An Overview of the Potential Impacts of Honey Bees to Native Bees, Plant Communities, and Ecosystems in Wild Landscapes: Recommendations for Land Managers

XERCES SOCIETY
for Invertebrate Conservation

Protecting the Life that Sustains Us

www.xerces.org

Richard Hatfield
Sarina Jepsen
Mace Vaughan
Scott Black
Eric Lee-Mäder

Please cite this document as:

Hatfield, R. G., S. Jepsen, M. Vaughan, S. Black, E. Lee-Mäder. 2018. *An Overview of the Potential Impacts of Honey Bees to Native Bees, Plant Communities, and Ecosystems in Wild Landscapes: Recommendations for Land Managers.* 12 pp. Portland, OR: The Xerces Society for Invertebrate Conservation.

Introduction

The question of whether introduced honey bees belong on public lands and natural areas in North America has been debated for decades (Pyke 1999, and references therein). As more areas of natural habitat that formerly provided resources for pollinators are converted to agricultural and suburban uses, the pressures for the beekeeping industry to find pesticide-free areas in which honey bees can forage while they are not actively pollinating crop fields are increasing. As a result, there is a critical need to present evidence-based considerations for landowners and managers of public lands and natural areas to review when deciding whether honey bees would be appropriate in these landscapes, and if so, the timing, duration, and numbers of hives that should be allowed.

In recognition of the potential risks that honey bees pose to native pollinators and their associated landscapes (see below for details), the final decision about whether to allow honey bees access to public lands and natural areas should be left to land managers who have the best understanding of the local conditions, local management goals, the needs of the flora and fauna, and the sensitivity of the habitat. We also recommend that land managers consider any federal or local laws pertaining to natural areas management. These laws include, but are not limited to, the National Environmental Policy Act (NEPA), the National Forest Management Act (NFMA), the Clean Water Act, and the Endangered Species Act, as well as all relevant state and municipal legislation.

Honey bees are critical for agriculture, and honey production is an important industry. Plus, beekeepers—professional and hobbyist alike—are some of the most engaged advocates for improved pollinator habitat across the US. The Xerces Society does want to ensure, however, that native pollinators and other land management or conservation goals are considered a priority in decisions about apiary placement on public lands and natural areas.

Recommendations for Land Managers

Where local and federal laws permit the placement of honey bees, and managers are deciding whether to include hives on their land, we suggest that managers consider the following potential impacts of honey bees. Following this set of recommendations is a review of the literature relevant to these issues.

Are populations of endangered or threatened pollinators present on the land?

- If rare species of bees and butterflies, including threatened or endangered species, special status, sensitive, or other species of concern, are known to exist within the flight area where the hives are to be placed, assessment of potential risks to these populations should be undertaken.

- If it is possible that rare or declining pollinator species can be found in the area, efforts should be made to determine if they are present. Consulting scientists with expertise in pollinator surveys and species identification is recommended. In cases where a particular pollinator species is critically imperiled, every remaining population and individual may be essential to the species' immediate and long-term survival. There is potential that honey bees may transmit diseases to native bees (e.g., spread of deformed wing virus from honey bees to bumble bees causing wing damage) and may compete for floral resources (e.g., decreased fecundity in bumble bees).

Are there invasive plant populations, or ongoing efforts to eradicate invasive plant species, that would be affected by the inclusion of honey bees?

- Honey bees may not be compatible with invasive plant species management. If honey bees pollinate and increase seed production of the invasive species in question (e.g., yellow star thistle), land managers may want to exclude honey bees during periods of bloom.

What are the potential impacts to other wildlife?

- Are there bears in the area that will be attracted to the apiary as a food source? Land managers need to work with beekeepers to determine if placement of an apiary will increase the potential for human–bear conflicts. If this is a risk, then electric fencing and maintenance of that fencing to prevent intrusion from bears should be mandated on public lands to avoid bear damage to apiaries and to prevent habituation of bears to hives.

Is there sufficient infrastructure to support the drop-off and storing of the proposed operation?

- Commercial beekeepers may bring anywhere between 4 and 400 hives, depending upon the size of the operation. Hives are delivered using a range of vehicles from flatbed trucks to semi-tractor trailers. Access roads must be appropriate for the required transport, and should not result in excess erosion, road damage, or other infrastructure challenges.
- Apiary sites also must be of sufficient size, with level and firm ground to accommodate small forklifts or Bobcat-type loaders used to move pallets of bees. An apiary location will also need sufficient space for trucks to turn around.

If the above considerations have been made and a decision to move forward with apiary placement is under consideration, we recommend:

- Any apiary (no matter the number of hives), needs to be more than 4 miles from:
    - Known locations of pollinators that are listed on state or federal endangered species acts, or designated as special status, sensitive, or other species of concern (this includes plants with specific and important native pollinator relationships that can lead to decline in plant production);
    - Wilderness and wilderness study areas, as well as congressionally designated preserves and monuments.
    - Habitats of special value for biodiversity and/or pollinators (e.g., high-elevation meadows, wet meadows, etc.).
- Each apiary should have no more than 20 hives.
- Apiaries should be separated by at least 4 miles.

A Summary of the Potential Impacts of Honey Bees on Native Ecosystems

The importance of honey bees and native bees

Pollinators support the reproduction of nearly 85% of the world's flowering plants (Ollerton et al. 2011) and 35% of global crop production (Klein et al. 2007). The great majority of pollinators are insects, including bees, wasps, flies, beetles, ants, butterflies, and moths. Bees are considered the most important group of pollinators in temperate climates. There are over 3,600 species of bees in the United States and Canada (Ascher & Pickering 2018); almost all of these are native.

The honey bee (*Apis mellifera*) is not native to North America and was introduced in the early 17th century by Europeans for honey and wax production (DeGrandi-Hoffman 2003). As honey bees were moved around for honey production, the value of their contribution to pollination services on farms became apparent. Eventually, with the advent of the removable frame beehive, introduced in 1852 by L. L. Langstroth, modern apiculture took shape, and honey bees began their long-standing relationship with North American agriculture (LeBuhn 2013).

The honey bee is the most widely managed crop pollinator in the United States. Studies indicate that honey bees are important for more than $15 billion in crop production annually (Morse & Calderone 2000; Calderone 2012). The number of managed western honey bee hives is increasing at the global scale (IPBES 2016) although seasonal colony losses of up to 40% have been seen in recent years in some European countries and in North America (Bee Informed Partnership 2014). Colony losses may not always result in irreversible declines, as losses can be mitigated somewhat by beekeepers splitting colonies.

Native bees are also important crop pollinators. A recent survey found that native bees universally increased fruit set in 41 crop systems worldwide, independent of honey bee presence (Garibaldi et al. 2013). Native, unmanaged bees provide free pollination services, and are often more efficient than honey bees on an individual bee basis at pollinating particular crops, such as squash, berries, and tree fruits (e.g., Tepedino 1981; Bosch & Kemp 2001; Javorek et al. 2002; Garibaldi et al. 2013). Native bees are important in the production of an estimated $3 billion worth of crops annually to the United States economy (Losey & Vaughan 2006; Calderone 2012) although this is thought to be an underestimate of actual worth. Beyond agriculture, pollinators are keystone species in most terrestrial ecosystems: they pollinate the seeds and fruits that feed everything from songbirds to grizzly bears. Thus, conservation of pollinating insects is critically important to conserving both biodiversity and agriculture.

Evidence of honey bee and native bee decline

Little is known about the population status of most of the more than 3,600 species of native bees in the United States and Canada, especially across the entire range of individual species. However, what little information we do have suggests that many native species are experiencing population declines. A recent global analysis found that 40% of pollinator species may be at risk of extinction in the coming years (IPBES 2016). Also, an analysis of North America's bumble bees (*Bombus* spp.) conducted by the International Union for the Conservation of Nature (IUCN) Bumblebee Specialist Group indicates that 28% of bumble bees in Canada, the United States, and Mexico have experienced significant declines and may be at risk of extinction (Hatfield et al. 2015). These include several bumble bees that were formerly among our most common species. This analysis is corroborated by many recent studies that have documented bumble bee declines throughout North America (Colla & Packer 2008; Evans et al. 2008; Grixti et al. 2009; Colla & Ratti 2010; Cameron et al. 2011; Colla et al. 2012; Koch & Strange 2012; Bartomeus et al. 2013).

The ultimate cause of bumble bee and other native bee declines continues to be investigated, although many factors appear to be contributing. While land use change and habitat fragmentation are likely contributors to decreasing populations in some species (Williams et al. 2009; Potts et al. 2010), disease (Thorp et al. 2003; Colla et al. 2006; Williams et al. 2009; Cameron et al. 2011; Koch & Strange 2012), pesticide use (Whitehorn et al. 2012; Desneux et al. 2007; Laycock et al. 2012, 2013; Fauser-Misslin et al. 2013; Baron et al. 2014; Feltham et al. 2014), and climate change (Williams et al. 2009; Kerr et al. 2015; Miller-Struttman et al. 2015) are all also likely significant factors (Goulson et al. 2015).

Because of concerns about high annual honey bee losses and declines in native bee species, there has been a focus on development of national policies to support bee habitat. Most importantly, the 2008 and 2014 Farm Bills make pollinators a conservation priority for USDA agencies like the Natural Resources Conservation Service (NRCS) and Farm Service Agency (FSA). As a result, Farm Bill conservation programs are now providing farmers and ranchers with technical and financial assistance to create pollinator habitat on their lands. Because of the ongoing honey bee hive losses each winter and the challenges this poses to the beekeeping industry, the USDA also launched a special initiative in March 2014 specifically targeting $3 million to plant honey bee forage in five Upper Midwest and Northern Plains states where 65% of honey bee hives are rested in the summer. Similar levels of targeted funding for honey bee habitat was set aside in the years that followed. Another challenge to the beekeeping industry has been the steady loss of land enrolled in the Conservation Reserve Program (CRP). Between 2007 and 2017, close to 12 million acres came out of CRP, much of it in the Upper Great Plains. This has led to a considerable loss of honey bee forage in key resting and honey production areas.

Overall, the increased focus on bee health reflects a growing awareness of the importance of pollinators, and a motivation by government agencies and the public to take action. While the Xerces Society applauds all efforts to conserve pollinators, there is a need to ensure that actions to help beekeepers also benefit, and do not negatively impact, North America's native pollinators.

Our increasingly complex, fragmented landscape makes public lands and natural areas an important resource for the conservation of native pollinator communities. These public lands and natural areas have served as refugia for native bees and other pollinators for decades. These same public lands also hold the potential to provide pesticide-free forage for honey bees. There are, however, inherent possible risks to populations of native bees presented by the large scale placement of honey bees on public lands and natural areas. As the conservation of native bees is paramount to ecosystem health, we need conservation measures that focuses on the drivers of pollinator declines and beyond the protection of a single, non-native, primarily agricultural species (Geldmann & González-Varo 2018). The purpose of this report is to provide a summary of the current research that addresses the real, or potential threats that managed honey bees pose to native bees and native plant communities, so that the managers of public lands and natural areas can be informed when deciding whether or not to allow managed honey bees access to these areas.

Do honey bees pose a risk to wild bees, plant communities, and other wildlife?

While honey bees are essential pollinators in our agricultural environment, their role in public lands and natural areas is less clear. Though research examining the effects of honey bees on wild bees and plant communities has conflicting results, there is evidence that, at least in some cases, honey bees can alter plant and native bee communities because of their foraging habits, relatively high level of pathogen loads, degree of resource (pollen and nectar) removal, and their interactions with native bees.

Competition with native bees

A single honey bee colony requires substantial resources to survive. Estimates of single hive consumption vary from 20–130 lbs/year for pollen and 45–330 lbs/year of honey—representing 120–900 lbs/year of nectar (Goulson 2003, and references therein). Depending on the environment and the density of honey bee hives in an area and the time of year, this could represent a substantial percentage of the resources available. Significantly, Cane and Tepedino (2016) estimate that a standard 40 hive apiary extracts the pollen equivalent of 4 million wild bees from the surrounding landscape in 3 months. The proportion of resources used by honey bees, as well as the effects of this resource depletion on the native bee community, are likely to vary by location, the time of year, the species involved, floral abundance and diversity, as well as climatic and other environmental conditions.

Recent research documents that under controlled conditions honey bees displace native bees from flowers, alter the suite of flowers that native bees were visit, and have a negative impact on native bee reproduction (Hudewenz and Klein 2015). There is also evidence that honey bees can potentially impact the native bee community by removing the available supplies of pollen and nectar (Anderson & Anderson 1989; Paton 1990, 1996; Wills et al. 1990;

Dafni & Shmida 1996; Horskins & Turner 1999), or by competitively excluding native bees, thus forcing them to switch to other, less abundant, and less rewarding plant species (Wratt 1968; Eickwort & Ginsberg 1980; Pleasants 1981; Ginsberg 1983; Paton 1993, 1996; Buchmann et al. 1996; Horskins & Turner 1999; Dupont et al. 2004; Thomson 2004; Walther-Hellwig et al. 2006; Tepedino et al. 2007; Roubik 2009; Shavit et al. 2009; Hudewenz & Klein 2013; Rogers et al. 2013; but see Butz Huryn 1997; Steffan-Dewenter & Tscharntke 2000; Minckley et al. 2003). Likewise, Cane and Tepedino (2016) found significant competitive pressures (a 15:1 ratio of honey bees to native bees on a plant attractive to bees) even 4 km from a large apiary (90 hives)—but none of these studies have addressed population level effects on native bees. The long-term implications of this shift in resource use are not entirely clear, although there is a growing body of research on bumble bees that demonstrates negative competitive effects of honey bees on bumble bees, including lower reproductive success, smaller body size, and changes in bumble bee foraging behavior—and most notably, a reduction in pollen gathering (Evans 2001; Goulson et al. 2002; Thomson 2004, 2006; Paini & Roberts 2005; Walther-Hellwig et al. 2006; Goulson & Sparrow 2009; Elbgami et al. 2014). A recent study in California documented a decline in two species of bumble bees over 15 years with an associated increase in honey bee densities, which intensified competition for floral resources, and forced bumble bees to shift to less abundant and less rewarding flowers (Thomson 2016).

Additional evidence shows that honey bees are regularly using, and depleting, the most abundant resources in the surrounding environment (Paton 1996; Mallick & Driessen 2009; Shavit et al. 2009), and that upon removal of honey bees, native bees exhibit signs of competitive release by returning to plants that were formerly used by honey bees (Pleasants 1981; Wenner & Thorp 1994; Thorp 1996; Thorp et al. 2000). A number of studies have shown more neutral effects (Steffan-Dewenter & Tscharntke 2000; Minckley et al. 2003; Forup & Memmott 2005; Hudewenz & Klein 2013). The effects on other species of native bees, such as ground-nesting solitary bees, have not been well documented due to the difficulty in studying their rates of reproduction.

In a recent review of the effects of managed bees on native bees Mallinger et al. (2017) found that the majority of studies concluded that managed bees (including honey bees) had negative effects on native bees through competition. This competitive pressure was greater when the managed bee species was outside of their native range (such as honey bees in North America). However, they also found that the majority of studies did not explore mechanisms nor explanatory variables and thus the majority of studies did not show causal or direct effects. They conclude that the existing evidence may warrant the use of the precautionary principle when considering the placement of managed bees, particularly in areas of conservation concern, but caution that more detailed studies are needed to assess the long-term effects of managed bees on ecosystems (Mallinger et al. 2017).

Disease transmission to native bees

The spillover of infectious disease from domesticated livestock to wildlife populations is one of the main sources of emerging infectious disease (Daszak et al. 2000; Fürst et al. 2014). While this phenomenon has not been well studied in invertebrates, there is recent evidence of the transmission of pathogens from commercial bumble bees to wild bumble bees (Colla et al. 2006; Otterstatter & Thomson 2008; Murray et al. 2013). Evidence has also emerged demonstrating that honey bees can transmit diseases to many different species of native bees, including bumble bees, when they interact at shared flowers (Singh et al. 2010; Fürst et al. 2014). Bumble bees placed close to honey bee hives were found to have an 18% higher prevalence of the parasite *Crithidia bombi* than bumble bees placed away from honey bees (Graystock et al. 2014). A number of RNA viruses that were formerly thought to be specific to honey bees have now been reported to infect bumble bees (Genersch et al. 2006; Morkeski & Averill 2010; Singh et al. 2010; Meeus et al. 2011; Evison et al. 2012). The virulence of most of these RNA viruses in bumble bees has not yet been evaluated or demonstrated. However, in at least one study (Genersh et al. 2006) bumble bees infected with Deformed Wing Virus (DWV) developed malformed wings. Another recent study showed that DWV significantly reduced survivorship of bumble bees (Fürst et al. 2014). The same study (Fürst et al. 2014) showed that bumble bees with an overt inoculation of DWV produced non-viable offspring and had reduced longevity. In addition, while the primary disease implicated in recent bumble bee declines is the microsporidian *Nosema bombi*, bumble bees have recently been seen to harbor *Nosema ceranae*, a common disease of honey bees that can be particularly virulent to honey bee colonies, and has been implicated as a factor in Colony Collapse Disorder (Paxton 2010; Graystock et al. 2013; Fürst et al. 2014). *Nosema ceranae* has been detected in honey bees in Canada, and the United States (Williams et al. 2008), and more recently been detected in bumble bees in South America (Plischuk et al. 2009). It is likely only a matter of time until this pathogen is detected in wild bumble bees in North America.

A review paper that looked at disease transmission between managed and wild bees concluded that the commercial use of pollinators is a key driver of emerging disease in wild pollinators, and that avoiding anthropogenic induced pathogen spillover is crucial to preventing disease emergence in native pollinators (Manley et al. 2015). To help mediate this potential, the authors suggest that it is crucial to prevent the introduction of diseased pollinators into natural environments (Manley et al. 2015). Another review paper looked at the global effect that managed pollinators (including commercial bumble bees and honey bees) are having on wild bees (Graystock et al. 2015a). Graystock et al. (2015a) documented three mechanisms for managed bees causing negative effects on wild bees: pathogen spillover, when transmission occurs from managed to wild pollinators; pathogen spillback, the transmission of pathogens from wild populations to managed pollinators, where the pathogen becomes more prevalent and then is further transferred back to other populations/areas; and facilitation, which makes wild bees more susceptible to disease because of stress due to competition. Graystock et al. (2015b) also documented that pathogen transmission occurs between bumble bees and honey bees at shared flowers, showing a clear mechanism and vector for infection. However, Mallinger et al. (2017) found that the majority of studies do not document direct or causal population-level effects from disease transmission. They also found that disease transmission was more significant when the managed bee was being used within its native range (e.g., commercial bumble bees in North America) (Mallinger et al. 2017). Given this information, and since small, fragmented, and declining populations are especially susceptible to infectious disease (Fürst et al. 2014), and disease is already implicated as a likely causal factor of some native bee declines in North America (Cameron et al. 2011), this emerging body of research suggests that caution should be exercised when considering the placement of managed bees of any species in habitat that supports vulnerable or declining native bee populations.

Risks to Native Plant Communities

Because more than 85% of all flowering plants depend upon an animal pollinator for reproduction (Ollerton et al. 2011), healthy pollinator populations are essential to the maintenance of plant communities. Since the early Cretaceous period, native plants and pollinators have been coexisting in a symbiotic relationship that is essential to ongoing biodiversity. Today, our public lands and natural areas serve as important refugia for the many native plant species that are otherwise threatened by habitat fragmentation (due to agricultural intensification and urban expansion), climate change, invasive species, and a host of other pressures.

Significantly, a study found that competitive pressures from managed honey bees (even within their native range) restructured the plant–pollinator network in natural areas adjacent to agricultural fields at a cost to native plant reproduction (Magrach et al. 2017). While one plant species benefitted from high densities of honey bees (likely due to a forced resource shift for native bees due to honey bees dominating their normal forage plants), another plant had reduced fecundity with increased honey bee visitation (either due to physiological or behavioral reasons that were not determined in the study) (Magrach et al. 2017). This study shows that not only are honey bees (particularly at high densities) exerting pressures on native bee populations, but that those pressures have real effects on the plant community, with the potential for long-term consequences by jeopardizing and/or enhancing, plant reproduction.

In addition to affecting plant reproduction, non-native pollinators are a potential threat to native plant populations as they sometimes preferentially forage on invasive plants (Thorp et al. 1994; Butz Huryn & Moller 1995; Morales & Aizen 2002; Hanley & Goulson 2003). There is evidence that, particularly for self-incompatible plants (see Butz Huryn & Moller 1995), honey bee visitation increases seed set, and may initiate an invasive mutualism between the two species (Barthell et al. 2001, 2005; Morales & Aizen 2002; Hanley & Goulson 2003; Goulson 2005). The risk of increasing the spread of invasive plant species by increasing the abundance of their key pollinators could cause significant economic and ecological damage to ecosystems (Goulson 2005), and at a significant cost to native plant populations (Brown et al. 2002).

Moreover, while honey bees are effective pollinators of the majority of plants that they visit (Butz Huryn 1997, and references therein), research from several regions of the world suggests that honey bees are only collecting pollen from 25–42% of plant species available in natural areas (Wills et al. 1990; Thorp et al. 1994, 2000; Buchmann 1996). Furthermore, approximately 15,000–20,000 species of flowering plants are more efficiently pollinated by a behavior known as buzz pollination (De Luca & Vallejo-Marín 2013), which is something that many native bee species can do quite well, but that honey bees are incapable of performing. Thus, if an ecosystem were to become dominated by honey bees, with a concomitant decline in the abundance of native bees, many species of native plants may potentially be left under-pollinated.

In a recent review paper, Dohzono and Yokoyama (2010) looked at studies on the effects of introduced honey bees and bumble bees on native plant populations. They found that while these introduced bees are unlikely to affect the pollination system in bird pollinated plants, they can exhibit potential negative effects on native plant populations generally in the form of (1) decreased pollen transfer, (2) competition for resources and exclusion of native pollinators, and (3) changes in native pollinator visitation rates and efficiency. However, negative effects in most systems have not been quantified. So, while the mechanisms for the negative impacts of honey bees do exist, there are few studies that clearly document negative effects on plant populations due to pollen limitation. Therefore, while it is possible that the disruption of native pollinators by non-native bees disrupts plant populations, it is also possible that non-native bees may alter native pollinator populations (items 1–3 above) without having a net negative effect on plant populations (for more details see Dohzono & Yokoyama 2010). More research in this area is needed, but finding locations for comparative studies without non-native pollinators is an increasingly difficult challenge.

Based on best available research, honey bees can be described as good pollinators of some native plants. However, they cannot be considered effective pollinators of all native flora, and are not essential to the pollination of native plant populations (Wills et al. 1990; Thorp et al. 1994, 2000; Buchmann 1996; Butz Huryn 1997; De Luca & Vallejo-Marín 2013).

Risks to other wildlife

An additional concern is that black bears may try to get at honey in hives, and become more habituated to feeding on these hives. As bears are increasingly interfacing with humans, and as beekeepers seek high-quality forage for their apiaries, bear–honey bee conflicts are likely to increase (Caron & Bowman 2004). The economic effect of black bears on honey bee operations is significant (O'Brien & Marsh 1990). Less well understood are the effects of these depredation events on black bears. Electric fences have proven to be an effective measure to protect apiaries from bear depredation, and therefore bears from human–bear conflicts. Where bears pose a risk to apiaries, fences should be erected and maintained (Clark et al. 2005).

Conclusion

A diversity of pollinators is vital to ecosystems, and pollinators' contributions to biodiversity are well documented. As such, efforts to maintain a diverse suite of pollinators should be a priority for all public lands and natural areas. Honey bees, while not native to North America, play an essential role for pollination in agriculture. Conservation measures, particularly the creation of high-quality, insecticide-free foraging habitat in agricultural landscapes, are necessary for long-term honey bee health.

Public lands and natural areas are essential for our native pollinator and plant populations as they serve as important refugia from ongoing threats in more populated and manipulated landscapes. Evidence exists to suggest that through competition, disease transmission, and foraging habits (e.g., preference for invasive plant species) that honey bees have the potential to negatively affect native bee and plant populations in these habitats, particularly under certain environmental conditions and at high densities. The degree of these effects is variable, and certainly warrants further investigation. Yet, while some counter examples are available, the majority of studies show negative effects and the threats from these effects have the potential to alter native bee populations.

Because of the potential threats to our native pollinators, until additional evidence exists documenting that honey bees have a net neutral effect on our native biota, we urge land managers to consider these potential impacts and their relevance when making a decision about the placement of apiaries on public lands and natural areas. Importantly, land managers need to ensure that honey bee placement is consistent with existing legislation and with ongoing and future management priorities.

Literature Cited

Anderson, G. J., and M. K. Anderson. 1989. Assaying pollinator visitation to *Solanum* flowers. *Solanaceae Newsletter* 3:71.

Ascher, J. S., and J. Pickering. 2018. "Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila)." http://www.discoverlife.org/mp/20q?guide=Apoidea_species (accessed April 30, 2018).

Baron, G. L., N. E. Raine, and M. J. Brown. 2014. Impact of chronic exposure to a pyrethroid pesticide on bumblebees and interactions with a trypanosome parasite. *Journal of Applied Ecology* 51:460–469.

Barthell, J. F., J. M. Randall, R. W. Thorp, and A. M. Wenner. 2001. Promotion of seed set in yellow star-thistle by honey bees: evidence of an invasive mutualism. *Ecological Applications* 11:1870–1883.

Barthell, J. F., R. W. Thorp, A. M. Wenner, J. M. Randall, and D. S. Mitchell. 2005. Seed set in a non-native, self-compatible thistle on Santa Cruz Island: implications for the invasion of an island ecosystem. In *Proceedings of the Sixth California Islands Symposium*, edited by D. Garcelon and C. A. Schwemm, 269–273. Arcata, CA: Institute for Wildlife Studies.

Bartomeus, I., J. S. Ascher, J. Gibbs, B. N. Danforth, D. L. Wagner, S. M. Hedtke, and R. Winfree. 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Sciences* 110:4656–4660.

Bee Informed Partnership. 2014. "Bee Informed Partnership | Using beekeepers' real world experience to solve beekeepers' real world problems." http://beeinformed.org/ (accessed April 30, 2018).

Berenbaum, M., P. Bernhardt, S. Buchmann, N. Calderone, P. Goldstein, D. W. Inouye, P. Kevan, C. Kremen, R. A. Medellin, and T. Ricketts. 2007. *Status of Pollinators in North America*. 326 pp. Washington, D.C.: The National Academies Press.

Bosch, J., and W. P. Kemp. 2001. *How to Manage the Blue Orchard Bee as an Orchard Pollinator*. (Sustainable Agriculture Network handbook series; bk. 5.) 88+viii pp. Beltsville, MD: National Agricultural Library.

Brown, B. J., R. J. Mitchell, and S. A. Graham. 2002. Competition for pollination between an invasive species (purple loosestrife) and a native congener. *Ecology* 83:2328–2336.

Buchmann, S. L. 1996. Competition between honey bees and native bees in the Sonoran Desert and global bee conservation issues. In *The Conservation of Bees*, edited by A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, and I. H. Williams, 125–142. London: Academic Press.

Butz Huryn, V. M. 1997. Ecological impacts of introduced honey bees. *Quarterly Review of Biology* 72:275–297.

Butz Huryn, V. M., and H. Moller. 1995. An assessment of the contribution of honey bees (*Apis mellifera*) to weed reproduction in New Zealand protected natural areas. *New Zealand Journal of Ecology* 19:111–122.

Calderone, N. W. 2012. Insect pollinated crops, insect pollinators and US agriculture: Trend analysis of aggregate data for the period 1992–2009. *PLoS ONE* 7:e37235.

Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences* 108:662–667.

Cane, J. H., and V. J. Tepedino. 2017. Gauging the effect of honey bee pollen collection on native bee communities: *Apis* pollen depletion and native bees. *Conservation Letters* 10:205–210.

Caron, D. M., and J. L. Bowman. 2004. *Bears and Bees*. (MAAREC Publication 4.10, MidAtlantic Apicultural Research & Extension Consortium.) Newark: University of Delaware.

Clark, J. D., S. Dobey, D. V. Masters, B. K. Scheick, M. R. Pelton, and M. E. Sunquist. 2005. American black bears and bee yard depredation at Okefenokee Swamp, Georgia. *Ursus* 16:234–244.

Colla, S., F. Gadallah, L. Richardson, D. Wagner, and L. Gall. 2012. Assessing declines of North American bumble bees (*Bombus* spp.) using museum specimens. *Biodiversity and Conservation* 21:3585–3595.

Colla, S. R., M. C. Otterstatter, R. J. Gegear, and J. D. Thomson. 2006. Plight of the bumble bee: pathogen spillover from commercial to wild populations. *Biological Conservation* 129:461–467.

Colla, S. R., and L. Packer. 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. *Biodiversity and Conservation* 17:1379–1391.

Colla, S. R., and C. M. Ratti. 2010. Evidence for the decline of the western bumble bee (*Bombus occidentalis* Greene) in British Columbia. *Pan-Pacific Entomologist* 86:32.

Dafni, A., and A. Shmida. 1996. The possible ecological implications of the invasion of *Bombus terrestris* (L.)(Apidae) at Mt. Carmel, Israel. In *The Conservation of Bees*, edited by A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, and I. H. Williams, 183–200. London: Academic Press.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife—threats to biodiversity and human health. *Science* 287:443–449.

DeGrandi-Hoffman, G. 2003. Honey Bees in U.S. Agriculture: Past, Present, and Future. In *For Nonnative Crops, Whence Pollinators of the Future?*, edited by K. Strickler and J. H. Cane, 11–20. Annapolis, MD: Entomological Society of America.

De Luca, P. A., and M. Vallejo-Marín. 2013. What's the "buzz"about? The ecology and evolutionary significance of buzz-pollination. *Current Opinion in Plant Biology* 16:429–435.

Desneux, N., A. Decourtye, and J. M. Delpuech. 2007. The sublethal effects of pesticides on beneficial arthropods. *Annual Review of Entomology* 52:81–106.

Dohzono, I., and J. Yokoyama. 2010. Impacts of alien bees on native plant-pollinator relationships: A review with special emphasis on plant reproduction. *Applied Entomology and Zoology* 45:37–47.

Dupont, Y. L., D. M. Hansen, A. Valido, and J. M. Olesen. 2004. Impact of introduced honey bees on native pollination interactions of the endemic *Echium wildpretii* (Boraginaceae) on Tenerife, Canary Islands. *Biological Conservation* 118:301–311.

Eickwort, G. C., and H. S. Ginsberg. 1980. Foraging and mating behavior in Apoidea. *Annual Review of Entomology* 25:421–446.

Elbgami, T., W. E. Kunin, W. O. H. Hughes, and J. C. Biesmeijer. 2014. The effect of proximity to a honeybee apiary on bumblebee colony fitness, development, and performance. *Apidologie* 45:504–513.

Evans, E. C. 2001. "Competition between European honey bees and native bumblebees: resource overlap and impact on reproductive success." (Master's thesis, University of Minnesota.)

Evans, E., R. W. Thorp, S. Jepsen, and S. H. Black. 2008. "Status review of three formerly common species of bumble bee in the Subgenus *Bombus*." Portland, OR: The Xerces Society for Invertebrate Conservation. (Available at http://www.xerces.org/bumblebees/.)

Evison, S. E. F., K. E. Roberts, L. Laurenson, S. Pietravalle, J. Hui, J. C. Biesmeijer, J. E. Smith, G. Budge, and W. O. H. Hughes. 2012. Pervasiveness of parasites in pollinators. *PLoS ONE* 7:e30641.

Fauser-Misslin, A., B. M. Sadd, P. Neumann, and C. Sandrock. 2013. Influence of combined pesticide and parasite exposure on bumblebee colony traits in the laboratory. *Journal of Applied Ecology* 51: 450–459.

Feltham, H., K. Park, and D. Goulson. 2014. Field realistic doses of pesticide imidacloprid reduce bumblebee pollen foraging efficiency. *Ecotoxicology* 23:317–323.

Forup, M. L., and J. Memmott. 2005. The relationship between the abundances of bumblebees and honeybees in a native habitat. *Ecological Entomology* 30:47–57.

Fürst, M. A., D. P. McMahon, J. L. Osborne, R. J. Paxton, and M. J. F. Brown. 2014. Disease associations between honeybees and bumblebees as a threat to wild pollinators. *Nature* 506:364–366.

Garibaldi, L. A., I. Steffan-Dewenter, R. Winfree, M. A. Aizen, R. Bommarco, S. A. Cunningham, C. Kremen et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339:1608–1611.

Geldmann, J., and J. P. González-Varo. 2018. Conserving honey bees does not help wildlife. *Science* 359:392–393.

Genersch, E., C. Yue, I. Fries, and J. R. de Miranda. 2006. Detection of deformed wing virus, a honey bee viral pathogen, in bumble bees (*Bombus terrestris* and *Bombus pascuorum*) with wing deformities. *Journal of Invertebrate Pathology* 91:61–63.

Ginsberg, H. S. 1983. Foraging ecology of bees in an old field. *Ecology* 64:165–175.

Goulson, D. 2003. Effects of introduced bees on native ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 34:1–26.

Goulson, D. 2005. Risks of increased weed problems associated with introduction of non-native bee species. *Journal of Food, Agriculture & Environment* 3:11–13.

Goulson, D., and K. R. Sparrow. 2009. Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. *Journal of Insect Conservation* 13:177–181.

Goulson, D., J. C. Stout, and A. R. Kells. 2002. Do exotic bumblebees and honeybees compete with native flower-visiting insects in Tasmania? *Journal of Insect Conservation* 6:179–189.

Goulson, D., E. Nicholls, C. Botías, and E. L. Rotheray. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 334:1255957.

Graystock, P., K. Yates, B. Darvill, D. Goulson, and W. O. H. Hughes. 2013. Emerging dangers: deadly effects of an emergent parasite in a new pollinator host. *Journal of Invertebrate Pathology* 114:114–119.

Graystock, P., D. Goulson, and W. O. H. Hughes. 2014. The relationship between managed bees and the prevalence of parasites in bumblebees. *PeerJ* 2:e522. DOI:10.7717/peerj.522.

Graystock, P., E. J. Blane, Q. S. McFrederick, D. Goulson, and W. O. H. Hughes. 2015a. Do managed bees drive parasite spread and emergence in wild bees? *International Journal for Parasitology: Parasites and Wildlife* 5:64–75.

Graystock, P., D. Goulson, and W. O. H. Hughes. 2015b. Parasites in bloom: flowers aid dispersal and transmission of pollinator parasites within and between bee species. *Proceedings of the Royal Society B: Biological Sciences* 282:20151371.

Grixti, J. C., L. T. Wong, S. A. Cameron, and C. Favret. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. *Biological Conservation* 142:75–84.

Hanley, M. E., and D. Goulson. 2003. Introduced weeds pollinated by introduced bees: Cause or effect? *Weed Biology and Management* 3:204–212.

Hatfield, R. G., S. R. Colla, S. Jepsen, L. L. Richardson, and R. W. Thorp. 2015. "IUCN Assessments for North American *Bombus* spp." (for the North American IUCN Bumble Bee Specialist Group). Portland, OR: The Xerces Society for Invertebrate Conservation. (Available at http://www.xerces.org/wp-content/uploads/2015/03/Hatfield_etal_14_rs.pdf.)

Horskins, K., and V. B. Turner. 1999. Resource use and foraging patterns of honeybees, *Apis mellifera*, and native insects on flowers of *Eucalyptus costata*. *Australian Journal of Ecology* 24:221–227.

Hudewenz, A., and A.-M. Klein. 2013. Competition between honey bees and wild bees and the role of nesting resources in a nature reserve. *Journal of Insect Conservation* 17:1275–1283.

Hudewenz, A., and A.-M. Klein. 2015. Red mason bees cannot compete with honey bees for floral resources in a cage experiment. *Ecology and Evolution* 5:5049–5056.

Javorek, S. K., K. E. Mackenzie, and S. P. Vander Kloet. 2002. Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: *Vaccinium angustifolium*). *Annals of the Entomological Society of America* 95:345–351.

IPBES [Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services] (2016) *Summary for policymakers of the assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production*, edited by S. G. Potts, V. L. Imperatriz-Fonseca, H. T. Ngo, J. C. Biesmeijer, T. D. Breeze, L. V. Dicks, L. A. Garibaldi et al. Bonn: IPBES Secretariat.

Kerr, J. T., A. Pindar, P. Galpern, L. Packer, S. G. Potts, S. M. Roberts, P. Rasmont et al. 2015. Climate change impacts on bumblebees converge across continents. *Science* 349:177–180.

Klein, A.-M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* 274:303.

Koch, J. B., and J. P. Strange. 2012. The status of *Bombus occidentalis* and *B. moderatus* in Alaska with special focus on *Nosema bombi* incidence. *Northwest Science* 86:212–220.

Laycock, I., K. C. Cotterell, T. A. O'Shea-Wheller, and J. E. Cresswell. 2013. Effects of the neonicotinoid pesticide thiamethoxam at field-realistic levels on microcolonies of *Bombus terrestris* worker bumble bees. *Ecotoxicology and Environmental Safety* 100:153–158.

Laycock, I., K. M. Lenthall, A. T. Barratt, and J. E. Cresswell. 2012. Effects of imidacloprid, a neonicotinoid pesticide, on reproduction in worker bumble bees (*Bombus terrestris*). *Ecotoxicology* 21:1937–1945.

LeBuhn, G. 2013. *Field Guide to the Common Bees of California: Including Bees of the Western United States*. 192 pp. Oakland: University of California Press.

Losey, J. E., and M. Vaughan. 2006. The economic value of ecological services provided by insects. *Bioscience* 56:311–323.

Magrach, A., J. P. González-Varo, M. Boiffier, M. Vilà, and I. Bartomeus. 2017. Honeybee spillover reshuffles pollinator diets and affects plant reproductive success. *Nature Ecology & Evolution* 1:1299–1307.

Mallick, S. A., and M. M. Driessen. 2009. Impacts of hive honeybees on Tasmanian leatherwood *Eucryphia lucida* Labill.(Eucryphiaceae). *Austral Ecology* 34:185–195.

Mallinger, R. E., H. R. Gaines-Day, and C. Gratton. 2017. Do managed bees have negative effects on wild bees?: A systematic review of the literature. *PLoS ONE* 12:e0189268.

Manley, R., M. Boots, and L. Wilfert. 2015. REVIEW: Emerging viral disease risk to pollinating insects: ecological, evolutionary and anthropogenic factors. *Journal of Applied Ecology* 52:331–340.

Meeus, I., M. J. Brown, D. C. De Graaf, and G. U. Y. Smagghe. 2011. Effects of invasive parasites on bumble bee declines. *Conservation Biology* 25:662–671.

Miller-Struttmann, N. E., J. C. Geib, J. D. Franklin, P. G. Kevan, R. M. Holdo, D. Ebert-May, A. M. Lynn, J. A. Kettenbach, E. Hedrick, and C. Galen. 2015. Functional mismatch in a bumble bee pollination mutualism under climate change. *Science* 349:1541–1544.

Minckley, R. L., J. H. Cane, L. Kervin, and D. Yanega. 2003. Biological impediments to measures of competition among introduced honey bees and desert bees (Hymenoptera: Apiformes). *Journal of the Kansas Entomological Society* 76:306–319.

Morales, C. L., and M. A. Aizen. 2002. Does invasion of exotic plants promote invasion of exotic flower visitors? A case study from the temperate forests of the southern Andes. *Biological Invasions* 4:87–100.

Morkeski, A., and A. L. Averill. 2010. Managed pollinator CAP-coordinated agricultural project: Wild bee status and evidence for pathogen 'spillover' with honey bees. *American Bee Journal* 150:1049–1052.

Morse, R. A., and N. W. Calderone. 2000. The value of honey bees as pollinators of US crops in 2000. *Bee Culture* 128:1–15.

Murray, T. E., M. F. Coffey, E. Kehoe, and F. G. Horgan. 2013. Pathogen prevalence in commercially reared bumble bees and evidence of spillover in conspecific populations. *Biological Conservation* 159:269–276.

O'Brien, J. M., and R. E. Marsh. 1990. Vertebrate pests of beekeeping. In *Proceedings of the Fourteenth Vertebrate Pest Conference 1990*, edited by L. R. Davis and R. E. Marsh, 228–232. Davis: University of California–Davis.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? *Oikos* 120:321–326.

Otterstatter, M. C., and J. D. Thomson. 2008. Does pathogen spillover from commercially reared bumble bees threaten wild pollinators? *PLoS ONE* 3:e2771.

Paini, D. R., and J. D. Roberts. 2005. Commercial honey bees (*Apis mellifera*) reduce the fecundity of an Australian native bee (*Hylaeus alcyoneus*). *Biological Conservation* 123:103–112.

Paton, D. C. 1990. Budgets for the use of floral resources in mallee heath. In *The Mallee Lands: A Conservation Perspective (Proceedings of the National Mallee Conference)*, edited by J. C. Noble, P. J. Joss and G. K. Jones, 189–193. East Melbourne: CSIRO

Paton, D. C. 1993. Honeybees in the Australian environment. *Bioscience* 43:95–103.

Paton, D. C. 1996. *Overview of Feral and Managed Honeybees in Australia: Distribution, Abundance, Extent of Interactions with Native Biota, Evidence of Impacts and Future Research*. 71 pp. Canberra: Australian Nature Conservation Agency. .

Paxton, R. J. 2010. Does infection by *Nosema ceranae* cause "Colony Collapse Disorder" in honey bees (*Apis mellifera*)? *Journal of Apicultural Research* 49:80–84.

Pleasants, J. M. 1981. Bumblebee response to variation in nectar availability. *Ecology* 62:1648–1661.

Plischuk, S., R. Martín-Hernández, L. Prieto, M. Lucía, C. Botías, A. Meana, A. H. Abrahamovich, C. Lange, and M. Higes. 2009. South American native bumblebees (Hymenoptera: Apidae) infected by *Nosema ceranae* (Microsporidia), an emerging pathogen of honeybees (*Apis mellifera*). *Environmental Microbiology Reports* 1:131–135.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25:345–353.

Pyke, G. H. 1999. The introduced honeybee *Apis mellifera* and the precautionary principle: Reducing the conflict. *Australian Zoologist* 31:181–186.

Rogers, S. R., P. Cajamarca, D. R. Tarpy, and H. J. Burrack. 2013. Honey bees and bumble bees respond differently to inter-and intra-specific encounters. *Apidologie* 44:621–629.

Roubik, D. W. 2009. Ecological impact on native bees by the invasive Africanized honey bee. *Acta Biológica Colombiana* 14:115–124.

Shavit, O., A. Dafni, and G. Ne'eman. 2009. Competition between honeybees (*Apis mellifera*) and native solitary bees in the Mediterranean region of Israel—Implications for conservation. *Israel Journal of Plant Sciences* 57:171–183.

Singh, R., A. L. Levitt, E. G. Rajotte, E. C. Holmes, N. Ostiguy, D. vanEngelsdorp, W. I. Lipkin, C. W. dePamphilis, A. L. Toth, and D. L. Cox-Foster. 2010. RNA viruses in hymenopteran pollinators: evidence of inter-taxa virus transmission via pollen and potential impact on non-*Apis* hymenopteran species. *PLoS ONE* 5:e14357.

Steffan-Dewenter, I., and T. Tscharntke. 2000. Resource overlap and possible competition between honey bees and wild bees in central Europe. *Oecologia* 122:288–296.

Tepedino, V. J. 1981. The pollination efficiency of the squash bee (*Peponapis pruinosa*) and the honey bee (*Apis mellifera*) on summer squash (*Cucurbita pepo*). *Journal of the Kansas Entomological Society* 54:359–377.

Tepedino, V. J., D. G. Alston, B. A. Bradley, T. R. Toler, and T. L. Griswold. 2007. Orchard pollination in Capitol Reef National Park, Utah, USA. Honey bees or native bees? *Biodiversity and Conservation* 16:3083–3094.

Thomson, D. 2004. Competitive interactions between the invasive European honey bee and native bumble bees. *Ecology* 85:458–470.

Thomson, D. M. 2006. Detecting the effects of introduced species: a case study of competition between *Apis* and *Bombus*. *Oikos* 114:407–418.

Thomson, D. M. 2016. Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecology Letters* 19:1247–1255.

Thorp, R., K. Strickler, and J. Cane. 2003. Bumble bees (Hymenoptera: Apidae): commercial use and environmental concerns. In *For Nonnative Crops, Whence Pollinators of the Future?*, edited by K. Strickler and J. H. Cane, 21–40. Annapolis, MD: Entomological Society of America.

Thorp, R. W. 1996. Resource overlap among native and introduced bees in California. In *The Conservation of Bees*, edited by A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, and I. H. Williams, 143–152. London: Academic Press.

Thorp, R. W., A. M. Wenner, and J. F. Barthell. 1994. Flowers visited by honey bees and native bees on Santa Cruz Island. In *Proceedings of the Fourth California Islands Symposium: Update on the Status of Resources*, edited by W. L. Halvorson and G. J. Maender, 351–365. Santa Barbara: Santa Barbara Museum of Natural History.

Thorp, R. W., A. M. Wenner, and J. F. Barthell. 2000. Pollen and nectar resource overlap among bees on Santa Cruz Island. In *Proceedings of the Fifth California Islands Symposium*, edited by D. R. Browne, K. L. Mitchell, and H. W. Chaney, 261–267. Santa Barbara: Santa Barbara Museum of Natural History.

Walther-Hellwig, K., G. Fokul, R. Frankl, R. Büchler, K. Ekschmitt, and V. Wolters. 2006. Increased density of honeybee colonies affects foraging bumblebees. *Apidologie* 37:517–532.

Wenner, A. M., and R. W. Thorp. 1994. Removal of feral honey bee (*Apis mellifera*) colonies from Santa Cruz Island. In *Proceedings of the Fourth California Islands Symposium: Update on the Status of Resources*, edited by W. L. Halvorson and G. J. Maender, 513–522. Santa Barbara: Santa Barbara Museum of Natural History.

Whitehorn, P. R., S. O'Connor, F. L. Wackers, and D. Goulson. 2012. Neonicotinoid pesticide reduces bumble bee colony growth and queen production. *Science* 336:351–352.

Williams, G. R., A. B. A. Shafer, R. E. L. Rogers, D. Shutler, and D. T. Stewart. 2008. First detection of *Nosema ceranae*, a microsporidian parasite of European honey bees (*Apis mellifera*), in Canada and central USA. *Journal of Invertebrate Pathology* 97:189–192.

Williams, P., S. Colla, and Z. Xie. 2009. Bumblebee vulnerability: common correlates of winners and losers across three continents. *Conservation Biology* 23:931–940.

Wills, R. T., M. N. Lyons, and D. T. Bell. 1990. The European honey bee in Western Australian Kwongan: foraging preferences and some implications for management [*Apis mellifera*; shrublands]. *Proceedings of the Ecological Society of Australia* 16:167–176.

Wratt, E. C. 1968. The pollinating activities of bumble bees and honey bees in relation to temperature, competing forage plants, and competition from other foragers. *Journal of Apicultural Research* 7:61–66.