

Aspects and consequences of competition

The effects of honey bees (Apis mellifera) on wild bee populations

Front cover picture by Annette Meyers, retrieved from https://pixabay.com/photos/lavender-flowers-purple-bloom-4348354/ on 09-05-2020

Abstract

Pollinator populations have been experiencing increasing pressures in recent years, constituting to population declines. Decreases in abundance of wild bee and honey bee populations have sparked the interest in conserving and protecting pollinators. However, in addition to the existing danger of diseases, pesticides, parasites, and predators, the introduction of honey bees has been hypothesised to threaten native pollinator populations. This leads to the question "How do honey bees (Apis mellifera) affect native bee populations?". To answer this question, different aspects of competition and their consequences have been discussed, including interspecific and intraspecific interactions, resource overlap and resource harvesting, visitation rates, aggressive interactions, and resource partitioning. Furthermore, it has been discussed whether or not the effects of honey bees differ depending on whether they were introduced within or outside of their natural distribution. Most competitive interactions between honey bees and native pollinator populations result in negative or no impacts on the native species. It seems that impacts of honey bees introduced outside of their natural distribution are mainly negative, whereas introduction within the natural distribution seems to mainly have no impact. Aggressive interactions are mainly interspecific, but occur as intraspecific as well. Resource partitioning could limit competition between honey bees and wild populations, however, this may only be possible in flower-rich, heterogeneous habitats.

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Introduction

Pollinator populations have been under increasing pressure in recent years, following dangers posed by diseases, pesticides, parasites and predators (Roffet-Salque et al., 2016). As a result, populations decline. This decline in pollinators, among which are wild bees and honey bees (Apis mellifera), and the realisation of the importance and need for pollinator conservation have become more pronounced for both scientists and the public (Cane & Tepedino, 2017). As a result, there has been a great interest concerning wild and agricultural pollination to preserve and promote bee populations (Roulston & Goodell, 2011).

Humans have been associated with honey bees since as early as approximately 9.000 years ago (Dams & Dams, 1977). It has been found that the exploitation of honey bees for their honey and beeswax has been happening continuously through the ages, however, it is unknown exactly where and when the regular association of honey bees with beekeeping came to be (Roffet-Salque et al., 2016). Honey bees occur naturally in large parts of Eurasia and Africa (Figure 1.) (Borst, 2015). From the four presented species of honey bees in Figure 1., A. mellifera is most commonly known to be a domesticated species Figure 1. Natural distribution map of the modern honey bee. which is kept by beekeepers. However, honey



Adapted from (Borst, 2015).

bees have also been introduced outside their natural distribution. This led to A. mellifera becoming a worldwide managed agricultural species. Recently, it has become a more pressing question whether or not these introduced honey bees form a potential threat to native pollinators. It has been suggested that introduced managed honey bee colonies could threaten wild bee populations due to their presence in large numbers (Requier et al., 2019). This presence could also trigger competition between honey bees and wild bees, for example, intra- and interspecific competition for resources (Paini, 2004). Reductions in bee diversity caused by competition with honey bees can lead to insufficient pollination of crops in agricultural fields, resulting in lower crop yields, as A. mellifera deems to be an inefficient pollinator for such purposes (Franklin, Carroll, Blake, Rickard, & Diaz, 2018). Thus, taking into consideration that bee populations are already experiencing stress due to modern disturbances as named above, wild bees may also experience negative effects caused by introduced honey bees.

This leads to the question 'How do honey bees (A. mellifera) affect native bee populations?'. To answer this question, competition between honey bees and wild bees will be discussed, as well as what the consequences of competition are. In addition, a comparison will be made between honey bees that have been introduced within and outside of their natural distribution.

Competition and Consequences between Honey Bees and other pollinators

Competition occurs when individuals within (intraspecific) or between (interspecific) species compete for a limited resource, which for example could be nesting grounds, pollen, or nectar. When competition for a resource occurs, it can result in negative consequences for one or all parties involved, however, usually one party will suffer more, such as reductions in survival, reproduction and growth (Paini, 2004). Multiple aspects of competition will be discussed in this essay, including resource overlap, resource harvesting, visitation rates, aggressive interactions, and resource partitioning.

Competition between honey bees and native pollinators is mainly triggered by honey bees foraging at the same sites as native populations. When honey bees additionally forage on the same flowering species, and subsequently remove certain amounts of resources, there are two possible outcomes. 1) only a small amount of resource is harvested, which has minimal or no further effects on native bees and flora, or 2) a substantial amount of resourced is harvested. When this second option happens, there could be potential effects on flora and fauna, however, only fauna will be discussed in the form of native bee populations for this essay. Such effects on native bees depends on whether the resource, such as pollen and nectar, is limited or unlimited. Substantial harvesting of resources from an unlimited source would lead to minimal competition, whereas a limited resource would lead to competition (Figure 2.) (Butz Huryn, 1997).

In a review article, Paini (2004) discusses a multitude of studies investigating the impact of honey bees on native bees. The studies had been



Figure 2. Potential effects of honey bee foraging on native flora and fauna. Heavier arrows indicate a potential for stronger effects. Adapted from (Butz Huryn, 1997).

grouped into the different measurements that had been used to determine the impact, which were resource overlap, resource harvesting, visitation rates, adult survival, fecundity, and population density (Paini, 2004). Here, resource overlap, resource harvesting, and visitation rates will be further discussed, as these interactions lay the basis for competition as a result of foraging by honey bees as can be seen in Figure 2. Adult survival and fecundity will not be discussed here, as these aspects are for most parts not directly influenced by honey bees.

Resource overlap and harvesting

Resource overlap occurs when multiple species, in this case *A. mellifera* and native bee populations, coexist in the same area and additionally share the same resources such as flower species. Such floral resources, which consist of pollen and nectar, are the primary food source for both adult and larval bees. Whereas nectar is the main energy source for the adult workers, both adults and larvae consume pollen (Requier et al., 2015). Thus, if competition were to arise due to a limited

resource, either one or both species will experience losses in food income, which in turn could lead to lower fitness and reduced survival.

'If two species compete for a resource, it must be limiting in such a way that an increase in resource harvest by one species corresponds to diminished harvest by the other,' (Roubik, 1978).

Research on how introduced honey bee densities affect native bee populations has been conducted by experimentally manipulating the

Forager	Floral resource					
class	Mimosa*	Rhynchospora	Melochia	Borreria		
Africanized honey bees						
During	9.6	81.5	111.3	371.0		
After	0.0	7.5	72.0	365.0		
F ratio	25.78†	27.89†	8.11±	0.05		
Stingless bees§				0100		
During	25.3	65.6	23.3	124.5		
_	32.0¶					
After	19.1	100.0	61.0	189.5		
	44.5¶			10710		
F ratio	2.10	1.08	6.80±	14.5†		
	2.26					
Other native foragers						
During			51.8	22.5		
After	Not present	Not present	60.1	59.0		
F ratio	-		2.32	11.89†		

*Bees per 100 flowers. †P < .001. ‡P < .05. §Mimosa: Melipona fulva and M. favosa favosa; Rhynchospora: Trigona (Tetragonal) clavipes; Melochia: M. fulva and T. (Trigona) cilipes: Borreria: M. fulva, M. favosa favosa, and T. (Trigona) cilipes. Melipona fulva. ¶Melipona favosa favosa.

Table 1. F ratios for mean daily forager number during the presence and after removal of Africanised honey bee hives. Degrees of freedom are Mimosa (1,12), Rhynchospora (1,18), Melochia (1,8), and Borreria (1,12). Adapted from (Roubik, 1978).

number of invasive bees present. Due to low densities of Africanised honey bees, which is a feral hybrid of the African and European A. mellifera, at the time of experimentation, Roubik (1978) manufactured hives by capturing feral Africanised honey bee swarms and transferring them. While being used in the experiments, each hive contained around 6.000 to 15.000 bees. The hives were first placed and later removed near areas of flowering plants, which were visited by native stingless bees, wasps, flies, and other bees, as well as the Africanised honey bees (Table 1.). Pollen collected by foraging bees were solely derived from Rhynchospora and Mimosa, however, both pollen and nectar were taken from other flowers (Roubik, 1978). This would suggest that competition for pollen on Rhynchospora and Mimosa would be higher compared to other flowering species.

Following increases in number of the Africanised honey bees on *Melochia villosa*,



Figure 3. The relations of Africanised and stingless bee abundances on flowering Melochia villosa. The dashed line gives the best fit to the points in the form of a quadratic polynomial (given by $y = -0.516 + 1.08x - 0.023x^2$). Adapted from (Roubik, 1978).

stingless bees became less abundant (*Figure 3*.). Similarly, after removal of the bee hives, abundances of stingless bees increased again (Roubik, 1978). This supports the hypothesis that the presence of honey bees negatively affects the abundance of native bee populations.

Visitation rates

Visitation rates of pollinators on certain flowering species could provide information on whether there may be competition between pollinator populations, or if perhaps resource partitioning is taking place (*Figure 4.*).

As a foraging bee, it is of importance to maximise resource harvest relative to the cost of harvesting (Roubik, 1981). Thus, if competition were to displace a species from their resource, this species has to readjust to find a new way to maximise. To induce intense competition between native stingless bees (*Trigona corvina*) and introduced honey bees (*Apis mellifera*), Roubik (1981) surveyed a site with flowering plants (*Baltimora recta*) which were visited by both bee species, and removed a large portion of these plants. As a result of plant removal, resource abundance declined and the number of honey bees within adjacent study plots rose by 44%, whereas the abundance of stingless bees remained stable with an increase of only 17% (Roubik, 1981).

When determining floral visitation rates, Roubik (1981) looked at the average duration of three successful floral visits. Overall, visitation rates of honey bees were relatively constant, foraging for 14.3 to 16.1 seconds per three flowers. In contrast, stingless bees foraged for 23.0 to 27.9 seconds per three flower visits, in addition to experiencing an increase on one day. Over the course of the experiment, the means of floral visitation by stingless and honey bees were 25.6 and 15.1 seconds per three flowers, respectively (Roubik, 1981).

Successful floral visits had been defined by Roubik (1981) as visits during which the forager obtained nectar in the manner of 'multiple probing of florets by a bee on a flower'. The lower foraging time of honey bees can be explained by both their somewhat larger size than stingless bees, as well as honey bees landing near the flower's centre instead of landing on ray petals like stingless bees did (Roubik, 1981). It would seem that less time spent on floral visitations would imply better maximisation of resource harvesting, and thus that honey bees are superior to stingless bees. However, in his article, Roubik (1981) does not specify whether this is true or not, as only the mean times spent are given without further conclusions (Roubik, 1981).

Aside from measuring visitations, aggressive behaviour was also studied. After removal of the flowering plants, aggression by the stingless bees in response to the sudden increase in honey bee abundance. Both interspecific and intraspecific aggression had been observed. However, there was only one act of intraspecific aggression, which took place among stingless bees, whereas interspecific aggression towards honey bees had been observed on multiple occasions, totalling 11 interactions. Contrary to the stingless bees, honey bee workers were not aggressive (Roubik, 1981). From this behaviour it seems that stingless bees consider honey bees a threat, while honey bees do not consider stingless bees as a threat.

After removal of the flowering plants, stingless bees did not appear to shift to new foraging areas. Furthermore, proportionally more stingless bees abandoned *B. recta* in plots where flowering plants were removed than honey bees. By remaining in place while resources have been reduced suggest that aggressive stingless bees would rather fight for a foraging territory than scout for areas with



Figure 4. Flow chart depicting possible outcomes following competition between honey bees and native bee for floral resources. Adapted from (Paini, 2004).

less competition. Such foraging tactics are likely to be fitting in situations where other aggressive foragers have saturated the resources, or where bees will more easily leave when being attacked. However, as has been proven by this study, the stingless bees' foraging tactics had no significant effect on the foraging activity of honey bees. Honey bees are more flexible foragers when it comes to changes in resources, as can be concluded by honey bees quickly invading favourable foraging areas, giving them a competitive advantage over stingless bees (Roubik, 1981).

Aggressive interactions

Competition can lead to aggressive interspecific and intraspecific interactions. Such aggressive interactions are generally initiated by social insects towards individuals from other species and colonies. As a result of interaction with these aggressive bees, inferior bees may be displaced from their resources (Dworschak & Blüthgen, 2010). Being displaced from preferred resources could lead to a shift towards foraging less optimal resources, lowering fitness and thus survival rates.

Additionally, aggressive interactions can lead to one individual or species inflicting physical damage onto another individual or species. One example of such severe interspecific aggression between native bees and *A. mellifera* is highlighted in the box below as a case study on the article 'Fatal Attraction of Certain Large-Bodied Native Bees to Honey Bee Colonies' (Thoenes, 1993).

Case study - 'Fatal attraction of certain large-bodied native bees to honey bee colonies'

Thoenes (1993) set up a study to determine the response of native bees to the physical presence of honey bee colonies. In this study, 36 colonies of honey bees (*A. mellifera*) were equipped with "Todd dead bee traps", designed to catch any deceased insect over 1 centimetre in length that is removed from the colony. The colonies were moved into a new area and inspected three times per week over a period of nine months. At three and a half months in, an active bumble bee (*Bombus pennsylvanicus sonorus* Say) colony had been noticed at a distance of about 100 metres from the apiary site. After discovery, the bumble bee nest was carefully fully uncovered, and subsequently a wooden cover was installed to allow for observation of the nest with minimal disturbances. Additionally, any presence of bumble bees in the area of the apiary was noted, alongside the recording any bumble bee/honey bee interaction throughout the sampling period, with the bumble bee colony being attacked and destroyed by a rodent somewhere between August 15th and September 1st.

The experiment resulted in a total of 147 dead workers of *B. sonorus* in the dead bee traps from July 5th through August 2nd, however, no bumble bee queens were found. Additionally, they found five dead female carpenter bees (*Xylocopa californica arizonensis* Cresson).



Not only is the found number of dead bumble bees a clear sign of aggression from the honey bee colonies, the state that they were found in is too. As can be seen in the left photograph above (*A.*), several bumble bee worker corpses were found with dead honey bee corpses still attached to the bodies. These were either intact or only the heads of honey bees, with their mandibles still tightly attached to the corpse of the bumble bee. Moreover, several of the bumble bees were still covered by 15 to 20 live honey bees at the time of collection. These honey bees were described as being "balled" around the corpse. As for the photograph above on the right (*B.*), the image depicts bumble bee workers stripped of their dense body hair. The majority of bumble bees were found in states as such, where honey bees had partially or completely rid them of body hair. Additionally, some of the bumble bees' wings, legs, and antennae were either partially or completely damaged.

Honey bee colonies experience the evaporation of large quantities of water from fresh mesquite nectar at a certain time of the year. During this time, all native bees had been found in the dead bee traps. This indicates that the foraging native bees were attracted to the mesquite floral volatiles coming from the honey bee colonies. The bumble bees' large size enables the honey bees to attack them *en masse*, resulting in bumble bees getting "balled" by the honey bees.

The loss in number of workers for the bumble bee colony leads to it being more vulnerable with respect to attacks from a variety of enemies. It is hypothesized that this was also one of the factors accounting to the destruction of the bumble bee colony nearby the apiary.

In conclusion, when honey bee colonies are physically located in a natural environment, it can result in negative impacts on native bee populations due to honey bees weakening colonies.

Concerning competition between bees, it seems that interspecific competition occurs most often, wherein *A. mellifera* emerges victorious over native bee populations. Intraspecific aggression has been briefly mentioned before where one aggressive intraspecific interaction took place between stingless bees. However, aggressive intraspecific interactions also occur on larger scales. For example, when studying Africanised honey bees in Yucatan, Mexico, Roubik & Villanueva-Gutierrez (2018) found that alongside interspecific aggression, intraspecific aggression also regularly took place. Nearly two thirds out of all 7578 recorded aggressive interactions were denoted as intraspecific aggression (*Table 2.*). Taxa among which intraspecific aggression was most intensive were *Apis, Cephalotrigona* and *Trigona* (Roubik & Villanueva-Gutierrez, 2018). When looking at *A. mellifera* in particular, there were 1047 interactions between them and ten native species. 44 of these interactions included aggression by *A. mellifera*, which often occurred against large polistine wasps. However, *A. mellifera* suffered from persistent aggression as well by the common *Trigona fulviventris* (Roubik & Villanueva-Gutierrez, 2018).

It appears that the invasive *A. mellifera* population's only notable aggression was intraspecific. However, during uncommon circumstances under crowding during feeding, the invasive bees would lunge at, but refrain from biting, native species (Roubik & Villanueva-Gutierrez, 2018).

Taxa*	N total interactions	N Intraspecific attacks	N Interspecific attacks*	Total site days	Intraspecific attack site days	Mean interspecific aggression per site-day**
Apis mellifera	1227	131	44	23	8	2.5
Cephalotrigona	2016	744	1272	39	12	39.8
Trigona	469	227	242	40	12	4.9
Plebeia	1578	440	1138	46	16	9.3
Frieseomelitta	1661	456	1205	28	7	35.7
Polistinae	387	0	387	10	0	10.9

Table 2. Observation summary. *N attacks by listed taxa, species given in article; Plebeia and Polistinae are of >1 species.

 **Mean of total interspecific attacks per site-day.

 * total interspecific attacks per site-day.

Adapted from (Roubik & Villanueva-Gutierrez, 2018).

Resource partitioning

Competition between species can be limited if they could be practising resource partitioning, where limited resources are divided among species. For example, foraging abundances of bumble bees and honey bees have been studied on heathlands across the Poole Basin, Dorset, UK. Heathlands were chosen as study ground, probably due to their mosaic layout of varying habitat types, including dry, wet and mire habitats. Additionally, high floral densities can be found at the chosen location. Furthermore, the amount of available forage dynamically changes starting before May, and continuing throughout summer (Franklin et al., 2018).

The initial assumption that competition for resources would arise, can be derived from physical similarities between the species. Bumble bees have comparable tongue lengths to honey bees, especially short-tongued bumble bees. Due to this similarity, niche overlap and foraging competition between the species becomes highly likely, as tongue length determines the accessibility of resources (Franklin et al., 2018).

In the study mentioned above, 60 heathlands were surveyed twice per months for the months July, August and September. The identified pollinators were *A. mellifera*, and multiple bumble bee species. Interestingly, out of the bumble bee species, most had relatively shorter tongue lengths. Logically speaking this would result in higher competition found with *A. mellifera*.

However, it has been found that when both bumble bees and honey bees are present at the same site, there is only a weak negative correlation between honey bee abundance and bumblebee abundance (Figure 5B.). The separate presence of bumble bees or honey bees at a site were positively correlated with only the percentage floral cover of E. cinerea and C. vulgaris respectively (Figure 5A.). E. cinerea and C. vulgaris are both characteristic for dry heaths. Bumble bees and honey bees therefore share the same habitat, while experiencing limited competition due to the partitioning of resources (Franklin et al., 2018).

As for this study on resource partitioning by bumble bees and honey bees in heathlands, it should be noted that



Figure 5. (A) The mean number of bumble bee (dark) and honey bee (light) observations. (B) The number of sites shared by bumble bees and honey bees (BB and HB respectively), and those with only one of either species out of a total of 30 sites per month. Dark bars represent wet heath, light bars represent dry heath. Adapted from (Franklin et al., 2018)

resource partitioning was likely possible due to the heterogeneity of the landscape. Thus, the availability of both wet and dry heaths alongside vast floral resources may have enabled bumble bees and honey bees to coexist with limited competition. However, not all habitats in which bee populations exist provide such circumstances. For example, agricultural systems experience high fluctuations in forage availability as a result of mass flowering (Franklin et al., 2018). To further enable resource partitioning among bee populations worldwide in an attempt to reduce declines, attempts should be made to create more fitting heterogeneous sites. If such sites were to be created with the resource needs of *A. mellif*era in mind, it could be possible that the artificially placed flowering species shift foraging by honey bees away from wild bee populations. The decreased presence of *A. mellifera* would allow for the wild bees to forage more freely, possibly increasing their fitness and thus survival, which in turn is beneficial for colony growth.

The impact of introduced Honey Bees in relation to geographical location

Most published articles that discuss the introduction of honey bees are composed of studies on interactions between *A. mellifera* and native bee populations outside of the honey bee's natural distribution. This is a logical choice due to the possible drastic effects that a new species could bring with them as they are invasive to the native area. However, due to the declines in bee populations in general as mentioned before, it is also necessary to study whether honey bees affect wild bee populations within their natural distribution as well. When analysing the previously mentioned review by Paini (2004), Table 3 can be constructed. Out of all papers that had been reviewed, only four out of thirty-seven were studies done on honey bees within their natural distribution. Three out of the four studies (75% no impact) have found that the impact of honey bees on native bees were not significant, whereas only one found that there was a negative impact.

Impact	Within	Outside
Negative	1	23
None	3	7
None/positive	-	2

Table 3. Analysis of the review papers by (Paini, 2004).

When comparing this to the studies done outside of the natural distribution (32 studies), it appears that there are proportionally more studies that have concluded in a negative impact of honey bees instead of resulting in no impact, with respectively twenty-three and seven studies (21.9% no impact). However, due to the little number of studies within the honey bee's natural distribution, it cannot be said with certainty that most introduced honey bees within their natural distribution have no impact on native pollinator species. So, even though the reviewed studies within the natural distribution, it could still provide an indication as to whether negative impacts are to be expected or not.

Discussion

Most cited literature on competition between honey bees and native pollinators appears to be quite old, ranging from 10 to 60 sixty years (e.g. Ginsberg, 1983; Roubik, 1978; Sakagami, 1959; Wratt, 1968). It speaks for itself that experiments done such a long time ago might not lead to the same conclusions if they were to be done nowadays. Climate change has led to global warming over the past 50 years, which affects surface air temperatures (Oreskes, 2004). Research has already shown that due to climate change, the area of suitable habitats of all present bees species has declined in Brazil (Giannini et al., 2012). In order to assess whether or not conclusions made over 10 years ago can be extrapolated to future events or that they are outdated, similar experiments should be done to compare if there have been significant changes.

In addition to retesting old papers, it would also be interesting to research competition between honey bees and other pollinators that are not bees, flies, or wasps. Such pollinators could be ants, bats, and nectarivorous birds. Some research has already been done on these species. For example, Schaffer *et al.* (1983) found that by excluding ants, the available nectar to bees was increased, as the ants foraged on the flower's stalks during both day and night. Due to stalk's secretion of 90% of its nectar at night, ants had an advantage over bees since bees only foraged during the day. Therefore, it was possible for the ants to consume $\approx 85\%$ of the overnight accumulation, leaving less nectar available for the bees (Schaffer et al., 1983). It thus appears that instead of honey bees emerging victorious, they now suffer from competition other than bees.

However, in other instances honey bees still remain the victorious party as has been found by Hansen *et al.* (2002), where they studied competition between introduced honey bees and endemic nectarivorous birds. The birds only fed on certain flowering species in the early morning, until the activity of foraging honey bees quickly lowered nectar standing crops. Other flowering plant species that were less exploited by the honey bees still remained attractive for the birds, as they kept nectar feeding on them. So, in this case honey bees actually not only cause negative impacts on the nectarivorous birds, but on the flora as well because they replaced the birds as pollinators of the flowering plant species, yet were less efficient in doing so (Hansen, Olesen, & Jones, 2002).

Besides competition for food resources, there can also be competition for nesting sites. For example, by occupying tree cavities, feral honey bees exclude other roosting species such as endangered bat species for about three to seven years. However, impacts on bat populations are not just dependant on the frequency of occupation of cavities by honey bees, but also the overall availability of cavities (Welch & Leppanen, 2017). Perhaps by providing artificial tree cavities, competition for this resource could be lowered. This could improve survival for both bee and bat populations, which is desirable, as both species are experiencing pressure and declines.

Conclusion

Managed honey bees have been introduced worldwide for economical and agricultural purposes, both within and outside their natural distribution, with competition as a result. Competition can lead to losses for one or both parties involved, which results in reduced survival. It mainly seems that honey bees either have a negative or no impact on native bee populations. However, outside their natural distribution, negative impacts appear to occur more often than no impact, whereas within their natural distribution no impact seems to occur the most. Nonetheless, the evidence supporting the "no impact within the natural distribution" is weak due too little available literature. Extreme competition can take place in the form of aggression, where, in the discussed case, honey bees attacked *en masse* and killed bumble bees. Nonetheless, competition can also be limited when honey bees and wild pollinator populations practise resource partitioning, allowing for co-occurrence of the species. However, resource partitioning might only be possible in a flower-rich, heterogeneous habitats.

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