Cavity occupancy by wild honey bees: need for evidence of ecological impacts

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The European honey bee (*Apis mellifera*) is managed worldwide for honey production and crop pollination, and is an invasive species in many countries. Wild colonies occupy natural and human-made cavities and are thought to impact other cavity-using species. We reviewed documented evidence of wild *A mellifera* nesting sites globally via a literature review (27 relevant studies) and citizen-science observations of wild honey bee colonies on iNaturalist (326 observations). Honey bee occupancy rates from published studies were typically low and occupation was often temporary. Citizen-science data showed that most colonies in cavities had small or narrow entrance holes. Current evidence of perceived competition with honey bees in cavities is largely anecdotal and little is known about the long-term impacts on survival and reproductive success of other cavity-occupying species. To guide conservation policy and practice, more empirical research is needed to understand the ecological outcomes of competitive interactions in nesting cavities.

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The European honey bee (*Apis mellifera*), among the most economically important managed bee species worldwide, is renowned for its production of honey and other hive products and its contribution to global crop pollination services. The species' highly generalist traits and utility as a managed pollinator have facilitated its global translocation by humans, resulting in it becoming the most widely distributed managed bee species in the world. As such, however, it is also considered an invasive species in many countries (Vanbergen *et al*. 2018).

Wild honey bee colonies occupy a variety of natural and man-made cavities in their native and introduced ranges (Figure 1). In the process, they interact with multiple animal species that also occupy and use these cavities. In regions where European honey bees have been introduced or are invasive, the presence of feral populations raises concern about potential ecological impacts, including antagonistic interactions with native species (Paini 2004; Stout and Morales 2009; Aizen *et al*. 2014). Most of the research investigating the impacts of *A mellifera* on native species has focused on potential resource competition between introduced honey bees and native pollen- or nectar-feeding taxa around the world (Kato *et al*. 1999; Hansen *et al*. 2002; Thomson 2004). More recently, other negative effects have received attention, such as the bees' role in pathogen transmission (Graystock *et al*. 2016). However, few studies have documented direct effects of honey bees on the community composition, health, abundance, or diversity of native taxa (Mallinger *et al*. 2017), thereby limiting the understanding of how localized observations translate to broader community-level interactions.

In a nutshell:

- Honey bees (*Apis mellifera*) are the most widespread managed insects in the world, and are invasive in many countries
- Wild colonies typically build nests in natural and human-made cavities; in the honey bee's introduced range, it is often claimed that these colonies have detrimental ecological impacts on other cavity-using animals
- Evidence of competition between honey bees and other cavity-occupying species is largely anecdotal, however, and published occupancy rates are typically low
- Additional research is needed to improve understanding of the ecological effects of wild honey bee colonies

Wild honey bees establish colonies in natural cavities, particularly old tree hollows (Oleksa *et al*. 2013; Kohl and Rutschmann 2018). As occupation of tree hollows could displace other native species, it is thought that wild or unmanaged *A mellifera* compete with cavity-nesting birds and mammals, with detrimental effects on the survival and reproductive success of these animals (Paton 1996). This assumption appears regularly in scientific literature, is promoted in popular science and social media, and, in Australia, has been included as evidence for listing "competition from feral honey bees" as a key threat under state environmental legislation (NSW Scientific Committee 2002). However, systematic reviews of the available evidence for this potentially competitive interaction are scarce.

The capacity for wild honey bees to have negative impacts on other cavity-occupying animals likely depends on a range of ecological and local environmental factors. The proportion of obligate cavity-nesting animals varies across regions (Newton 1994), as does the proportion of different animal groups that may utilize cavities in other contexts. The likelihood of

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Figure 1. Examples of feral honey bee colonies: (a) attached to a branch in a forest (Upper Crystal Creek, Australia); (b) on a cliff face above a waterfall (Dorrigo, Australia); (c) within the wall cavity of a building (Mayfield, Australia); and (d) inside a fallen dead tree (Armidale, Australia).

competition between cavity-nesting species may also depend on the availability of suitable cavities in the landscape (Lindenmayer *et al*. 2014). Here, we assess current evidence available on wild honey bee nesting sites, and evaluate the potential for competition for nest sites between wild honey bees and cavity-occupying birds and other animals. We highlight key knowledge gaps and identify major research questions that require immediate attention to increase understanding of the impact of nest-site interactions between wild honey bees and other animals. More evidence of the spatial and temporal scale of these interactions and their ecological outcomes is essential to inform conservation policy aiming to protect biodiversity from threatening processes associated with this species in its introduced range.

Methods

We used a multistage comprehensive search strategy to collate available evidence of wild *A mellifera* nesting sites in their native and introduced range. We conducted (1) a traditional literature review using the Scopus database and (2) a search of the iNaturalist database to collate citizen-science observations of wild honey bee colonies in areas where the species has been introduced and within its native range.

To collate peer-reviewed literature documenting natural nest sites of wild *A mellifera*, we conducted a systematic search of the Scopus literature database using two search strings: (1) (TITLE-ABS-KEY ((honeybee OR "honey bee" OR "Apis mellifera")) AND TITLE-ABS-KEY ((feral OR wild OR unmanaged)) AND TITLE-ABS-KEY ((nest OR colony OR comb OR hive))); and (2) (TITLE-ABS-KEY ((honeybee OR "honey bee" OR "Apis mellifera")) AND TITLE-ABS-KEY ("nest box")). Searches were conducted in March 2020 and returned a total of 556 papers, which were screened to remove irrelevant papers. Our goal was to identify scientific publications that documented original data on nesting sites of unmanaged honey bee colonies, and therefore studies of managed bee colonies, simulated data, reviews, and opinion papers were not included (however, relevant review or opinion papers were screened for other empirical references). We further supplemented the database searches with papers sourced from the references of relevant papers and Google Scholar searches using combinations of the search terms. In combination, these searches yielded a total of 27 papers that documented original data on wild *A mellifera* colonies in tree hollows, nest boxes (defined here as boxes deployed to provide nesting sites for vertebrates, not pheromone traps targeted at swarming bees), or other cavities.

To collate recorded citizen-science observations of wild honey bee colonies, we used the iNaturalist database. We searched *A mellifera* observations (over 74,000 observations) and saved nest-site observations to a dedicated project page on the iNaturalist website (www.inaturalist.org/projects/feral-honey-bee-hives) to aid data collection. Data were searched in batches by country (eg Australia) or continental regions (eg Europe). For each region, we first filtered the total results to search for observations tagged with the words "nest", "colony", or "hive", and collated all relevant observations. Second, because not all users tag their observations with notes or keywords, we then searched through the remaining observations. For regions with more than 3,500 observations, we searched until at least 3,500 unique observations had been screened; this number was chosen as a threshold because the majority of countries had fewer than 3,000 records. Observations with poor-quality photos that made it impossible to identify local context or substrate of the nest were excluded. This process resulted in 326 observations of wild honey bee colonies that met our search criteria. From each of these observations, we extracted data on the country of observation, whether the combs were exposed or internal, what substrate the combs were attached to, and the size or characteristics of the nest entrance.

Results

Literature search

We found a total of 27 studies that documented use of cavities by wild honey bee colonies (1) in areas where *A mellifera* has been introduced and (2) within the species' native range (WebTable 1). Of the areas where the honey bee has been introduced, most studies were carried out in Australia (*n* = 10) and the US (*n* = 10), with the remaining studies conducted in South America (Brazil and Argentina; *n* = 2). In regions where *A mellifera* is endemic, studies were performed in Africa (South Africa, Kenya; *n* = 3), Europe (Germany, Poland; *n* = 2), and West Asia (Israel; *n* = 1). All of the studies were subject to selection bias because authors documented nest sites based on pre-selected criteria (ie known locations) or that were part of experimental treatments (eg nest-box deployment). Published studies typically involved measurements of characteristics of known bee nest locations, surveys of known areas specifically for tree cavity nests, or determinations of occupancy rates in nest boxes established specifically for experimental purposes.

Evidence of interspecific competition directly attributed to cavity occupation was limited. Sixteen studies did not provide any information about interspecific competition (WebTable 1), and only a single study included an anecdotal observation that direct competition occurred ("in one season [1975] two nests failed [one on eggs, one on nestling] because bees swarmed into the hollows and established hives there"; Saunders 1979). Studies that inferred potential competition largely focused on birds and a few charismatic mammal species, whereas impacts on other animals were largely unexamined (eg other invertebrates, bats; Welch and Leppanen 2017). Even so, evidence and inferences presented in the remaining studies suggested that direct competition impacting bird survival and reproductive success was rare. In studies in which occupancy rates across comparative sites (eg nest boxes) were empirically measured, honey bee occupancy rates were typically low (less than 10%). Multiyear studies often showed that nest occupancy was temporary, and several studies reported that birds and other animals were not deterred from using sites formerly occupied by honey bees.

Citizen-science observations

Our search process sourced 326 photographic observations of wild honey bee nests on iNaturalist: 260 in the species' introduced range and 66 in the native range. Most nests (86%) were aboveground, 12% were at ground level (eg at the base of a tree), and nine nests (2.8%) were underground. Most observations (65%) depicted internal nests constructed within a natural or artificial cavity, while the remaining nests were exposed combs attached to a substrate. Of the internal nests (*n* = 211), 57% had small or very small entrance holes, 26% were entered via a narrow slit, and 15% had wide entrances (Figure 2). Four nests were located within internal cavities of houses that had been exposed through renovations; because entrance holes could not be identified in these cases, they were therefore categorized as "unclear".

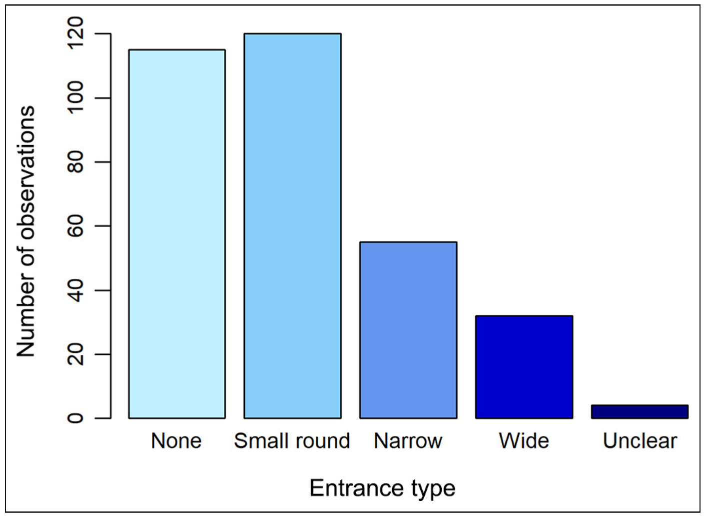

Figure 2. Number of honey bee nests with different entrance sizes. "None" indicates exposed nests that did not occupy a cavity. "Small round" refers to entrance holes that are round holes of approximately <10 cm (eg wood knots in a tree trunk). "Narrow" refers to narrow slits (eg in tree trunks), approximately 1–2 cm wide. "Wide" refers to large and open entrance holes. "Unclear" indicates nests inside buildings where entrance holes could not be identified.

Most of the nests (internal and exposed) were attached to natural substrates (Figure 3), such as tree trunks or branches (external attachment and internal cavities), cliff faces, and eroded soil or rock cavities. A total of 48 nests were built within human structures, including buildings, bridges, underground and aboveground utility meter boxes, and hollow concrete poles. A few colonies were located in abandoned nests constructed by other animals: for instance, a termite mound and an underground wombat burrow.

Discussion

Understanding the circumstances in which cavity-nesting species interact with one another in native and introduced ranges is essential to inform sustainable conservation and management policies. Current evidence of perceived competition between honey bees and other cavity-nesting taxa is largely anecdotal and based on short-term observations. Importantly, our review does not confirm that wild honey bees have neutral or positive effects on other cavity nesters; rather we show that data are currently limited and that there is a need for more research to confirm the scale and magnitude of their ecological effects (Panel 1). There are many outcomes of wild honey bee colony occupancy that remain unknown and require further study, including how

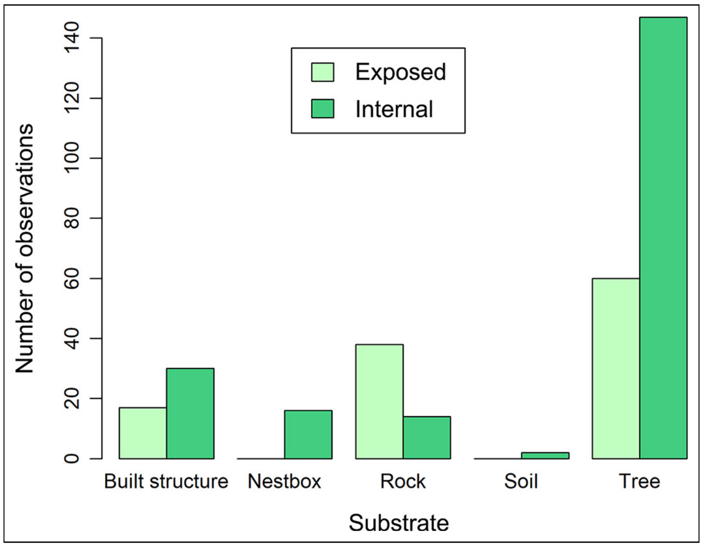

Figure 3. Number of honey bee nests (internal and exposed) attached to different substrates. Not included in the graph were nests constructed within a Saguaro cactus (*Carnegiea gigantea*) and inside a termite mound.

bees affect local wildlife diversity and communities of interacting species, such as plant–pollinator networks.

The current literature indicates that permanent displacement of other animals by *A mellifera* may be rare. In several studies, the authors noted that vertebrates used artificial nest boxes in subsequent years (Delnicki and Bolen 1977; Goldingay *et al.* 2015), while others noted that honey bees shared cavities with vertebrates and invertebrates (McComb and Noble 1982). Of the studies that documented honey bee use of nest boxes or tree cavities, most showed that *A mellifera* occupancy rates were typically low. In addition, multiyear studies often noted that most colonies only temporarily occupied cavities. These findings likely reflect the influence of climate, parasites, pathogens, and resource availability in driving honey bee colony growth, survival, and swarm behavior under natural conditions (Winston *et al.* 1981). Wild colonies generally survive for only a few years and swarm frequently (Loftus *et al.* 2016; Seeley 2017). They may also be less likely to survive in harsh environments or where they face greater exposure to predation by humans and other vertebrates (Kajobe and Roubik 2006; Moritz *et al.* 2007) or pests and pathogens (Manning *et al.* 2007; Thompson *et al.* 2014; Youngsteadt *et al.* 2015). Yet, while the capacity of wild honey bee colonies to permanently displace other cavity-nesting animals appears limited, the spatiotemporal magnitude of their ecological effect is most likely dependent on species identity and environmental context.

Studies documenting nest-site characteristics of wild honey bee colonies suggest that they may prefer large internal cavities – often in large old trees – with moderate exposure, and generally with small or narrow nest entrances that are at least 3–5 m above ground surface (Seeley and Morse 1976, 1978; Avitabile *et al.* 1978; Oldroyd *et al.* 1994). Our assessment of iNaturalist observations agrees with these generalizations. Competition would potentially occur with other cavity-nesting animals that prefer similar cavities; however, we could not locate a quantitative assessment of honey bee nest-site attributes globally, and therefore it is unclear how these observations compare across different habitats or bioregions. In addition, a systematic assessment of nest-site preferences for other cavity-nesting animals would be necessary to determine the likelihood of competition with honey bees, and this is likely to vary depending on species (including a species' ability to excavate or enlarge holes), habitat type, and climate regions (Gutzat and Dormann 2018). In Australia, previous studies of nest characteristics of black cockatoos (*Calyptorhynchus* spp) suggest no particular preferences for nest sites, but it is possible they are more likely to use hollows with larger entrances (Saunders 1979; Johnstone *et al.* 2013), which honey bees may avoid. In modified landscapes, honey bees may also be more likely to use cavities in anthropogenic structures, such as buildings or farm infrastructure (Morse *et al.* 1990; Manning *et al.* 2007), which are less likely to be used by cavity-nesting vertebrates. Reptiles and invertebrates would be the most likely animals to prefer similar cavities to honey bees, and anecdotal evidence from the studies we sourced in our review suggest that these animals are less likely to be deterred by the presence of honey bees (McComb and Noble 1982), but no research has tested these relationships empirically. Several studies found that native social wasps had higher occupancy rates than honey bees, were often more aggressive, and were more likely to displace vertebrates (McComb and Noble 1982; Twedt and Henne-Kerr 2001). In some cases, it was difficult to determine actual occupancy rates of honey bees because the authors grouped wasps and bees together in their data (Lindenmayer *et al.* 2009; Liébana *et al.* 2013).

More than half of the relevant studies we sourced through the literature review focused on vertebrate-targeted nest boxes,

Panel 1. Priority research questions to understand the ecological effects of wild honey bees on cavity-occupying animals

- How do wild honey bee colonies interact with non-avian cavity-using animals?
- How do wild honey bee colonies interact with other animals in nest boxes compared to natural cavities?
- How do wild honey bee colonies interact with other cavity-using animals in their native range compared to their introduced range?
- How does wild honey bee colony occupancy of a cavity affect the health, survival, reproductive success, abundance, and diversity of animal species that use the same cavity?
- How does wild honey bee colony occupancy of a cavity affect pollinator community composition and effectiveness, or plant–pollinator network structure?

and these often reported higher occupancy rates than studies based on surveys of natural systems. Anecdotal evidence of competition is possibly biased by detectability (ie people are more likely to witness competition occurring in experimental systems when they are monitoring nest boxes or designated cavities). For example, a study of nest-site competition among bumblebees, social wasps, and cavity-nesting birds in the northern hemisphere found no empirical evidence of widespread competition, and concluded that anecdotal evidence appears to be a "nest-box phenomenon", whereby social insects may occasionally interfere with nest-box studies but their effect appeared to be negligible in natural nests (Broughton *et al.* 2015).

Our review highlights the lack of evidence available to support claims of competition between wild honey bees and cavity-nesting animals. More published studies are available of artificial nest boxes intended for vertebrate use than of natural systems, which could lead to overestimates of the likelihood of competition. It is well known that wild honey bee colonies are difficult to detect in natural systems, even with targeted searching, and therefore detectability in artificial nest boxes deployed as part of an existing research project will be much higher. The observations collated from iNaturalist citizen-science records illustrate the potential for honey bees to occupy natural cavities that may be used by other animals, but do not provide evidence that competition occurs. Although most observations were of aboveground nests inside tree cavities, entrances to these nests typically consisted of very narrow slits or small knot-holes in trunks and branches. These holes are likely too constricted for most birds and mammals to enter and establish a nest (without further excavation), but could be used by small reptiles or other invertebrates. Because the iNaturalist observations are biased by detectability (exposed aboveground colonies are more likely to be observed and recorded, and countries with fewer iNaturalist users will be undersampled) and do not provide any information on colony age or survival, they cannot provide evidence of long-term effects. They do, however, illustrate the wide range of locations and substrates that unmanaged honey bees use for nest construction. Urban pest controllers or beekeepers, who are often brought in to remove honey bee colonies from buildings and recreational areas, potentially represent additional sources of data, and targeted interviews of these practitioners may provide further insight into wild honey bee nesting sites and potential for competition with other animals.

Conclusion

There is limited understanding of the long-term impacts of honey bee cavity occupation on the survival and population viability of other cavity-nesting species. Current evidence of perceived competition is largely anecdotal and based on short-term observations. There are many outcomes of wild honey bee colony occupancy that are still unknown and require further research (Panel 1), particularly the potential effects on community-level interactions and ecological processes.

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2347/suppinfo