produce harmful consequences for colonies already vulnerable to disease (Thompson 2003; Vidau et al. 2011; Aufauvre et al. 2012). One study suggested that individual honey bee vulnerability to *Nosema* infection is enhanced by the presence of the neonicotinoid imidacloprid, but the parent colonies failed to show increased *Nosema* levels due to exposure in this study (Pettis et al. 2012).

Simulated exposure events on free-ranging foragers showed that exposure of honey bees to the neonicotinoid thiamethoxam at low levels caused mortality, perhaps due to homing failure, and that this may contribute to colony loss (Henry et al. 2012). However, the bioavailability of the active ingredient in the treated bees was not measured in this study, and is a critical issue to investigate in general. Studies have detected low levels of neonicotinoids (1–10 $\mu\text{g kg}^{-1}$) in the pollen and nectar of treated plants throughout the blooming period (Creswell 2011) and some scientists argue that bees likely ingest nectar repeatedly through several flower visits, thus increasing their exposure (Yang et al. 2008; Creswell 2011). Other research has shown that chronic exposure to the neonicotinoid imidacloprid at similar sublethal doses has negligible effects at the colony level (Nguyen et al. 2009). Field exposure of bees to flowering canola (*Brassica napus*) grown from seed treated with the neonicotinoid clothianidin

had negligible impact on acute mortality, longevity, brood development, and over-winter survival (Cutler and Scott-Dupree 2007). However, control and treatment fields in that study were in close proximity (295 m), with a small radius (1 km) surrounding the test areas for which alternative foraging options were controlled. Elevated levels of the crop fungicide chlorothalonil have been reported in entombed pollen (pollen presumably sealed off within the hive as a protective measure) (vanEngelsdorp et al. 2009a), and the presence of entombed pollen has been associated with increased colony mortality. However, larvae and adult bees that were fed diets supplemented with entombed pollen did not experience increased mortality (vanEngelsdorp et al. 2009a). Similarly, a laboratory study (Girolami et al. 2009) found extremely high concentrations of neonicotinoids in the guttation drops of corn plants and demonstrated that when bees consumed this fluid, death occurred within a few minutes. The guttation drops were supplemented with a sugar solution to stimulate consumption and there is continued debate as to whether honeybees use guttation fluid as a source of water in relevant crop species. Other studies did not find detrimental effects when conducting similar research with sugar beets, and when alternative drinking sources were available as might occur in nature (Keppler et al. 2010; OPERA 2011). While several recent studies have used models to suggest colony level effects (Henry et al. 2012; Whitehorn et al. 2012), a confirmed causal relationship between environmental pesticide residues and CCD or significant colony loss has yet to be demonstrated (Johnson et al. 2010). The most difficult challenge facing experimental researchers lies in deducing whether sublethal effects on individuals play a role in colony loss under real field conditions.

Beekeepers commonly use miticides to reduce the impact of varroasis. Miticides are placed directly in the hive, and are lipophilic and accumulate in the wax, particularly in the comb where the brood develops (Johnson 2009). Exposure may be exacerbated by synergism, which occurs between low doses of the miticides coumaphos and tau-fluvalinate for example due to binding competition for P450, a class of enzymes important for detoxification (Johnson 2009). Some fungicides found in hives inhibit ergosterol biosynthesis and thus synergize the toxicity of pyrethroid insecticides to honey bees (Johnson 2009). Finally, bees exposed to the antibiotic oxytetracycline which is applied within the hive, were significantly more sensitive to coumaphos and tau-fluvalinate (Hawthorne and Dively 2011). Effects of additive exposure to cholinergic pesticides such as imidacloprid and coumaphos have also been found

(Palmer et al. 2013). Further, recent studies examining in-hive chemicals have detected a high diversity of miticides and agricultural pesticides in bee colonies (vanEngelsdorp et al. 2009b; Mullin et al. 2010). Although high levels of intoxicants were detected, no direct correlation between pesticides found in hives and colony loss was found (aside from higher levels of coumaphos in healthy colonies) (vanEngelsdorp et al. 2009b). Although recent studies are beginning to address how bees process these toxins by determining what factors affect the ability of honey bees to upregulate P450 detoxification genes in response to in-hive chemicals (Johnson et al. 2012), additional research into the potential additive and synergistic effects is still needed.

Other Causal Hypotheses

Some authors have proposed that multiple drivers act together, or secondarily to broader changes that may affect the ability of honey bees to resist declines, or that they directly cause immunosuppression. These broader changes include poor genetic diversity, weather events, stress, or inadequate nutrition (Potts et al. 2010a). There has been little research on whether long distance transportation of colonies causes stress, but it has not been linked to losses (vanEngelsdorp et al. 2007, 2008, 2010, 2011, 2012). Agricultural intensification, the increase of monoculture acreage, and loss of natural habitat may affect honey bee nutrition, and theoretically colony health; however, this has not been fully investigated (Brodschneider and Crailsheim 2010).

What is the Most Likely Causal Candidate for Annual Colony Losses?

As with any large-scale biological phenomenon, competing and often conflicting hypotheses are difficult to resolve. However, the evidence from the current state of the field suggests that some individual drivers appear to be more important in honey bee annual losses than others. For example, surveys of beekeepers and published reports suggest elevated colony losses in much of Europe and Canada are attributed to *V. destructor* and its associated pathogens, as well as known environmental and managerial challenges such as weather events and starvation (Aston 2010; Chauzat et al. 2010; Gajger et al. 2010; Le Conte et al. 2010; Mutinelli et al. 2010; Neumann and Carreck 2010; Vejsnaes et al. 2010; Potts et al. 2010b). Similarly, the majority of losses in the U.S. have been attributed to one or more known causes such as weather events, starvation, queen failure, and mites by

beekeepers in recent surveys (vanEngelsdorp et al. 2010, 2011, 2012). However, these reports do not take into consideration the presence or absence of rigorous health surveillance in these colonies prior to the loss.

The hypothesis that honey bees have become immunosuppressed, making them more susceptible to pathogens or pests, parallels similar arguments used for wildlife population declines that were later attributed to single causal factors, e.g., amphibian declines due to the emerging disease chytridiomycosis (Daszak et al. 2003). Caution needs to be applied to this hypothesis, particularly when so little is known of honey bee innate and social immunity. Honey bees have approximately one-third of the immunity genes of other insects, but as colonial insects they also rely on social immunity where colonial behavior protects the colony (Evans and Spivak 2010). Additionally, balanced nutrition including pollen and propolis has recently been demonstrated to induce detoxifying enzymes in individual honey bees (Mao et al. 2013). Therefore, studies that experimentally show an effect on immunity in individual honey bees cannot be readily extrapolated to an effect on the colony in the field.

Perhaps the most parsimonious hypothesis for the cause of annual losses is that the relatively recent introduction of *Varroa* mites, and the resultant expansion of the range, prevalence, or intensity of infection of viral strains they harbor, has had a dramatic impact on honey bees. Thus, rather than immunosuppression of honey bee immunity as the underlying condition, it may be the relative naivety of bee colonies to *Varroa* and viral strains causing their decline and susceptibility to other factors. This hypothesis is supported by recent findings that the increase in prevalence and dominance of virulent viral strains lags behind *Varroa* introduction and leads to a complex, but probably significant, relationship between pest introduction, pathogen emergence, and honey bee colony losses (Martin et al. 2012). In a similar scenario, arguments that disease-induced amphibian population declines were only possible due to immunosuppression by another driver have now been largely refuted. In this case, the international trade in amphibians has now been widely accepted as the primary driver of the emergence of this disease (Daszak et al. 2003; Fisher et al. 2012). This is consistent with the increasing importance of trade and travel in the emergence and spread of diseases in humans, livestock, and wildlife globally (Smolinski et al. 2003; Karesh et al. 2005; Fevre et al. 2006; Hosseini et al. 2010) and in other types of biological invasions (Levine and D'Antonio 2003).

CRITICAL RESEARCH AND POLICY GAPS

New Approaches to Investigating Causal Factors

Investigating the causes of long-term population declines and die-offs in wildlife or free-ranging domesticated species requires long-term data on all hypothesized causal drivers. In cases where multiple drivers may be involved, a framework to deduce the importance, or strength, of each driver is required. Similar problems abound in disease ecology, where pathogens responsible for population declines are affected by climate, land use change, trade, pollutants, and the interaction of a myriad of other drivers. In these cases, traditional hypothesis testing may be supplemented by modeling, risk analysis and strong inference methods that provide a measure of the relative role of each driver (Plo-wright et al. 2008). A macroecology approach (Gaston and Blackburn 2000; Blackburn and Gaston 2004) involving a broad view of ecological systems based on model selection could complement experimental studies on honey bee colony losses. For example, it would be possible to make statistical comparisons among different potential hypotheses at a broader scale (Fig. 3). Each hypothesis could be ranked and weighted giving a quantifiable measure of support. When similar levels of support for each hypothesis is found, model averaging can be used to make robust estimations and predictions (Burnham and Anderson 2002; Johnson and Omland 2004).

For honey bee colony losses, long-term datasets on bee colony dynamics, land use change, *Varroa destructor* prevalence, bee pathogen distribution and prevalence, pesticide exposure, and a range of other hypothesized causes are not uniformly available across the geographic range of reported losses. Furthermore, there are differences among regions in the manner data have been collected, and honey bee losses defined and reported. While specific tests of some hypotheses have been published, these are relatively few and are still insufficient to deduce cause. More importantly, there are a large number of hypothesized drivers that have not yet been studied at a scale relevant to understanding the ecology of bee losses.

Varroa destructor Research

Studies to deduce the role of *V. destructor* in colony losses would require information on the introduction of *Varroa* into new regions. At the individual apiary level, there are rarely adequate monitoring history and records available of *Varroa* levels in each colony over time prior to a loss event. Rather,

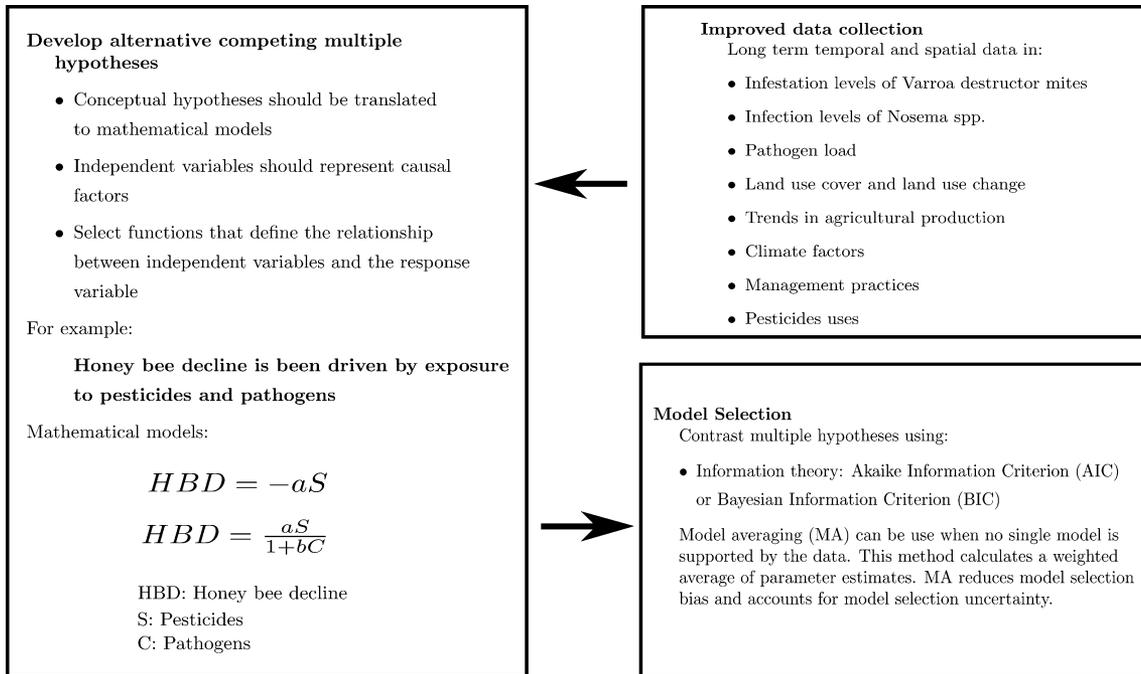


Fig. 3. A complementary analysis framework to study honey bee losses. This macroecological approach uses a top-down perspective and statistical methodologies (e.g., model selection) to contrast and to explain observed patterns at different temporal and spatial scales.

investigation into the role of *Varroa* in losses is usually attempted after the fact. Until more rigorous health monitoring techniques are implemented, mathematical modeling of the spread of *Varroa* at a regional level might provide insight, and models could be back-tested by using data on first reports of the pest from states, provinces, and counties following introduction. Metapopulation models which explicitly estimate the connectivity among colonies may provide a way to estimate the seasonal spread of pathogens, their ability to cause the extensive colony loss in some regions, and their likely patterns of persistence. Testing this hypothesis might be aided by the presence of regions where *Varroa* is absent (e.g., Victoria, British Columbia) and by studies that monitor the impact of the mite over a number of years on longitudinal experimental colonies.

Intensification of Honey Bee Production

The ratio of commercial beekeeper to (small-scale) hobbyist operations has increased in many countries due to the increasing demand for pollination services to commercial crops (Daberkow et al. 2009; Potts et al. 2010b) and rising competition from international honey markets (Le Conte and Navajas 2008). Given the current condition of the U.S. honey market, American beekeepers are less economically

rewarded to produce honey and provide their bees with a varied diet compared to providing pollination services. Bees devoted to pollination services are primarily exposed to monoculture nutritional sources (Le Conte and Navajas 2008; Champetier et al. 2010). Between 1987 and 2002 in the U.S., there was a 40% decline in beekeepers owning fewer than 25 colonies, and a 66% increase in colonies managed by commercial beekeepers (Daberkow et al. 2009). Thus, the intensification of bee production in the U.S. is similar to much earlier intensification of livestock production, e.g., the movement from backyard poultry production to commercial rearing in the early twentieth century. This process led to the emergence of agricultural pathogens historically (e.g., *Salmonella enteritidis*) and currently (e.g., influenza A/H5N1). However, there are important differences between honey bee management and intensively managed livestock. These include a paucity of regulations on veterinary care, disease testing and quarantine of traded animals, use of treatments, nutrition studies to develop dietary supplements, and health and welfare inspection. The manner in which health care, management plans, nutrition modification, and record-keeping are applied in beekeeping operations may need to adapt to the changing levels of intensification to avoid further declines in bee health and increased annual losses. Trained bee

health consultants (e.g., extension workers, state apiculturists, veterinarians) may help in this transition. These workers could assist beekeepers in adapting management schemes based on local environmental and disease threats, size of operation, and diagnostic and treatment needs.

Pesticides

There has been a great deal of work on the role of pesticides in bee colony loss leading to significant concern over their effects. Despite this concern and a recent European policy changes on the use of neonicotinoid pesticides, scientific studies examining the overall impact of neonicotinoid pesticides on managed honey bee colony loss are yet to demonstrate colony level losses in field settings and at field doses. Critical issues to be addressed are the lack of comparable losses in some regions where pesticides are used, uncertainty about appropriate field doses, and the methods used in experimental studies. Further research on sublethal and additive or synergistic effects of agricultural chemicals and their residues, using field-based colony level data, and application of spatial analysis methodologies to past and ongoing losses may help elucidate the role of pesticides in losses.

Longitudinal Epidemiological Monitoring and Disease Investigations

The lack of standardized reporting within and among countries makes it difficult to track patterns of colony loss on local or regional scales. Longitudinal epidemiological monitoring that includes long-term studies of patterns of colony loss, disease incidence and pathogen prevalence in single populations, with standardized sampling and data collection protocols would allow effective comparisons among different geographic areas experiencing losses. The COLOSS network (Prevention of Honeybee Colony Losses—<http://coloss.org/>), the German Honey Bee Monitoring Program (Genersch et al. 2010), the Bee Informed Project (www.beeinformed.org), and USDA's Managed Pollinator Coordinated Agricultural Project (CAP—www.beeccdcap.uga.edu), have begun efforts along these lines.

Environmental and Ecological Implications

The full range of environmental implications of honey bee colony declines and losses is unclear and some suggest that the role of the managed honey bee in pollinating native and even some crop plants is overestimated (Winfree et al.

2007; Ollerton et al. 2012; Garibaldi and Winfree 2013). Thus, it is difficult to assess how honey bee colony losses relate to global native pollinator declines. Honey bees are an introduced species in many parts of their range (e.g., North America), and they are extensively managed throughout. They do, however, have free contact with wild native pollinators, allowing pathogen exchange, resource competition, and exposure to similar environmental hazards. Yet stressors may or may not affect managed honey bees differently than native or non-managed species. Despite evidence of transmission, the impact of *Varroa* mites and viruses on native bees at the population level remains unclear. Similarly, pesticides have the potential to affect native pollinators (Potts et al. 2010a), particularly bumble bee (*Bombus terrestris*) foraging behavior and reproductive success (Gill et al. 2012; Laycock et al. 2012; Whitehorn et al. 2012) although bumble bee life cycle characteristics differ from that of the honey bee. Regardless of the true extent of native pollinator declines (Levine and D'Antonio 2003), it is uncertain if managed honey bee declines and losses are related to native or free-ranging pollinator declines. Regardless, past lessons learned from impacts of agricultural intensification on wildlife should be applied when investigating the potential health links between honey bees and native pollinators, while accounting for the unique nature of managing a semi-free-ranging species.

CONCLUSION

Causes of long-term declines of honey bees in the U.S. and Europe are most likely due to the loss of beekeepers to the industry and intense competition for bee products. More research is needed on honey bee annual losses, but the global spread of pathogens and pests through the trade in bees and bee products likely plays a key role. These losses compound two critical environmental problems: the role of anthropogenic movement and manipulation of wildlife and their habitat and the role of agricultural intensification on managed species. In many ways, the state of research on honey bee losses mirrors the situation of livestock production in the early twentieth century, with poor coordination of best management practices (including lack of adequate knowledge of health threats and treatments) and a low appreciation of the impact of rapid demographic change on a managed population.

For this issue, some lessons can be learned from amphibian population declines, which were first brought to

global attention in the late 1980s and considered enigmatic by their occurrence in presumed pristine locations (Blaustein and Wake 1990). Despite several initial hypotheses of driver interactions (Kiesecker and Blaustein 1995; Davidson et al. 2001; Pounds 2001), the identification of an emerging disease, chytridiomycosis (Berger et al. 1998) led to a marked shift in emphasis. The emergence of this disease, driven by the global trade in amphibians is now widely accepted as the major driver of enigmatic global amphibian population declines (Stuart et al. 2004; Mendelson et al. 2006; Fisher et al. 2012) and has led to the adoption of global policies to reduce its spread (Mendelson et al. 2006; Schloegel et al. 2010). Applying these lessons to the current state of honey bee health suggests that filling research gaps, particularly in management impacts and techniques, will complement additional studies on environmental factors such as nutrition, pesticides, pests, and pathogens to formulate comprehensive solutions to what may become an economically and environmentally costly phenomenon.

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REFERENCES

- Aizen MA, Harder LD (2009) The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Current Biology* 19:915–918
- Al-Afaleq AI, Hussein MF (2011) The status of Rift Valley fever in animals in Saudi Arabia: a mini review. *Vector-Borne and Zoonotic Diseases* 11(12):1513–1520
- Alaux C, Ducloz F, Crauser D, Le Conte Y (2010) Diet effects on honeybee immunocompetence. *Biology Letters* 6(4):562–565
- Anderson PK, Cunningham AA, Patel NG, Morales FJ, Epstein PR, Daszak P (2004) Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. *Trends in Ecology & Evolution* 19(10):535–544
- Aston D (2010) Honey bee winter loss survey for England, 2007–8. *Journal of Apicultural Research* 49:111–112
- Aufauvre J, Biron DG, Vidau C, Fontbonne R, Roudel M, Diogon M, Vignes B, Belzunces LP, Delbac F, Blot N (2012) Parasite–insecticide interactions: a case study of *Nosema ceranae* and fipronil synergy on honeybee. *Scientific Reports* 2:326
- Berger L, Speare R, Daszak P, Green DE, Cunningham AA, Goggin CL, Slocombe R, Ragan MA, Hyatt AD, McDonald KR, Hines HB, Lips KR, Marantelli G, Parkes H (1998) Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proceedings of the National Academy of Sciences of the United States of America* 95(15):9031–9036
- Blackburn, T. and K. Gaston (2004). “Special Feature: Macroecology.” *Basic and Applied Ecology* 385–387.
- Blaustein AR, Wake DB (1990) Declining amphibian populations: a global phenomenon. *Trends in Ecology & Evolution* 5:203–204
- Brodtschneider R, Crailsheim K (2010) Nutrition and health in honey bees. *Apidologie* 41:278–294
- Burnham KP, Anderson DR (2002) *Model selection and multi-model inference: a practical information-theoretic approach*, New York: Springer
- Champetier A, Sumner D, Wilen JE (2010) *The Bioeconomics of Honeybees and Pollination*.
- Chauzat MP, Martel AC, Zeggane S, Drajnudel P, Schurr F, Clement MC, Ribiere-Chabert M, Aubert M, Faucon JP (2010) A case control study and a survey on mortalities of honey bee colonies (*Apis mellifera*) in France during the winter of 2005–6. *Journal of Apicultural Research* 49(1):40–51
- Chen Y, Evans JD, Smith BI, Pettis JS (2008) *Nosema ceranae* is a long-present and wide-spread microsporidian infection of the European honey bee (*Apis mellifera*) in the United States. *Journal of Invertebrate Pathology* 97:186–188
- Creswell JE (2011) A meta-analysis of experiments testing the effects of a neonicotinoid insecticide (imidacloprid) on honey bees. *Ecotoxicology* 20:149–157
- Cunningham AA, Daszak P, Rodríguez JP (2003) Pathogen pollution: defining a parasitological threat to biodiversity conservation. *Journal of Parasitology* 89:S78–S83
- Currie RW, Pernal SF, Guzmán-Novoa E (2010) Honey bee colony losses in Canada. *Journal of Apicultural Research* 49:104–106
- Cutler GC, Scott-Dupree CD (2007) Exposure to clothianidin seed-treated canola has no long-term impact on honey bees. *Journal of Economic Entomology* 100:765–772
- Daberkow S, Korb P, Hoff F (2009) Structure of the US beekeeping industry: 1982–2002. *Journal of Economic Entomology* 102(3):868–886
- Daszak P, Cunningham AA, Hyatt AD (2000) Emerging infectious diseases of wildlife—threats to biodiversity and human health. *Science* 287:443–449
- Daszak P, Cunningham AA, Hyatt AD (2003) Infectious disease and amphibian population declines. *Diversity and Distributions* 9:141–150
- Davidson C, Shaffer HB, Jennings MR (2001) Declines of the California red-legged frog: climate, UV-B, habitat, and pesticides hypotheses. *Ecological Applications* 11(2):464–479
- Desneux N, Decourtye A, Delpuech JM (2007) The sublethal effects of pesticides on beneficial arthropods. *Annual Review of Entomology* 52:81–106
- Evans JD, Spivak M (2010) Socialized medicine: individual and communal disease barriers in honey bees. *Journal of Invertebrate Pathology* 103:S62–S72
- Fevre EM, Bronsvoort BMDC, Hamilton KA, Cleaveland S (2006) Animal movements and the spread of infectious diseases. *Trends in Microbiology* 14(3):125–131

- Fisher MC, Henk DA, Briggs CJ, Brownstein JS, Madoff LC, McCraw SL, Gurr SJ (2012) Emerging fungal threats to animal, plant and ecosystem health. *Nature* 484(7393):186–194
- Gajger IT, Tomljanovic Z, Petrincic Z (2010) Monitoring health status of Croatian honey bee colonies and possible reasons for winter losses. *Journal of Apicultural Research* 49:107–108
- Gallai N, Salles JM, Settele J, Vaissiere BE (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics* 68(3):810–821
- Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, KKremen C, Carvalheiro LG, Harder LD, Afik O, Bartomeus I, Benjamin F, Boreux V, Cariveau D, Chacoff NP, Dudenhöffer JH, Freitas BM, Ghazoul J, Greenleaf S, Hipólito J, Holzschuh A, Howlett B, Isaacs R, Javorek SK, Kremenka KM, Srishnan S, Mandelik Y, Mayfield MM, Motzke I, Munyuli T, Nault BA, Otieno M, Petersen J, Pisanty G, Potts SG, Rader R, Ricketts TH, Rundlöf M, Seymour CL, Schüepp C, Szentgyörgyi H, Taki H, Tscharrntke T, Vergara CH, Viana BF, Wanger TC, Westphal C, Williams N, and, Klein AM (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339(6127):1608–1611
- Gaston KJ, Blackburn TM (2000) *Pattern and Process in Macroecology*, Oxford: Wiley-Blackwell
- Genersch E, Aubert M (2010) Emerging and re-emerging viruses of the honey bee (*Apis mellifera* L.). *Veterinary Research* 41(6):54
- Genersch E, von der Ohe W, Kaatz H, Schroeder A, Otten C, Buchler R, Berg S, Ritter W, Muhlen W, Gisder S, Meixner M, Liebig G, Rosenkranz P (2010) The German bee monitoring project: a long term study to understand periodically high winter losses of honey bee colonies. *Apidologie* 41(3):332–352
- Gill RJ, Ramos-Rodriguez O, Raine NE (2012) Combined pesticide exposure severely impacts individual- and colony-level traits in bees. *Nature* 491:105–109
- Girolami V, Mazzon L, Squartini A, Mori N, Marzaro M, Di Bernardo A, Greatti M, Giorio C, Tapparo A (2009) Translocation of neonicotinoid insecticides from coated seeds to seedling guttation drops: a novel way of intoxication for bees. *Journal of Economic Entomology* 102(5):1808–1815
- Gisder S, Aumeier P, Genersch E (2009) Deformed wing virus: replication and viral load in mites (*Varroa destructor*). *Journal of General Virology* 90(2):463–467
- Gisder S, Hedtke K, Möckel N, Frielitz M-C, Linde A, Genersch E (2010) Five-year cohort study of *Nosema* spp. in Germany: does climate shape virulence and assertiveness of *Nosema ceranae*? *Applied and Environmental Microbiology* 76(9):3032–3038
- Guzman-Novoa E, Eccles L, Calvete Y, McGowan J, Kelly PG, Correa-Benitez A (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(4):443–450
- Hawthorne DJ, Dively GP (2011) Killing them with kindness? In-hive medications may inhibit xenobiotic efflux transporters and endanger honey bees *PLoS ONE* 6(11):e26796
- Henry M, Beguin M, Requier F, Rollin O, Odoux JF, Aupinel P, Aptel J, Tchamitchian S, Decourtye A (2012) A common pesticide decreases foraging success and survival in honey bees. *Science* 336(6079):348–350
- Higes M, García-Palencia P, Martín-Hernández R, Meana A (2007) Experimental infection of *Apis mellifera* honeybees with *Nosema ceranae* (Microsporidia). *Journal of Invertebrate Pathology* 94:211–217
- Higes M, Martín-Hernández R, Botias C, Garrido Bailon E, Gonzalez-Porto AV, Barrios L, Jesus del Nozal M, Bernal JL, Jimenez JJ, Garcia Palencia P, Meana A (2008) How natural infection by *Nosema ceranae* causes honeybee colony collapse. *Environmental Microbiology* 10(10):2659–2669
- Highfield AC, El Nagar A, Mackinder LCM, Noel LMLJ, Martin SJ, Schroeder DC (2009) Deformed wing virus implicated in overwintering honeybee colony losses. *Applied and Environmental Microbiology* 75(22):7212–7220
- Hosseini P, Sokolow SH, Vandegrift KJ, Kilpatrick AM, Daszak P (2010) Predictive power of air travel and socio-economic data for early pandemic spread. *PLoS ONE* 5(9):e12763
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends in Ecology & Evolution* 19(2):101–108
- Johnson RM (2009) Managed pollinator CAP Coordinated Agricultural Project: a national research and extension initiative to reverse pollinator decline when varroacides interact. *American Bee Journal* 149:1157–1159
- Johnson RM, Ellis MD, Mullin CA, Frazier M (2010) Pesticides and honey bee toxicity—USA. *Apidologie* 41(3):312–331
- Johnson RM, Dahlgren L, Siegfried BD, Ellis MD (2012) Acaricide, fungicide and drug interactions in honey bees (*Apis mellifera*). *PLoS ONE* 8(1):e54092
- Karesh WB, Cook RA, Bennett EL, Newcomb J (2005) Wildlife trade and global disease emergence. *Emerging Infectious Diseases* 11(7):1000–1002
- Kepler J, Becker R, Spatz R, Dechet F (2010) *Systemische insektizide Beizmittel—Auftreten und Relevanz von Guttation für die Entwicklung von Honigbienenkolonien*, Quedlinburg, Germany: Deutsche Pflanzenschutztagung. J. K.-I. BfKeVG
- Kiesecker JM, Blaustein AR (1995) Synergism between UV-B radiation and a pathogen magnifies amphibian embryo mortality in nature. *Proceedings of the National Academy of Sciences of the United States of America* 92:11049–11052
- Kilpatrick AM, Chmura AA, Gibbons DW, Fleischer RC, Marra PP, Daszak P (2006) Predicting the global spread of H5N1 avian influenza. *Proceedings of the National Academy of Sciences of the United States of America* 103:19368–19373
- Kilpatrick AM, Kramer LD, Jones MJ, Marra PP, Daszak P (2006) West Nile virus epidemics in North America are driven by shifts in mosquito feeding behavior. *PLoS Biology* 4(4):e82
- Klee J, Besana AM, Genersch E, Gisder S, Nanetti A, Tam DQ, Chinh TX, Puerta F, Ruz JM, Kryger P, Message D, Hatjina F, Korpela S, Fries I, Paxton RJ (2007) Widespread dispersal of the microsporidian *Nosema ceranae*, an emergent pathogen of the western honey bee, *Apis mellifera*. *Journal of Invertebrate Pathology* 96(1):1–10
- Krupke CH, Hunt GJ, Eitzer BD, Andino G, Given K (2012) Multiple routes of pesticide exposure for honey bees living near agricultural fields. *PLoS ONE* 7(1):e29268
- Laycock I, Lenthall KM, Barratt AT, Creswell JE (2012) Effects of imidacloprid, a neonicotinoid pesticide, on reproduction in worker bumble bees (*Bombus terrestris*). *Ecotoxicology* 21(7):1937–1945
- Le Conte Y, Ellis M, Ritter W (2010) *Varroa* mites and honey bee health: can *Varroa* explain part of the colony losses? *Apidologie* 41(3):353–363
- Le Conte Y, Navajas M (2008) Climate change: impact on honey bee populations and diseases. *Revue scientifique et technique (International Office of Epizootics)* 27(485–497):499–510

- Levine JM, D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. *Conservation Biology* 17(1):322–326
- Mao W, Shuler MA, Berenbaum MR (2013) Honey constituents up-regulate detoxification and immunity genes in the western honey bee *Apis mellifera*. *Proceedings of the National Academy of Sciences of the United States of America* 110(22):8763–8764
- Martin SJ, Highfield AC, Brettell L, Villalobos EM, Budge GE, Powell M, Nikaido S, Schroeder DC (2012) Global honey bee viral landscape altered by a parasitic mite. *Science* 336(6086):1304–1306
- Mendelson JR, Lips KR, Gagliardo RW, Rabb GB, Collins JP, Diffendorfer JE, Daszak P, Ibanez R, Zippel KC, Lawson DP, Wright KM, Stuart SN, Gascon C, da Silva HR, Burrowes PA, Joglar RL, La Marca E, Lotters S, du Preez LH, Weldon C, Hyatt A, Rodriguez-Mahecha JV, Hunt S, Robertson H, Lock B, Raxworthy CJ, Frost DR, Lacy RC, Alford RA, Campbell JA, Parra-Olea G, Bolanos F, Domingo JJC, Halliday T, Murphy JB, Wake MH, Coloma LA, Kuzmin SL, Price MS, Howell KM, Lau M, Pethiyagoda R, Boone M, Lannoo MJ, Blaustein AR, Dobson A, Griffiths RA, Crump ML, Wake DB, Brodie ED (2006) Biodiversity—confronting amphibian declines and extinctions. *Science* 313(5783):48
- Mullin CA, Frazier M, Frazier JL, Ashcraft S, Simonds R, vanEngelsdorp D, Pettis JS (2010) High levels of miticides and agrochemicals in North American apiaries: implications for honey bee health. *PLoS ONE* 5(3):e9754
- Mutinelli F (2011) The spread of pathogens through trade in honey bees and their products (including queen bees and semen): overview and recent developments. *Revue Scientifique et Technique—Office International des Epizooties* 30:257–271
- Mutinelli F, Costa C, Lodesani M, Baggio A, Medrzycki P, Formato G, Parrini C (2010) Honey bee colony losses in Italy. *Journal of Apicultural Research* 49:119–120
- Neumann P, Carreck NL (2010) Honey bee colony losses. *Journal of Apicultural Research* 49:1–6
- Nguyen BK, Saegerman C, Pirard C, Mignon J, Widart J, Tuironet B, Verheggen FJ, Berkvens D, De Pauw E, Haubruge E (2009) Does imidacloprid seed-treated maize have an impact on honey bee mortality? *Journal of Economic Entomology* 102(2):616–623
- Ollerton J, Price V, Armbruster WS, Memmott J, Watts S, Waser NM, Totland O, Goulson D, Alarcon R, Stout JC, Tarrant S (2012) Overplaying the role of honey bees as pollinators: a comment on Aebi and Neumann (2011). *Trends in Ecology & Evolution* 27(3):141–142
- OPERA (2011) *Bee health in Europe—facts & figures*, Italy: U. C. d. S. Cuore
- Palmer MJ, Moffat C, Saranzewa N, Harvey J, Wright GA, Connolly CN (2013) Cholinergic pesticides cause mushroom body neuronal inactivation in honeybees. *Nature Communications* 4(1634). doi:10.1038/ncomms2648
- Pettis JS, vanEngelsdorp D, Johnson J, Dively G (2012) Pesticide exposure in honey bees results in increased levels of the gut pathogen *Nosema*. *Naturwissenschaften* 99(2):153–158
- Plowright RK, Sokolow SH, Gorman ME, Daszak P, Foley JE (2008) Causal inference in disease ecology: investigating ecological drivers of disease emergence. *Frontiers in Ecology and the Environment* 6(8):420–429
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25(6):345–353
- Potts SG, Roberts SPM, Dean R (2010) Declines of managed honey bees and beekeepers in Europe. *Journal of Apicultural Research* 49:15–22
- Pounds JA (2001) Climate and amphibian declines. *Nature* 410(6829):639–640
- Ribiere M, Ball B, Aubert M (2008) Natural history and geographic distribution of honey bee viruses. In: *Virology and the Honey Bee*, Aubert M, Ball B, Fries I et al. (editors), Luxembourg: European Communities, pp 15–84.
- Rosenkranz P, Aumeier P, Ziegelmann B (2010) Biology and control of *Varroa destructor*. *Journal of Invertebrate Pathology* 103:S96–S119
- Schloegel LM, Daszak P, Cunningham AA, Speare R, Hill B (2010) Two amphibian diseases, chytridiomycosis and ranaviral disease, are now globally notifiable to the World Organization for Animal Health (OIE): an assessment. *Diseases of Aquatic Organisms* 92(2–3):101–108
- Smolinski MS, Hamburg MA, Lederberg J Committee on Emerging Microbial Threats to Health in the 21st Century (2003) *Microbial Threats to Health: Emergence, Detection, and Response*, Washington D.C.: The National Academies Press
- Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL, Waller RW (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* 306(5702):1783–1786
- Sumner DA, Boriss H (2006) Bee-economics and the leap in pollination fees. *Agricultural and Resource Economics Update* 9:9–11
- Tapparo A, Marton D, Gioro C (2012) Assessment of the environmental exposure of honeybees to particulate matter containing neonicotinoid insecticides coming from corn coated seeds. *Environmental Science & Technology* 46:2592–2599
- Thompson H (2010) Risk assessment for honey bees and pesticides—recent developments and 'new issues'. *Pest Management Science* 66:1157–1162
- Thompson HM (2003) Behavioural effects of pesticides in bees—their potential for use in risk assessment. *Ecotoxicology* 12(1–4):317–330
- van der Zee R, Pisa L, Andonov S, Brodschneider R, Charriere JD, Chlebo R, Coffey MF, Crailsheim K, Dahle B, Gajda A, Gray A, Drazic MM, Higes M, Kauko L, Kence A, Kence M, Kzic N, Kiprijanovska H, Kralj J, Kristiansen P, Hernandez RM, Mutinelli F, Nguyen BK, Otten C, Ozkirim A, Pernal SF, Peterson M, Ramsay G, Santrac V, Soroker V, Topolska G, Uzunov A, Vejsnaes F, Wei S, Wilkins S (2012) Managed honey bee colony losses in Canada, China, Europe, Israel and Turkey, for the winters of 2008–9 and 2009–10. *Journal of Apicultural Research* 51(1):91–114
- vanEngelsdorp D, Caron D, Hayes J, Underwood R, Henson M, Rennick K, Spleen A, Andree M, Snyder R, Lee K, Roccasecca K, Wilson M, Wilkes J, Lengerich E, Pettis J Bee Informed Partnership (2012) A national survey of managed honey bee 2010–11 winter colony losses in the USA: results from the Bee Informed Partnership. *Journal of Apicultural Research* 51(1):115–124
- vanEngelsdorp D, Evans JD, Donovall L, Mullin C, Frazier M, Frazier J, Tarpay DR, Hayes J, Pettis JS (2009) Entombed pollen: a new condition in honey bee colonies associated with increased risk of colony mortality. *Journal of Invertebrate Pathology* 101(2):147–149
- vanEngelsdorp D, Evans JD, Saegerman C, Mullin C, Haubruge E, Nguyen BK, Frazier M, Frazier J, Cox-Foster D, Chen YP, Underwood R, Tarpay DR, Pettis JS (2009) Colony collapse disorder: a descriptive study. *PLoS ONE* 4(8):e6481

- vanEngelsdorp D, Hayes J, Underwood RM, Caron D, Pettis J (2011) A survey of managed honey bee colony losses in the USA, fall 2009 to winter 2010. *Journal of Apicultural Research* 50(1):1–10
- vanEngelsdorp D, Hayes J, Underwood RM, Pettis J (2008) A survey of honey bee colony losses in the US, fall 2007 to spring 2008. *PLoS ONE* 3(12):e4071
- vanEngelsdorp D, Hayes JJ, Underwood R, Pettis JS (2010) A survey of honey bee colony losses in the United States, fall 2008 to spring 2009. *Journal of Apicultural Research* 49(1):7–14
- vanEngelsdorp D, Meixner MD (2010) A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. *Journal of Invertebrate Pathology* 103:S80–S95
- vanEngelsdorp D, Underwood R, Caron D, Hayes J (2007) An estimate of managed colony losses in the winter of 2006–2007: a report commissioned by the Apiary Inspectors of America. *American Bee Journal* 147(7):599–603
- Vejsnaes F, Nielsen SL, Kryger P (2010) Factors involved in the recent increase in colony losses in Denmark. *Journal of Apicultural Research* 49:109–110
- Vidau, C., M. Diogon, J. Aufauvre, R. Fontbonne, B. Vignes, J. L. Brunet, C. Texier, D. G. Biron, N. Blot, H. El Alaoui, L. P. Belzunces and F. Delbac (2011). “Exposure to Sublethal Doses of Fipronil and Thiacloprid Highly Increases Mortality of Honeybees Previously Infected by *Nosema ceranae*.” *PLoS ONE* 6(6).
- Whitehorn PR, O’Connor S, Wackers FL, Goulson D (2012) Neonicotinoid pesticide reduces bumblebee colony growth and queen production. *Science* 336(6079):351–352
- Williams GR, Tarpay DR, VanEngelsdorp D, Chauzat MP, Cox-Foster DL, Delaplane KS, Neumann P, Pettis JS, Rogers REL, Shutler D (2010) Colony collapse disorder in context. *Bioessays* 32(10):845–846
- Williamson SM, Wright GA (2013) Exposure to multiple cholinergic pesticides impairs olfactory learning and memory in honeybees. *Journal of Experimental Biology* 216(10):1799–1807
- Winfrey R, Williams NM, Dushoff J, Kremen C (2007) Native bees provide insurance against ongoing honey bee losses. *Ecology Letters* 10(11):1105–1113
- Yang EC, Chuang YC, Chen L, Chang LH (2008) Abnormal foraging behavior induced by sublethal dosage of imidacloprid in the honey bee (Hymenoptera: Apidae). *Journal of Economic Entomology* 101:1743–1748