Best practices for colony management: A neglected aspect for improving honey bee colony health and productivity in Africa

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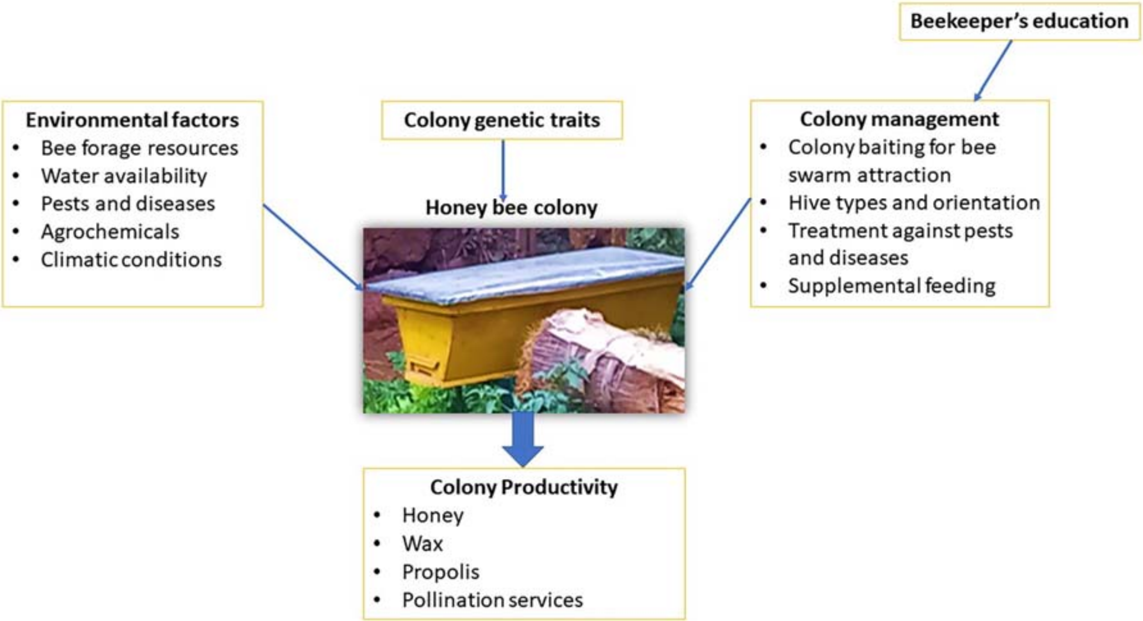
Abstract

Apiculture has a well-recognized role in enhancing food security by pollination services around the globe. Besides, apiculture is an extremely valuable income-generating and job-creating activity for millions of men, women, and youths across Africa through trade of hive products, especially honey. However, the yields of honey and other hive products are apparently below the optimum in most African countries. In this review, we discuss the characteristics of the local honey bee subspecies and current apicultural practices in relation to the factors that can potentially influence colony productivity. We highlight some potential factors affecting colony management and productivity and discuss research gaps that need to be addressed in order to improve the profitability and the sustainability of apiculture on a large scale in Africa.



Keywords: African honey bees, genetics, hive types, landscape, colony management

1.0. Introduction

Apiculture is an important livelihood option for millions of men, women, and youth in Africa, especially for those living in resource-poor communities. It contributes to income-generation and employment through the sale of honey bee products as well as food and nutritional security via pollination services. For example, the apiculture value chain in Ethiopia creates jobs for nearly two million people and increases household and individual income by 11 and 51%, respectively (Shenkute et al., 2012;

Abro et al., 2022). In Kenya, apiculture directly supports about 144,000 people, who earn annually about US$7.8 from honey sales per colony (Carroll & Kinsella, 2013). In Uganda, approximately 630 people are involved in apiculture (Amulen et al., 2019), which contributes to 7% of the annual household incomes in primary honey producing areas (Amulen et al., 2017). However, the apiculture sector remains far behind its estimated economic potential in most if not all African countries. For example, where information is available, we see countries like Ethiopia (Nega & Eshete, 2018), Tanzania (Namwata et al., 2013), Uganda (Amulen et al., 2017), Kenya (Carroll & Kinsella, 2013), and Ghana (Akamiti, 2020) realized only 10, 22.8, 1, 25, and 1% of their estimated annual honey production potential of 500,000, 138,000, 500,000, 100,000 and 500,000 tons, respectively. Nevertheless, the empirical bases for calculating honey production potential in Africa are not clear. The production of honey in the African continent is estimated to be less than 10% of the world's production (Wilson, 2006; Moinde, 2016). Besides honey, the other most known hive products in the continent are beeswax and propolis (Wilson, 2006; Nega & Eshete, 2018; Amulen et al., 2020). Whilst beeswax production is less than 25% of the world's production (Wilson, 2006; Moinde, 2016), the information on the actual production of propolis and other bee-hive products such as royal jelly, bee venom and pollen in the continent is not available.

In general, climatic conditions in most of the African continent are favorable as they support year-round survival and activity of honey bees, *Apis mellifera* L. (Hymenoptera, Apidae). Further, most honey bee subspecies in Africa are known for their inherent ability to resist different threats, in particular the invasive mite, *Varroa destructor* (Varroidae: Mesostigamata) and its associated viruses (Alghamdi et al., 2013; Strauss et al., 2013, 2016; Nganso et al., 2017, 2018; Gebremedhn et al., 2019; de Souza et al., 2021; El-Seedi et al., 2022). Both are considered the prime suspects for *A. mellifera* losses around the globe (Martin et al., 2012; Traynor et al., 2020). Hence, the low productivity of honey and other hive products is clearly a constraint that needs to be resolved urgently.

Colony productivity depends on many factors, which can be genetic, environmental, management and socio-political dependent as illustrated in Figure 1. Honey bees are naturally hoarding a surplus of nectar and converting it to honey to support their daily colony activities for periods when foraging conditions are not conducive (Hepburn & Radloff, 1998). Although nectar hoarding behavior has a genetic component (Maucourt et al., 2020), environmental, management and socio-political factors also play a crucial role in colony productivity. The aim of this review is therefore to highlight the impact of these individual factors on sustainable colony management and productivity and discuss knowledge gaps in honey bee health that need to be addressed in future research in order to ensure quality and quantity of hive products in Africa.

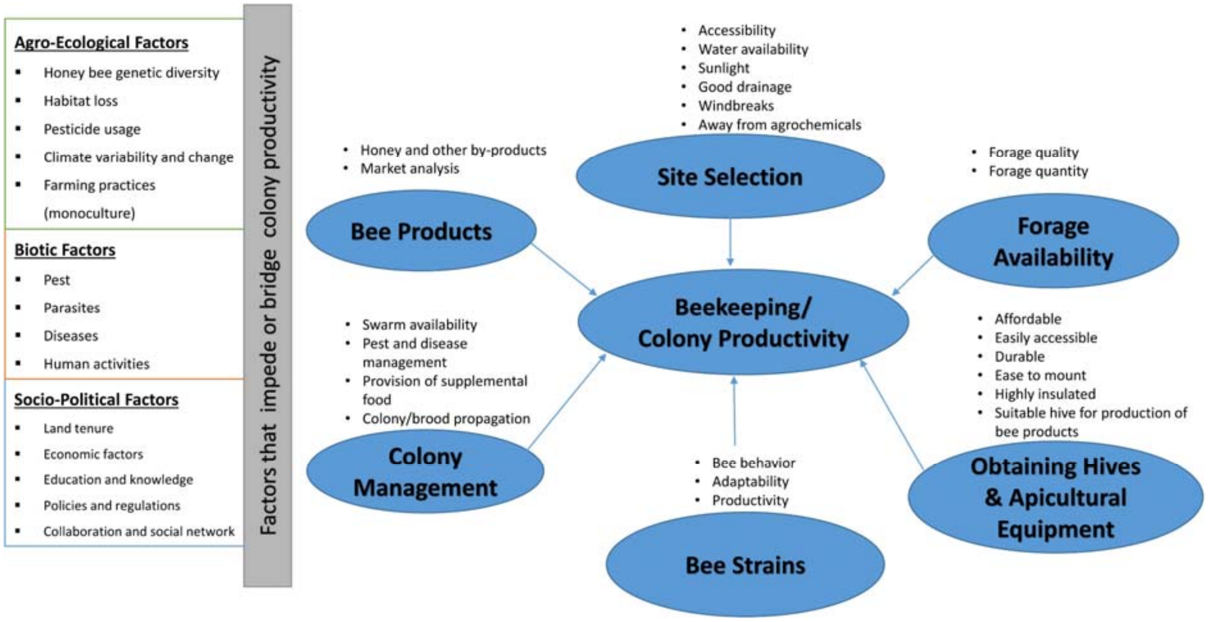


Figure 1. Main factors that affect colony management and productivity in Africa

2.0. Genetics of African honey bee subspecies and colony productivity

In Africa, apiculture is majorly based on swarm catching when colonies are reproducing by swarming. So far, 11 subspecies belonging to the different lineages namely A, O and Y have been identified based mainly on morphometric and molecular (e.g. microsatellite and mitochondrial DNA markers) analyses (Table 1; Franck et al., 2001; Ilyasov et al., 2020). These honey bee subspecies are wild, mostly unmanaged and exhibit high levels of polymorphism due to their pronounced migratory and swarming behaviors (Franck et al., 1998; Jaffe et al., 2010). In fact, discrepancies in the taxonomy of African honey bee populations are common as there are numerous transition zones where genetic exchange among the subspecies occurs, which gives rise to new genotypes of subspecies or hybrids (Ruttner, 1988; Raina & Kimbu, 2005). Both morphometric analyses and mitochondrial/microsatellite DNA markers have been extensively used to identify these subspecies (Radloff & Hepburn, 2000; Franck et al., 2001; Ilyasov et al., 2020). However, both tools have limited power to delineate the honey bee subspecies and hybrid individuals accurately when compared to the whole genome sequencing technique (Grozinger & Zayed, 2020). Unfortunately, most of the African honey bee subspecies do not have a reference genomic resource; and to date, only the North African honey bee *A. m. intermissa* has a draft reference genome assembly (Haddad et al., 2015).

Table 1. Behavioral characteristics of endemic honey bee subspecies in Africa.

Honey bee, *Apis mellifera* L., subspecies	Distribution according to Ilyasov et al., 2020	Information on resilience to Varroa mite and/or associated viruses	Good hygienic behavior (HB)	Good honey production	Good foraging rates for honey production	High defensive, absconding and swarming tendencies
A. m. simensis	Ethiopia	Gebremedhn et al., 2019	Gebremedhn et al., 2019	ND	ND	Gratzer et al., 2021
A. m adansonii	Nigeria, Burkina Faso, Uganda, Ghana, Tanzania, Zambia, Senegal, Sudan	Akinwande et al., 2013	Akinwande et al., 2013	*Kasangaki et al., 2018	ND	Fletcher, 1978; Kasangaki et al., 2018
A. m. scutellata	Kenya, Tanzania, Uganda, Republic of South Africa, Somalia	Strauss et al., 2013, 2016; Nganso et al., 2017, 2018; de Souza et al., 2021	Muli et al., 2014; Nganso et al., 2017	Bustamante et al., 2020	Fries & Raina, 2003	Hepburn & Radloff, 1988
A. m. monticola	Mountains of Kenya, Tanzania	Muli et al., 2014	ND	ND	ND	Hepburn & Radloff, 1988
A. m. litorea	Kenya	Muli et al., 2014	ND	ND	ND	Raina & Kimbu, 2005
A. m. capensis	South Africa	Martin et al., 2020; de Souza et al., 2021	Ellis et al., 2004	*Bustamante et al., 2020	W-Worswick, 1988	Allsopp & Hepburn, 1997; Spiewok et al., 2006; Neumann et al., 2018
A. m. lamarkii	Egypt	El-Seedi et al., 2022**;** Masry et al., 2013	El-Seedi et al., 2022**;** Masry et al., 2013	*Masry et al., 2013	*Masry et al., 2013	El-Seedi et al., 2022**;** Masry et al., 2013
A. m. jemenitica	Arabian Peninsula, Chad, Saudi Arabia, Somalia, Sudan, Uganda, Yemen	Al-Ghamdi et al., 2013	Al-Kahtani & Taha, 2022	Al-Ghamdi et al., 2017	Al-Ghamdi et al., 2017; Alqarni, 2020	Al-Ghamdi et al., 2013; Rashad & El-Sarrag, 1980
A. m. unicolor	Madagascar	Rasolofoarivao et al., 2015	Rasolofoarivao et al., 2015	ND	Rasolofoarivao et al., 2015	*Rasolofoarivao et al., 2015
A.m. intermissa	Morocco, Libya, Tunisia	Adjlane & Haddad, 2018; Haddad et al., 2018	Adjlane & Haddad, 2014	ND	ND	Gadbin et al., 1979; Ruttner, 1988
A. m. sahariensis	Morocco, Algeria,Tunisia, Libya, Mauritania, Western Sahara	Djlane et al., 2016	ND	ND	ND	Ruttner, 1988

*Indicates that the honey bee subspecies displays less of the character described.
ND-Indicates that the information is not available in the literature.

Information is available for some African subspecies regarding some beneficial traits for apiculture including high resilience to pests such as *Varroa* mite and its associated viruses via high hygienic behavior, good foraging, and honey production rates (Table 1). Unfortunately, the beekeepers cannot efficiently manage or manipulate the colonies of the African subspecies due to their higher defensiveness and propensity for absconding and swarming compared to the subspecies of European origin (Hepburn & Radloff, 1988, Ruttner, 1988). Despite these general limitations, we still see that some regions have higher production of honey, beeswax and/or other honey bee products than others in some African countries such as Cameroon (Njukang et al., 2021), Ghana (Letsyo & Ameka, 2019), Ethiopia (Tadesse et al., 2021), Uganda (Mubarik & Buyinza, 2020), Tanzania (Katani & Ndelolia, 2020). This country-level variability in productivity could be partly due to differences in the adaptation of honey bee genotypes to the local environmental factors such as climate, vegetation, occurrence of pests and pathogens (Radloff & Hepburn, 2000, Büchler et al., 2014; Meixner et al., 2014; Uzunov et al., 2014, Yusuf et al., 2015). In fact, a study conducted in Algeria demonstrated that while colony management practices are similar in the North and the South of the country, colony losses, infestation rates of *Varroa* and its associated viruses were higher for *A. m. intermissa* colonies in the North than *A. m. intermissa* and *A. m. sahariensis* colonies in the South, while prevalence of honey bee associated viruses and *Nosema* spp. were similar between both subspecies in the North and South (Adjlane et al., 2016). The mechanism behind these differences remains obscure, since this study did not compare hygienic behavior, colony growth and productivity between both subspecies maintained under the same environmental conditions. Could it be due to differences in forage availability, genetics of the subspecies or climate? Unfortunately, not much is known about differences in physiology, behavior or productivity among the African honey bee subspecies and/or their hybrids in various environmental conditions (Meixner et al., 2015). Such information is crucial for the enhancement of colony productivity through the selection and propagation of indigenous African honey bees and/or their hybrids that perform best under specific environmental conditions. When in 2000, Radolff and Hepburn, analyzed samples of nearly 15,000 workers from 825 colonies from 193 localities in East Africa, extending from South Africa to Ethiopia using morphometric measurements they revealed significantly different local honey bee populations (Radloff & Hepburn, 2000). The high variable populations mostly occur at transitional edges of major climatic and vegetation zones (Radloff & Hepburn, 2000).

It is worth mentioning that there exists a powerful evolutionary interaction between the honey bee genotypes and their adaptation to the local environmental factors (Ruttner, 1982; Meixner et al., 2010). Numerous studies conducted in Europe have shown that local honey bee stocks adapted to their immediate environment outperformed introduced or imported ones in terms of colony growth and vitality, honey production and resilience to biotic stressors (Büchler et al., 2014; Meixner et al., 2014;

Uzunov et al., 2014). Similarly, comparative studies between imported and local African honey bees such as *A. m. lamarckii* in Egypt (El-Seedi et al., 2022), *A. m. jemenitica* in Saudi Arabia (Al-Ghamdi et al., 2017; Alqarni, 2020) and Yemen (Al-kahtani & Taha, 2022) reported similar trends including a higher foraging and pollen-gathering activities by the local bees. Overall, all of these results suggest that sustainable apiculture should rely better on the use of indigenous honey bee populations, which have already adapted to the local environmental pressures while preserving local genetic diversity and may be more productive under their locally adapted environment (Büchler et al., 2014; Meixner et al., 2014; Uzunov et al., 2014).

3.0. Propagation of local African honey bee stocks for enhancement of colony productivity

Traditionally, apiculture around the globe was based on colony propagation via the selection of numerous traits of interest such as reducing swarming tendency, defensiveness and propolis usage to increase honey productivity (Ruttner, 1972; Crane, 1983; Simone-Finstrom et al., 2017). This led to neglecting the significance of other traits responsible for colony resilience. Parasite and pathogen challenges, especially *Varroa* mite and its associated viruses led to increasing effort to reinforce the colony resilience by targeted breeding eg. *Varroa* -sensitive hygiene (VSH) or suppressed mite reproduction (SMR) traits (Harbo & Harris, 2005; Spivak & Danka, 2021). The drawback of this approach is that it may reduce the efficacy of specific selection for other important life-history traits (e.g. survival or reproduction) and counteract natural selection processes that could improve colony fitness (Locke, 2012; Neumann & Blacquière, 2017). Nowadays, some bee scientists are advocating for propagation of local honey bee stocks through natural/Darwinian selection rather than artificial selection (queen rearing or insemination) (Neumann & Blacquière, 2017; Blacquière & Panziera, 2018; van Alphen & Fernhout, 2020). While the former preserves the social and individual immune traits and colony genetic diversity, the latter attempts to limit the positive effects of natural selection on colony fitness.

Artificial selection through queen rearing from the selected stocks has its benefits when breeding for the special desired apicultural traits but may offset the genetic diversity as it appears not to be a process driven by natural selection. The artificial selection process usually starts from the selection of the larvae to grow a new queen. Given the complex nature of queen supersedure, by choosing the larvae based mainly on the appropriate age to rear a new queen during artificial queen rearing, beekeepers are likely to miss out traits guiding the workers’ choices for larvae originating from the so called "royal subfamilies" as suggested earlier by Moritz et al. (1996) and later indicated by Withrow & Tarpy, 2018. Furthermore, the artificial insemination of queens from the selected families with sperm from an average of approximately 12-15 drones (although queens can naturally mate with up to 50 drones) from a few selected colonies may further reduce intracolonial and population genetic diversity with accompanied negative impacts on colony health, survival, and productivity (Mattila & Seeley, 2007; Tarpy et al., 2013; 2015; Delaplane et al., 2015). Recently, Espregueira Themudo et al. (2020) reported that the genetic diversity of native European subspecies over the last 150 years has severely declined due to several issues, one of which was artificial selection. Instead, we see that local honey bee populations in South Africa, Brazil, Russia, Sweden, France and USA that have been exposed to and eventually recovered from *Varroa* mite infestation without any human interference after some years later, have shown long-term survival but sometimes with low honey yield (reviewed in Locke et al., 2016). Thus, in order to avoid the above-mentioned problems, natural selection must be considered to avoid compromising the great genetic diversity of native African honey bee colonies that apparently exhibit strong resilience to common honey bee pests and diseases so far. In fact, it is well recognized that high intracolonial genetic diversity benefits foraging rates, food storage and colony population growth (Mattila & Seeley, 2007; Eckholm et al., 2011). It also benefits colony fitness in terms of thermoregulation efficiency (Jones et al., 2004), resistance to diseases (Palmer & Oldroyd, 2003; Desai & Currie, 2015), brood and colony survival (Tarpy et al., 2013; Delaplane et al., 2021) as well as colony defense traits against *Varroa* mite (Delaplane et al., 2021). As the interest of African beekeepers usually lies in selection for low absconding and defensiveness but high productivity, it will be important to compare the intra-colonial genetic diversity, colony survival, productivity and resilience to the local pests and pathogens among colonies of local subspecies derived from natural and artificial selected stocks.

Recently, using mitochondrial and microsatellite markers, Okwaro et al. (2021) demonstrated high genetic diversity and a queen mating frequency (between 27 to 38 drones) for the honey bee colonies in the Comoros Islands, which is within the normal for African subspecies. These findings may suggest an increased colony vigor against both biotic and abiotic stressors. Nevertheless, it remains to be determined whether this increase in mating number correlates with the number of viable discharged sperm being stored in the queens' spermatheca and queens' longevity. These should be compared to the information collected elsewhere in naturally mated queens (Woyke, 1962; Camazine et al, 1998; Delaney et al., 2011; Tarpy et al., 2012). Parameters that affect both drones and queen survival and reproductive success in Africa are largely unknown and should also be investigated in the future. They include diets fed during their ontogenetic development and adult life, adverse weather, exposure to pests, pathogens, and pesticides, among others (Amiri et al., 2017; 2020; Yániz et al., 2020). How the different classes of commonly used agrochemicals (e.g. fungicides, insecticides, and herbicides) in different African countries affect queen's egg laying rate and longevity, drones' longevity, semen quantity and quality (Irungu et al., 2016; Amulen et al., 2017; Darko et al., 2017; Bwatanglang et al. 2019; Fikadu, 2020; Mullié et al., 2023) remains to be studied. Another important factor to be evaluated in relation to queen and drones performances as they interact with common bee pests and diseases associated with the colonies is the quality and quantity of forage resources (Pirk et al., 2016; Cham et al., 2017; Makori et al., 2017; Ongus et al., 2018).

4.0. Conservation and management of bee pasture for enhancement of colony productivity

Honey bee colonies' survival and productivity rely on the availability of adequate floral and water resources. As generalist feeders, honey bees seem to satisfy their dietary needs based on the quality and quantity of local floral resources available in the landscape surrounding the apiary (reviewed in Vaudo et al., 2020). Honey bees visit a variety of flowering plants to collect nectar and pollen, but they also collect exudates like resin (a sticky plant exudate that honey bees collect and convert to propolis in the hive (Simone-Finstrom et al., 2017)) and latex (Walker & Crane 1987; Weissmann & Schaefer, 2015). These resources are essential for their development, immune system, and resilience to both biotic and abiotic stressors (Alaux et al., 2010; Di Pasquale et al., 2013, 2016; Weissmann & Schaefer, 2015; Alaux et al., 2017; Simone-Finstrom et al., 2017; Smart et al., 2019; Barascou et al., 2021). Their dietary needs vary with respect to caste, age, and task accomplishment (reviewed in Brodschneider & Crailsheim, 2010).

However, honey bees' local floral resources can be of poor-quality and/or unpredictable due to habitat loss and climate change (Goulson et al., 2015; Vaudo et al., 2015). As such, adequate understanding of the temporal and spatial availability of forage resources that support honey bee's nutrition, the conservation and management of these are paramount for sustaining bee health and improving revenues derived from the apiculture activity. Different types of honey and pollen substitutes have been used to nourish the colonies during the forage dearth periods in the temperate climates usually in the autumn to increase colonies' vigor and survival (Brodschneider & Crailsheim, 2010). They include casein, egg yolk, defatted soybean meal, brewer's dried yeast, skimmed milk powder, among others as pollen substitutes and a mixture of sucrose and water called "sugar or sucrose syrup" in a ratio of 2:1 and/or a high fructose corn syrup (HFCS) as honey substitutes. Although feeding colonies with sucrose syrup may improve colony strength and survival compared to HFCS (Sammataro & Weiss, 2013), neither of this substitute has been able to stimulate health-related physiological traits in honey bees significantly compared to honey (Wheeler & Robinson, 2014). In the same vein, pollen diet had superior health effects on honey bee colonies than their substitutes (Alqarni, 2006; Al-Ghamdi et al., 2011; Fine et al., 2018). Moreover, numerous studies have demonstrated the contribution of propolis and its ethanolic extracts to the health of European (Simone et al., 2009; Simone-Finstrom and Spivak, 2012; Wilson et al., 2015; Borba and Spivak, 2017; Dalenberg et al., 2020), African (Nganso &Torto, 2021) and Africanized (Bastos et al., 2008; Nicodemo et al., 2013, 2014) honey bees in the last decades. These studies suggest that beekeepers around the globe should encourage honey bees to collect and deposit propolis inside their hives, as opposed to previous beliefs due to its sticky nature (Simone-Finstrom et al., 2017).

Contrary to the situation in the temperate regions, the majority of beekeepers in Africa do not feed their managed honey bee colonies with honey and/or pollen during periods of resource dearth (Nganso, personal communication) with the exception of beekeepers in South Africa (Pirk et al., 2014). In fact, many beekeepers do not feed new swarms with honey and/or pollen. Some even harvest all the honey produced, leaving nothing for the colonies to feed on. Without supplemental feeding with their natural food resources, the hungry colonies might be at risk and abscond. On the other hand, excessive feeding not only poses an economic burden on the beekeeper but may also negatively affect colony health and the quality of bee products. Thus, the development of an appropriate recommendation of a feeding regime for managed African honey bee colonies that is based on local floral resources requires in-depth study.

The nutritional requirements of temperate honey bee subspecies have been extensively studied and their significance in boosting managed honey bee's resilience against pesticides and disease-causing pests and parasites have been highlighted repeatedly (Alaux et al., 2010; Di Pasquale et al., 2013; Schmehl et al., 2014; Vaudo et al., 2015; Dolezal & Toth, 2018). Unfortunately, this level of detail does not yet exist for African honey bee subspecies in the face of climate change. Moreover, increase in pesticide use and habitat loss have recently been suggested as potential drivers of pollinators' decline including bees in Africa (Fabre Anguilet et al., 2015; Dicks et al., 2021). Laboratory studies have shown the importance of protein to carbohydrate ratios and a pure carbohydrate diet on the survival and ovarian activation of the African savannah honey bee, *A. m. scutellata*, in South Africa (Pirk et al., 2010); as well as their ability to mitigate the effects of dual stressors, low temperature and pesticide (nicotine) (Archer et al., 2014). Additionally, recent studies in a limited area in North Kitui county of Kenya underscore the importance of natural landscape in fostering pollen quality and diversity, and consequently honey bee colony strength (Ochungo et al., 2021, 2022). Further, Ochungo et al. (2021)'s study confirmed that the composition of pollen in terms of protein concentration aligns with the seasonal activities of African honey bee colonies, as was suggested previously for European colonies (DeGrandi-Hoffman et al., 2018). However, the temporal and spatial distribution of key floral species supporting African honey bee nutrition have not yet been extensively studied. Additionally, just a limited amount of information exists about the nutritional composition of African bee forage plant species in terms of protein, lipid and carbohydrate concentrations that directly affects honey bee colony health and fitness (Ochungo et al., 2021; Vaudo et al., 2015). Moreover, studies on the identification and characterization of the landscape classes and weather variables favoring floral resource availability around the apiary using remote sensing are limited, and can immensely help beekeepers to predict landscape suitability for honey bee colony growth and honey production. Without a clear understanding of the impact of the above factors on bee productivity, beekeepers are limited in their ability to determine how many colonies their apiary/farm's vegetation can support to significantly enhance honey production. This can lead to over- or under-investment of time and resources in apiculture. Overall, we believe that an in-depth understanding of all these relevant aspects will tremendously boost the sustainability and profitability of the apiculture enterprise in Africa by promoting the management and conservation of bee pasturage in the landscape. It might also lead to the development of an effective science-based decision support system to help inform landscape suitability for apiculture (Robinson et al., 2021).

Maintenance of bee pasture on its own might be economically problematic in rural and purely developed areas unless combined into local agroecosystems due to the existence of rigorous right to ownership of rural and urban land, as well as of all natural resources. This is expected not only to improve food and nutritional security but also colony productivity (Carvalheiro et al., 2011). For example, a study on the integration of beekeeping in cashew orchards in Ghana and its neighboring country Benin found an increased yield of raw cashew nuts by 116.7% and 212.5%, with yield per tree increasing from 4.2 kg to 9.1 kg and 2.16 kg to 6.75 kg, respectively (Aidoo et al., 2014). In addition, honey bee products also increase drastically with 41.4 kg of honey, 2.8 kg of beeswax and 0.74 kg of propolis per hectare per 2 colonies amounting to US$ 208.53 in Ghana; and in Benin 27.48 kg of honey, 1.84 kg beeswax and 0.5 kg propolis worth US$ 138.40 was obtained.

5.0. Management strategies for parasites, predators, and pathogens

The highly populated honey bee hives are generally conducive for the spread of parasites, predators and pathogens owing to the presence of large amounts of food stores and extensive social interactions among highly related nestmates in a relatively stable microclimatic environment. However, these social insects have evolved both individual and several forms of social immune responses to avoid invasion, settlement, and replication of any threat inside their hives (Evans et al., 2006; Mondet et al., 2016; Pusceddu et al., 2021). The indigenous honey bee subspecies in Africa are of particular interest globally because their defense repertoire seems to be resistant to the invasive *Varroa* mite and its associated viruses that have recently significantly crippled the health of their counterparts in many countries around the globe (Pirk et al., 2016; Nganso et al., 2017, 2018; Nganso & Torto 2021; Gebremedhn et al., 2019; de Souza et al., 2021). Studies conducted in Kenya, South Africa and Ethiopia have identified potential tolerance and resistance mechanisms to *Varroa* mites (Strauss et al., 2016; Nganso et al., 2017, 2018; Cheruiyot et al., 2018; Gebremedhn et al., 2019; Fang et al., 2022). Thus, currently, beekeepers are advised not to treat their colonies with miticides as done in most *Varroa* affected countries (Mutinelli, 2016; Pirk et al., 2016; Brodshneider et al., 2023). This resistance of the wild African subspecies could be due to limited manipulations of the colonies by beekeepers in terms of selection for improved colony traits, thereby allowing natural selection to foster local adaptations and colony fitness. Nevertheless, it will be premature to assume that honey bees in Africa are not susceptible to the attacks from the other currently known parasites, predators and pathogens. In fact, beekeepers in certain parts of Ethiopia (Kebede et al., 2015; Gratzer et al., 2021), Uganda (Mujuni et al., 2012), Cameroon (Cham, 2017; Njukang et al., 2021), Kenya (Johansson, 2019; Wambua et al., 2019), Burkina Faso (Kaboré et al., 2021), and Tanzania (Njau et al., 2009) often complain about colony losses of up to 50% mainly due to infestations by wax moths, large hive beetles and ants (Figure 2). However, the exact causes for colony losses in most African countries are not clear and require further follow up studies on potential risk factors driving these losses.

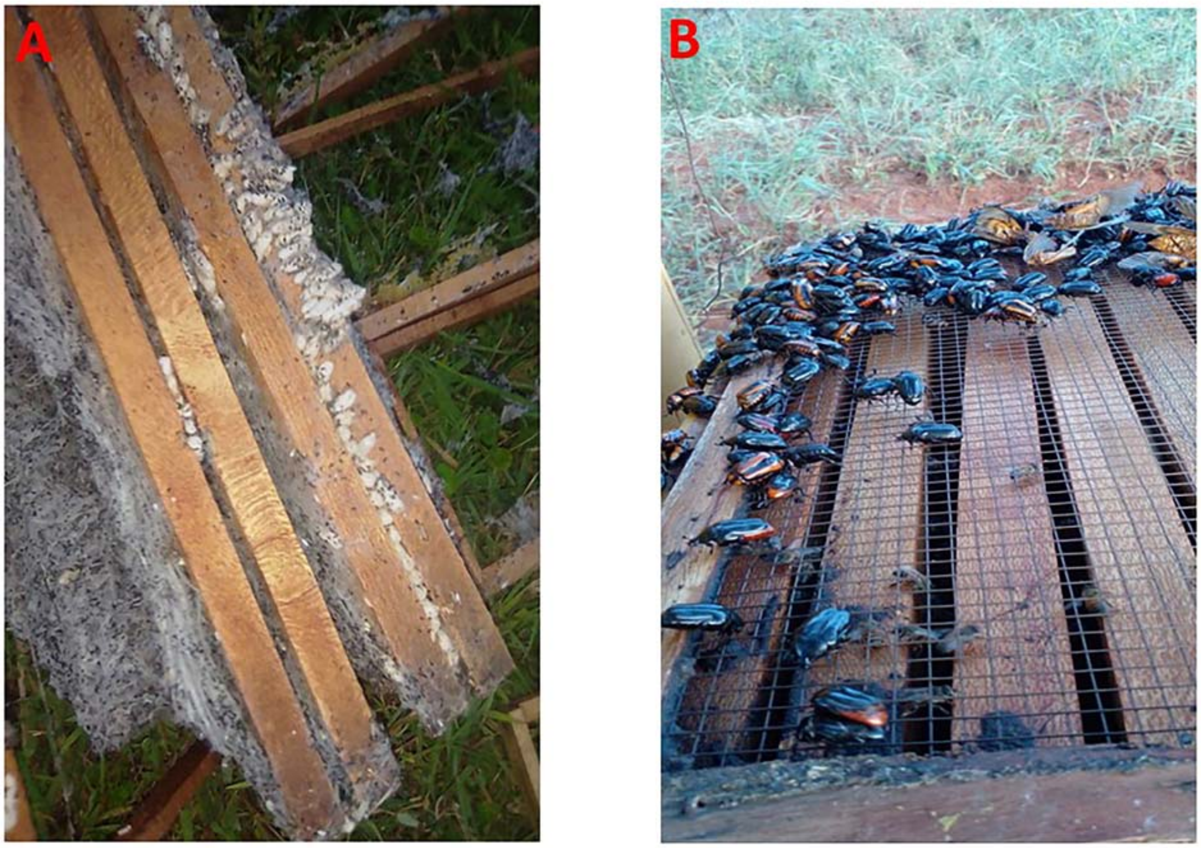


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Figure 2. Damage caused on African honey bee colonies by the wax moth (*Galleria mellonella*, Witte) (**A**) and the large hive beetle (*Oplostomus haroldi*, Linnaeus) (**B**)

In general, data on the extent of honey bee colony losses across the African continent as done over the last years in the USA (VanEngelsdorp et al., 2012; Spleen et al., 2013), China (Liu et al., 2016; Chen et al., 2017; Tang et al., 2020), Europe and some other countries (Gray et al., 2020) are lacking. So far, the few efforts that are available in this aspect have been done in South and Northern Africa. In South Africa, Pirk et al. (2014) surveyed beekeepers to assess the extent and the potential causes of colony losses over two consecutive years and reported losses of 29.6% in 2009-2010 and 46.2% in 2010-2011. These losses were more pronounced in migratory than stationary apiculture, and were majorly due to small hive beetles, *Varroa* mites, absconding and chalkbrood disease. In Egypt, loss rate of 35.5% in 2011-2012 and 38.8% in 2012-2013 were reported mainly due to oriental hornets, starvation, *Varroa* mite and poor quality of queens (Moustafa et al., 2014). Similarly, colony loss rates of 6.6% were reported in Algeria due to natural disasters and again queen problems in 2018-2019 (Gray et al., 2020). The latter issue can significantly affect African honey bee's resilience to diverse stressors as discussed above.

6.0. Hive types' economics, technology adoption and product quality

In Africa, the farmers keep the collected bee swarms in different hive types, ranging from locally made hives without any frames to the modern ones with movable top bars/frames, most commonly the Kenyan top-bar hive (KTBH) and the Langstroth hive (LH) (Figure S1). Modern hives are generally not affordable to African beekeepers due to their high costs. They are built with hardwood (e.g. *Cupressus lusitanica*, *Pinus patula* and *Grevillea robusta*) or softwood (e.g. *Polyscias kikuyuensis*, *Podocarpus latifolius*, and *Prunus africana*) timber species (Carroll, 2006; Zocchi et al., 2020), whereas the local hive types are made from a variety of low-cost materials that are readily available. These include clay soil, wood or bark of different tree species, gourds of pumpkin fruits, reed, grass or bamboo twigs that are woven together in a basket, cone or cylindrical form and are sometimes plastered with clay soil, animal dung or mud to enhance hives' durability, among others. Among the modern hives, the KTBHs are the cheapest and are more commonly used by African beekeepers than the LHs (Carroll & Kinsella, 2013; McMenamin et al., 2017; FAO, 2021; Tadesse et al., 2021). According to a recent report from FAO, more than 90% of the honey exported from Africa to the European market is harvested from the locally made hive types (FAO et al., 2021).

In different African communities, donor- and government-funded projects have attempted to promote the use of the modern LHs used in Europe and America over the local hives. These were conducted in the hope that the quality and quantity of harvested hive products as well as gender-neutral apiculture will be enhanced in the long-term (Carroll, 2006; Keeping, 2012; Adisu, 2016; FAO, 2021; Gratzer et al., 2021). These apiculture projects often provide the inexperienced rural communities with free and sometimes costly apiculture equipment including LHs and then leave without providing enough training and no access to local/international markets and/or knowledge on market requirements for bee products. In fact, lack of access to local/international markets and/or knowledge on market requirements for bee products along with a lack of best practices for harvest and post-harvest processing as well as product development, packaging, standardization, and certification are significant bottlenecks to enhancing the apiculture value chain in Africa (Berem, 2015; Munuo, 2015; Gratzer et al., 2021; Tadesse et al., 2021); and warrant intervention by developmental projects. The beneficiaries of these projects often showed no tangible production or long lasting impact. This kind of developmental projects are often based on biased cost-benefit analyses and false projections (Svensson, 2002), and will drive farmers into expenses that they cannot sustain in the long term since most of them lack the capital to purchase the costly LHs in the first place (FAO et al., 2021). In fact, according to Carroll (2006), there is no guarantee of increased colony productivity using LHs as some farmers in Kenya harvested more hive products from KTBHs than those having LHs. Similarly, Amulen et al. (2019) recently showed that local log hives in Uganda have the potential to improve honey yields to levels comparable to those of KTBHs and LHs, whereas previous studies refuted the idea and prone the adoption of modern over local hives for enhancement of honey production in Kenya and Ethiopia (Yirga & Teferi, 2010; Affognon et al., 2015; Beyene et al., 2016). Moreover, Carroll & Kinsella (2013) noted no significant difference in revenue per hive among the KTBHs, LHs and traditional hives in Kenya as the traditional hives are almost two- to four-fold and four-to seven-fold cheaper than the KTBHs and LHs, respectively. Furthermore, even though the quality of hive products derived from these locally made hives are not as high as those derived from LHs due to poor harvesting and post-harvest techniques, these products are still accepted in the local markets and meet the EU strict export criteria (Carroll & Kinsella, 2013; FAO et al., 2021). Thus, this implies that the quality of hive products is not a critical criterion to consider when selecting for a suitable hive type.

When considering the suitability of hive types for improving the productivity of hive products, there is a need to understand how the profitability varies according to the hive types in time and space based on the apiculture practices, climatic conditions and honey bee subspecies when selecting a suitable hive type. For example, Aregawi et al. (2014) compared honey and beeswax production, area of the comb covered by brood, pollen, or nectar among KTBH, LH, clay frame hive and a local/traditional hive, which contained *A. m. semensis* maintained under the same agro-ecological zone in Tigray Region of Ethiopia. They found that although honey production per hive was similar among the hive types, beeswax production was higher in traditional hive and KTBH than LH and clay frame hive. Their results also revealed that the area of the comb covered by brood, pollen or nectar was highest in the KTBHs, thereby suggesting that this hive type may be more suitable for use in this agro-ecological zone, even though disease and pest prevalence were not tested in their study. Additionally, there is also a need to investigate the risk of adopting the technology by beekeepers and the cost-effectiveness of the new technology. It seems that African beekeepers quickly adopted the KTBHs because of their low production cost, ease of use and management and/or high return on investment when compared to LHs (Belie, 2009; Carroll & Kinsella 2013) and traditional hives (Dathine, 2012; Abebe, 2011; Gorfu, 2005; Al-Ghamdi et al., 2017). As shown in Figure S1, the quality of KTBHs varies from traditional without queen excluder to improved/modern technology with queen excluders, and this can result in differential colony productivity and product quality. In this regard, developing policy guidelines on adopting hive quality standards can play an important role in ensuring standards in KTBH production.

Few studies have also tested for swarm attractiveness among the different types of hives and reported contradictory results. For example, studies in Uganda demonstrated that the local grass hives were the most attractive to migrating swarms when compared to the introduced KTBHs and LHs (Kugonza et al., 2009), whereas the local clay-pot hives and the KTBHs performed best when compared to the LHs in Nigeria (Ande et al., 2008). In contrast, McMenamin et al. (2017) found that the LHs performed best, followed by the Log hive, while the KTBHs were the least preferred in Kenya. These contradictory results might be due to several reasons including the materials used for hive construction, the orientation of the hive's entrance in different cardinal point directions, and the location of placement of hives. All these reasons may also to some extent explain why 33.3-100% of colonies absconded in LHs compared to 8.3-33% in local hives and 22% in KTBHs in Ethiopia and Nigeria (Ande et al., 2008; Adisu, 2016).

Ideally, a suitable beehive type should have good insulating properties to aid honey bees in maintaining brood nest microclimate within optimum range. In this regard, hives have been modified in various ways and some insulating material has also been used to optimize the regulation of brood nest microclimate. In Kenya, for example, hardwood timber species, especially *C. lusitanica* mentioned above, are often avoided because it absorbs water and their scent repels the honey bees, thus affecting bee establishment, health, and honey yields (Zocchi et al., 2020). Instead, beekeepers often use the softwood timber species mentioned above or insulate the inner hive surface with panels from the *Juniperus procera* tree to optimize the hive microclimate and improve bee establishment. In Saudi Arabia, for example, colonies provided with hives entirely covered with an Arnon insulating material had the highest amount of sealed brood, population and honey compared to standard LHs or other tested modified hive types due to better regulation of in-hive microclimate during extreme environmental conditions (Abou-Shaara et al., 2013). Hive's exposure to the sun (sunny and shaded areas) also influences microclimate homeostasis within honey bee hives (Seeley & Morse, 1978). However, the impact of these parameters on microclimatic regulation in different hive types of their African counterparts largely remains unknown.

7.0. Building beekeeper's capacity to enhance colony productivity

The level of experience in apiculture can also offset hive productivity as farmers in Kenya with more experience in apiculture earn nearly double per hive compared to those with less experience (Carroll & Kinsella, 2013). This highlights the importance of building capacity in best practices for colony management among African beekeepers. For example, beekeepers' inadequate knowledge of colony management can result in improper hive microclimate, low colony population size, high prevalence of pests and diseases, high colony losses and eventually low colony productivity. Swarms of African honey bees contain fewer individuals than those of European ones in general (Winston et al., 1983). As such, using larger catchment boxes for African bee swarms will force the newly established colonies to work harder to maintain the brood nest microclimate at an optimum level. Instead, a high level of experience in apiculture can offset possible tradeoffs of brood nest homeostasis's regulation with respect to honey bee biology and productivity through the provision of smaller boxes to catch bee swarms and transfer the colonies to the larger ones as the population builds up. Further, proper hives' insulation by placing them in the shade, using a smaller to larger lower entrance depending on the prevailing weather, an inner cover made of wood or foam beneath the roof top cover of the hive, and/or any other environmentally friendly material that will not allow moisture to get trapped within the hive can also help optimize brood nest microclimate (Gichora, 2003; Sheridan, 2020).

8.0. Diversification of bee-hive products to enhance revenues from apiculture

To improve livelihood and household income via apiculture, one should generally consider both the production costs and the revenue generated. The production costs are usually composed of expenses associated with hive production, colony management, product harvesting, post-harvesting processing techniques, packaging and colony losses. All these are heavily dependent on the issues discussed in the above section. Revenues are dependent on the number of target products and their market value. Today, honey remains the primary hive product harvested by African beekeepers followed by beeswax (Wilson, 2006; Amulen et al., 2020; Gratzer et al., 2021). The information on the production or commercialization of hive products besides honey and beeswax in the continent is still extremely limited (Wilson, 2006; Amulen et al., 2020; Gratzer et al., 2021). The value of other bee-hive products such as: propolis, royal jelly, bees pollen and venom are well recognized in the literature (The COLOSS BEEBOOK, Volume III, Dietemann et al., 2019). These additional hive products have a variety of uses and applications in the food, cosmetic and pharmaceutical industries (Pasupulet et al., 2017; Kocot et al., 2018; Ullah et al., 2022), and could have a high monetary value in local and international markets especially when derived from miticide-free African honey bee colonies if the costs of their production are economically balanced. However, product diversification has not been effective in this part of the world due to a lack of knowledge in the socio-economic value of these additional bee-hive products as the majority of beekeepers are poorly educated and/or have received adequate training in apiculture and production of these products (Amulen et al., 2017; Faji & Begna, 2017; Meutchieye et al., 2018; Mushonga et al., 2019; Bihonegn & Begna, 2021; Tutuba & Kapinga, 2022). Thus, efforts should be put in place to build the capacity of African beekeepers in producing and packaging these hive products, as well as assist them in creating formal market access for these products.

9.0. Concluding remarks and future perspectives

Apiculture is a valuable activity that can help the African continent achieve the sustainable development goals (SDGs) 1, 2, 3, 5, 8, 13 and 15 of the 2030 agenda for sustainable development adopted by the United Nations in 2015 (https://sdgs.un.org/goals, accessed on 12/12/2022). However, for this activity to be improved in the long-term, male and female beekeepers need to be educated on best practices for colony management. For this knowledge transfer to be effective, there is first a need to evaluate on a large scale the performance of different endemic African honey bee subspecies and their hybrids in terms of colony strength and productivity, and resilience to common bee pests and diseases under various climatic conditions. This will assist in the identification of the best productive bee genotypes, which are adapted to specific geographical areas. Additionally, it might hinder the importation of queens from other African countries and most importantly from other continents to conserve the genetic diversity of the local subspecies. Secondly, there is a need to investigate how land cover classes (low, medium, and high based on vegetation health and growth patterns) and local weather influence the spatio-temporal abundance and distribution of bee forage resources and consequently colony growth, health, and productivity. Third, there is also a need to set-up annual monitoring surveys to quantify swarm availability, colony loss rate and identify potential risk factors leading to a decline in honey bee health such as nutrition, pests and pathogens, agrochemicals, absconding, natural disasters, among others, as this has never been carried out in large-scale on the continent. Continued surveillance of the factors that can negatively affect the health of African honey bees is paramount to design critical management options that farmers can use against these stressors in the continent. Fourth, the impact of local and modern hive types on overall colony performance in different agro-ecological zones needs to be compared to identify the most suitable hive type for apiculture. Additionally, the impact of hive placement and orientation of hive entrances in relation to the solar position (sunny and shaded areas) on swarm attractiveness, colony growth and productivity needs to be examined. Lastly, product diversification is another critical issue that needs to be addressed to generate additional revenues from the sales of non-honey or -wax bee-hive products. To achieve this, there is a need to engage scientists, diverse public and private sector partners as well as non-governmental organizations with a complementary interest in apiculture for building the capacity of African beekeepers in best practices for product harvesting and post-harvest processing techniques, product development and packaging and assist them in creating markets through the development of certification standard for these products. Of course, documentation and assessment of indigenous knowledge of bee farmers in different African countries in hive making and placement, management practices of colonies, product harvesting and post-handling techniques will facilitate the design of effective management practices for colonies, which will be quickly adopted by the local people.

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