ANNUAL REVIEWS

Annual Review of Entomology

Ecology and Management of African Honey Bees (*Apis mellifera* L.)

Maryann Frazier,[1,*] Elliud Muli,[2] and Harland Patch[1]

[1]Department of Entomology and Center for Pollinator Research, Pennsylvania State University, University Park, Pennsylvania, USA; email: maryann.frazier15@gmail.com

[2]Department of Life Sciences, South Eastern Kenya University, Kitui, Kenya

Annu. Rev. Entomol. 2024. 69:439–53

The *Annual Review of Entomology* is online at ento.annualreviews.org

https://doi.org/10.1146/annurev-ento-020823-095359

*Corresponding author

Keywords

Apis mellifera, African honey bee, indigenous beekeeping, bee management

Abstract

In Africa, humans evolved as honey hunters of honey bee subspecies adapted to diverse geographical regions. Beekeeping today is practiced much as it was when Africans moved from honey hunting to beekeeping nearly 5,000 years ago, with beekeepers relying on seasonally available wild bees. Research suggests that populations are resilient, able to resist diseases and novel parasites. Distinct biomes, as well as environmental pressures, shaped the behavior and biology of these bees and in turn influenced how indigenous beekeeping developed. It appears that passive beekeeping practices that enabled free-living populations contributed to the overall resilience and health of the bee. There is clearly a need for research aimed at a deeper understanding of bee biology and the ecosystems from which they benefit and on which humans depend, as well as a growing realization that the management of these bees requires an indigenous approach that reflects a broader knowledge base and the economics of local communities and markets.

1. INTRODUCTION

Honey bees are among the most-studied insect species. The bulk of the work on honey bees has focused on temperate European subspecies. African honey bees have evolved in habitats from high desert to maquis and fynbos, savannah, dense rainforest, and high mountains and in the context of biodiverse communities of plants and animals. These climatic conditions have resulted in geographically unique and phenotypically distinct subspecies. Adaptive behaviors such as increased swarming, absconding, migration, and defensiveness led to an indigenous and variable form of beekeeping that made use of local materials for hive construction, required little to no management, and produced nominal honey yields. However, this form of beekeeping, still widely practiced today, provides a large number of nesting sites for highly mobile bees and contributes to maintaining large, free-living populations. High levels of gene exchange likely allow the bees to quickly adapt to environmental challenges.

Honey bees and beekeeping play an important role in the lives of people and ecosystems across Africa. The production of honey is a source of cash, calories, nutrients, and medicine for subsistence farmers (13, 60, 75, 85). Millions of households in Sub-Saharan Africa rely on beekeeping for some income (30, 48). Agricultural and natural ecosystems benefit from pollination services provided by many bee species, including the large free-living population of *Apis mellifera*.

While African landscapes appear to have significant potential for honey and beeswax production, in most countries, it appears that this potential has not been fully realized (14, 50). The income potential from the production of beeswax alone provides an untapped economic opportunity, given that many beekeepers simply discard it (29, 102). Although more data are needed, African beeswax appears to have less chemical contamination (71) from pesticides than beeswax from the United States (72). This puts African beekeepers in a unique position to benefit from beeswax production and export and should allow them to take advantage of growing niche markets such as those for organic and fair trade goods (101).

In many parts of Africa, forest conservation in association with beekeeping has been promoted (13, 58, 60). There is evidence for the positive link between beekeeping and forest management, since bee pollination fosters the maintenance of an entire ecosystem and not just a single crop or species (13, 52).

Honey bee pollination as an industry is not widespread, probably due to the lack of large pollinator-dependent monocultures and an abundance of wild pollinators. However, honey bees are used for crop pollination (52, 106); the most developed pollination industry is found in South Africa, where deciduous fruit growers are largely dependent on managed honey bees for pollination of apples, plums, pears, and apricots (7, 67).

Unemployment, especially among youth, is a challenge facing most African countries. Participation in the honey and wax production value chain has been promoted as a source of employment for young people. In Ethiopia, Africa's largest honey producer, the beekeeping industry purportedly employs over 2 million people (8). Additionally, beekeeping in many African communities is being promoted as a gender empowerment tool, allowing women to improve their status through income generation (3). Culturally, honey is widely used in preparation of traditional medicines (85) and as part of the bride price or dowry in traditional marriage ceremonies (51, 54). It is also a key ingredient in the brewing of alcoholic beverages such as beer and tej.

2. AFRICAN SUBSPECIES AND THEIR DISTRIBUTIONS

A synthesis of early work on African honey bees (43, 95, 96) using morphological characters suggested that there are 10 subspecies and that *A. mellifera* originated in Africa (119). A more recent reconstruction across the biogeographical range of *Apis* using 251 genomes from 18 subspecies

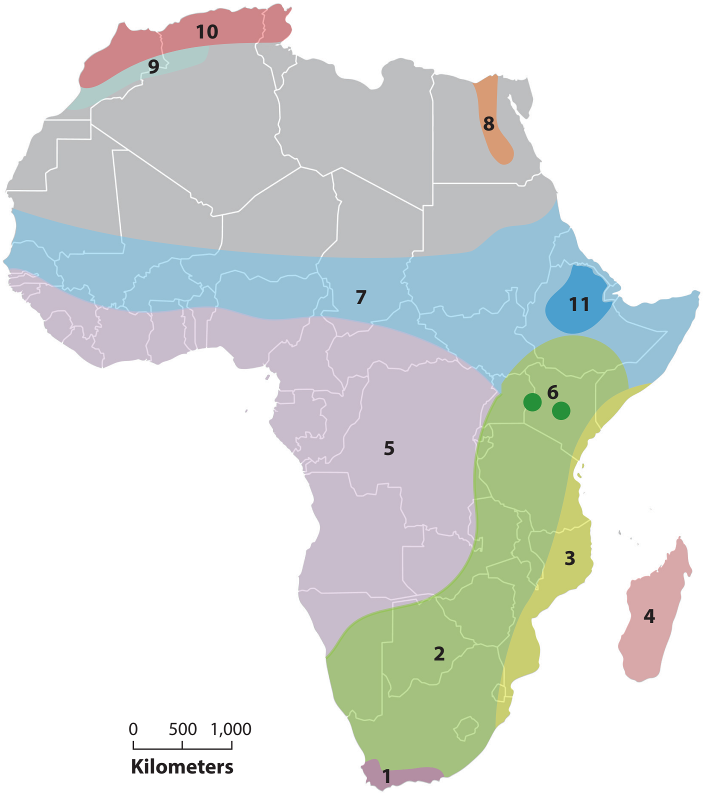

Figure 1

Geographic distribution of honey bee (*Apis mellifera*) subspecies in Africa based on morphoclusters identified by Hepburn & Radloff (43). (*Location 1*) *A. m. capensis*. (*Location 2*) *A. m. scutellata*. (*Location 3*) *A. m. litorea*. (*Location 4*) *A. m. unicolor*. (*Location 5*) *A.m. adansonii*. (*Location 6*) *A. m. monticola*. (*Location 7*) *A. m. jemenitica*. (*Location 8*) *A. m. lamarckii*. (*Location 9*) *A. m. sahariensis*. (*Location 10*) *A. m. intermissa*. (*Location 11*) *A. m. simensis*, added based on Meixner et al. (65). The extent of the range of these subspecies should be taken as an approximation. There is great need for resolution given the conflicts in the literature, particularly for *A. m. jemenitica*, the other desert species, and *A. m. adansonii*. The mountain honey bee, *A. m. monticola*, may not be the same subspecies across the range, as has been suggested elsewhere. It is represented only on Mount Elgon and Mount Kenya (see 37, 71, 117). Figure adapted with permission from Reference 43.

from Asia, Europe, and Africa suggested a western Asian origin of *A. mellifera* (28). There are seven major evolutionary lineages of western honey bee, three of which are found in Africa. The main A lineage is found across the continent and contains several subspecies, the L lineage is found in the Nile Valley in North Africa (*A. m. lamarckii*), and a unique U lineage is only found in Madagascar (*A. m. unicolor*). The African continent is approximately 1 billion hectares in size; thus, it is not surprising to find many subspecies with characteristic physiologies and behaviors associated with particular habitats.

Beyond the two subspecies mentioned, there are likely nine A-lineage subspecies, although the exact number is not clear (15, 37, 47) (**Figure 1**). The most widely distributed are *A. m. scutellata* in southern and east Africa and *A. m. adansonii* in the west to the edge of the Sahara Desert. Dogantzis et al. (28) found considerable introgression into African lineages; in particular, *A. m. intermissa* on the North African coast seems to be the result of high admixture, rather than a distinct lineage, as do the bees of the Nile Valley and Madagascar. *Apis mellifera saharensis* and *A. m. jemenitica* are both desert bees. The former is found in the western region of northern Africa, and the latter occurs from Mali east into the Arabian Peninsula; however, these subspecies need further resolution. The many synonyms for *A. m. jemenitica* underscore this need (47). *Apis mellifera simensis* is a recently described subspecies endemic to the volcanic dome system in Ethiopia (65). *Apis mellifera litorea* is confined to a band of tropical coast from Kenya to Tanzania and farther south (37, 96). Similarly, the Cape bee, *A. m. capensis*, is found only in the far southern coastal region of South Africa (96). *Apis mellifera capensis* bees are unique in that their workers are parthenogenic and can lay diploid eggs. They are also considered to be social parasites on *A. m. scutellata* when moved from their natural range into *A. m scutellata*'s territory (5, 79). The mountain bee of East Africa, *A. m. monticola*, has long been known to have gene flow with populations at lower altitudes, suggesting an ecotype, but may be a distinct subspecies at least in part of its range (66, 117). Additionally, European *A. mellifera* subspecies of various kinds have been purposely introduced across the continent for commercial production, and *Apis florea*, a small Asian species, has been accidentally introduced; was first discovered in Africa in Khartoum, Sudan in 1985; and is considered invasive (68, 107).

3. BEHAVIOR AND NEST ARCHITECTURE

Climate, unique biomes, and environmental pressures such as pests and predators including human honey hunters have shaped the natural history of African honey bees, which varies considerably from that of temperate-evolved bees. However, considerable variation in behavior and biology also exists among and within individual African subspecies. For example, Hepburn & Radloff (43, p. 227) ranked aggression across subspecies but characterized defensive behavior as follows: "whatever the perceived average level of aggressiveness for a subspecies, individual colonies will exhibit a range of behavior from docile to aggressive even within the same apiary, larger populous colonies are more aggressive and effective at nest defense and finally there is a high degree of unpredictability in this behavior making a clear-cut ethological analysis difficult." Frazier et al. (35) found significant differences in hygienic behavior expressed by *A. m. scutellata* colonies in two different locations in Kenya. An in-depth study of swarming and migration among Ethiopian subspecies showed that the temporal distribution of swarming varied within and among subspecies (83), although some of these Ethiopian subspecies designations have been challenged by Meixner et al. (65). While there is a significant body of research on some individual subspecies such as *A. m. scutellata*, few studies exist that compare behaviors across subspecies, and those that do may not be valid due to inaccurate subspecies identification. **Supplemental Table 1** summarizes the altitude where subspecies are typically found, the timing of their reproductive swarming and seasonal absconding, and a comparison of defensive behavior, based on the available literature. The behaviors discussed are those that are most frequently associated with tropical *A. mellifera* and have significant implications for survival and honey bee husbandry.

Supplemental Material >

3.1. Reproductive Swarming

Swarming is a characteristic behavior of honey bees, but factors that lead to reproductive swarming can vary. An influx of pollen even before colony buildup can induce swarming in African bees (103). These bees are also known to invest more food resources in reproduction than in food storage (98) and produce, on average, 6–12 swarms annually (84, 120). Hepburn & Radloff (43) review reproductive swarming among subspecies and its seasonality (see **Supplemental Table 1**). In general, colony buildup and reproduction is linked to floral resource availability, which ultimately depends on rainfall (43). With the exception of the Mediterranean far north and the fynbos of the southern cape, most of Africa is characterized by alternating wet and dry seasons. Thus, across most of the continent, the timing of swarming varies depending on the timing of local rainfall and flowering.

3.2. Absconding and Migration

The seasonal cycles of tropical and temperate honey bees are defined by periods of limited food and water availability. In temperate areas, bees have evolved to store nectar as honey and form clusters to survive winter, but tropical bees often abscond and migrate in response to dry periods of floral dearth. Absconding, while rare in temperate bees, is common in African bees (41, 102, 122) but is not well studied. It appears to be a response not only to resource depletion, but also to nest disruption. Many factors reportedly result in unprepared, short-distance moves, including disturbance by honey badgers and humans; beekeeper management; attacks by ants, wax moths (*Galleria mellonella* and *Achroia grisella*), hive beetles (*Aethina tumida* and *Oplostomus fuligineus*), and beewolves (*Philanthus* spp.); robbing among colonies; and untenable nest conditions caused by flooding or excessive heat (43, 97). However, absconding due to resource depletion often, but not always, appears to result in long-distance migration of 100 km or more and is seasonal (43, 63). It is typified by reduced brood production, eclosion of sealed brood, and adult bee consumption of resources (103). Migration has been proposed as a means to foster colonization of new habitats (32, 109) or to find areas favorable for reproductive swarming (34) or simply as a response to depleted environmental resources and an alternative to mass resource hoarding (16, 43). This movement of honey bees into areas rich in blooming plants will also have advantages for plants receiving the pollination services of migrating bees. Like other behaviors, migration is highly variable between and among subspecies. McMenamin et al. (62) found that, in Kenya, larger colonies were less likely to abscond during the dry season, while smaller colonies absconded and presumably migrated. The impressive mobility of African colonies is one of the key factors contributing to their expansion across the Americas and Mexico, extending their northern range approximately 500 km annually (97, 110).

3.3. Defense

African bees are notorious for their defensive behavior. Intense stinging episodes are well documented in Africa (32, 104). While there is a high degree of variability in nest defense, African bees have a considerably lower threshold of response to nest disturbance than bees of European origin (32). While there appears to be variation in defensive behavior among subspecies (**Supplemental Table 1**), there is also variation within a subspecies, and additional factors such as the size of the colony, altitude, availability of floral resources, continued disturbance, time of day, and changes in weather are reported to influence a colony's defensive response (32, 43).

Supplemental Material >

3.4. Amalgamation

Amalgamation is a well-documented behavior in African subspecies but is not well studied. While it appears most common in small reproductive swarms or absconding colonies, there are reports of multiple larger swarms amalgamating to form megaswarms (102). General observations of this behavior include individual colonies coming together, separating, coalescing, and eventually resolving into some number of colonies containing multiple queens where supernumerary queens are killed by balling (102, 103). It has been suggested that amalgamations allow for rapid buildup of populations while reducing the cost for survival (43).

3.5. Hygienic Behavior

The genetics of hygienic behavior was initially described by Rothenbuhler (93) in association with American foulbrood. Heritable hygienic behavior aimed specifically at the uncapping and removal of varroa-infested brood was later identified as varroa-specific hygiene (VHS) (42). It appears that hygienic behavior may be an important physiological and behavioral mechanism operating in African bees, allowing them to resist diseases like American foulbrood (35, 36) and parasites such as varroa mites (17).

3.6. Nest Architecture

Differences in nesting cavity preferences and nest architecture include, but are not limited to, differences in nest cavity size, bee space, and worker cell size. Dimensions vary between and among European and African subspecies, but in general, African bee nesting cavities are one-half to one-third the size of those of European bees; they average approximately 20 liters but can range from 5 to 150 liters (10). In South America, the average natural nest cavity volume of Africanized bees was 22 liters (122). European bees prefer a natural cavity volume of 40 liters (97). The center-to-center distance between adjacent combs in tropical *A. mellifera* is 32 mm (range 30–34), and worker cell diameter ranges from 4.8 to 5.0 mm (for reviews, see 43, 103). Temperate bees space their combs 35 mm (range 32–38) apart, and worker cell diameter ranges from 5.2 to 5.4 mm (121). Movable-frame hive designs and management practices are based on these measurements. In most cases, it is unlikely that these differences in African bee biology are taken into consideration when equipment and practices designed for temperature bees are promoted in Africa.

4. MANAGEMENT

It is impossible to know for certain when our early ancestors first encountered honey bees and the rich nutritional resources of brood, pollen, and honey that they can provide. However, it is likely that this interaction first occurred prior to us becoming modern humans (21). The earliest documentation of humans interacting with bees comes from Paleolithic cave art, which represents flying bees, comb, and human honey hunters. Such art is found in Europe, Asia, Australia, and southern Africa and dates back 7,000–8,000 years (23, 56). The most numerous images, some 4,000, found in southern Africa, are mainly the work of the San people, and are mostly undated (23, 86). Honey hunting is still practiced in parts of Africa today, particularly by hunter-gatherer peoples like the Hadza of Tanzania and the !Kung (a subgroup of the San people) in South Africa (61). Our earliest evidence of humans engaged in beekeeping comes from Egypt (23, 56). A relief from the Sun Temple of Newossera dating to 2450 BCE shows beekeepers tending cylindrical stacked hives and harvesting honey. Egyptian reliefs and paintings illustrate that, by this time, beekeeping was a sophisticated economic and cultural practice.

4.1. Beekeeping in the Present Day

Beekeeping in Africa today is widespread and highly diversified in its practice. *Apis mellifera* prefers to nest in cavities, although it will nest in the open in tropical environments, especially if cavities are in short supply (97). Human-provided nesting cavities range from traditional hives made from a variety of locally available materials requiring minimal management to movable-comb and movable-frame hives that require more intensive management to be successful. The origins and spread of traditional hive types and practices, reviewed by Crane (21) and Kidd & Schrimpf (53), have been influenced by many factors, including available materials, trade routes, and the introduction and distribution of cereal crops. Materials used to construct traditional hives include hollow logs and bark, cork, woven plant and crop residue, dung, clay, and gourds (28). Most of these hives are hung horizontally on trees, but some clay pot and fiber hives are used vertically and can be multichambered (23, 53, 76).

Although hive structure and practices vary depending on local environmental conditions, available materials, and cultural traditions, across much of Africa, beekeepers are totally dependent on the availability of wild populations to stock their hives (27). Hives or catcher boxes are placed in trees at specific times of year to maximize colonization by wild migratory colonies or reproductive swarms. They are often baited to increase attractiveness with materials including beeswax, honey, sugar, fruit juices, cow dung, fermented beans, and herbs (53). The colonized hives are left largely unmanaged until honey is harvested. How destructive the harvest is to the colony varies, and more destructive harvests often lead to absconding. As the season progresses, and food and water resources diminish, colonies often (but not always) abscond and presumably migrate, following resource availability. Beekeepers use this time to repair, clean, and rebait hives in preparation for the next rainy season. In South Africa and in Egypt and a few other northern African countries, where the environment is more temperate, a more industrialized form of beekeeping is practiced using movable-frame hives and associated methods (2, 32, 123).

4.2. Impacts of European Colonization and Economic Development

Since the early 1900s, beekeeping in Africa has been influenced by European colonization and Western economic development. European settlers found African bees to be unmanageable, and attempts were made to introduce European bees (33). By the mid-1900s, beekeeping was seen by governmental and nongovernmental agencies as a way to raise the incomes of small landholders and promote forest conservation (12, 19, 29, 60, 75). Beekeeping requires little to no land ownership and little capital investment, and the key component, the bees, constitute a free ecosystem resource. Benefits include nutrient- and calorie-dense food, medicine, and potential income from the sale of honey and beeswax. Additional benefits include discouraging deforestation and increased reforestation and ecosystem services in the form of pollination for both crops and wild flora. Many development efforts have focused on the introduction of hives and training in management methods designed for temperate bees (9, 14, 19, 29, 49, 53). Hives are typically donated, and training is often short term and nominal. While there are substantial data to support increased honey yields with movable-frame hives (26, 39, 102), these hives are expensive, require skilled carpentry and high-quality wood to construct, and do not last long in many African climates (38, 57). In addition, they require more intensive management and are highly subject to theft. For these reasons, intermediate movable-comb hives such as the Kenyan Top Bar hive, the Tanzania hive, and the Dadant transitional hive, were introduced (19, 113). These hives are mainly horizontal and use top bars rather than frames. However, even with the promise of higher honey yields associated with new hive designs (38, 102, 114), traditional hives and practices persist. In the Bamenda area of Cameroon around Mount Oka, where beekeeping is intensively practiced, the traditional Oku hive constitutes 80% of the 1,392 hives of the 58 members of the North West Bee Farmers' Association (47). In Kenya, 95% of the reported hives are still traditional log hives (91), and in Ethiopia, 95.57% of honey is produced in traditional hives (49). In Nigeria, various nesting structures are still used, including cane and straw hives, clay pots, gourds, and calabashes, along with traditional log hives (4).

A 2017 study of beekeeping in Uganda found significant barriers to small landholders' adoption of beekeeping, and the wellbeing status of beekeeping households was significantly lower than that of nonbeekeeping households (8). A comprehensive study of Kenyan Top Bar hive adoption in the Baringo District found that beekeepers had not adopted the new technology, mainly as a result of the lack of reliable technical support (40). There are many reasons why traditional hives and practices persist, why beekeeping has not been widely adopted by new individuals, and why beekeeping has failed to significantly contribute to the alleviation of poverty in Africa. Beyond increased education, reduced cost, increased availability of materials, and greater technical support, a deeper understanding of the basic biology of African bees is needed. Hepburn & Radloff (43, p. VIII), in their 1998 book *Honeybees of Africa*, argue that our knowledge of African honey bees is minute in comparison to what is known about European bees and that, "We fervently hope that the collection of what little there is will reveal some of the enormous gaps in the biology of these honey bees and in some way serve as a stimulus to broaden this base. Only then can the honeybees of Africa make their own contribution to the world corps of honeybee biology and at the same time translate the honeybee into an effective development tool for the people of Africa." This continues to be the case 25 years later.

5. KEY FACTORS IMPACTING HEALTH

In the past two to three decades, there has been considerable research effort aimed at honey bee health, mainly due to the large colony losses experienced around the world (69, 77, 105). Many of the critical drivers of colony losses, including pathogens, parasites, pesticides, and habitat loss (77, 89, 105, 115), are present in Africa (24, 36, 71, 73, 80, 87, 88, 108) (see **Supplemental Table 2**).

Supplemental Material >

5.1. Parasites and Pathogens

Pirk et al. (88) reviewed honey bee health in Africa. Despite the presence of the parasitic mite *V. destructor* and pathogens including *P. larvae*, both responsible for significant losses elsewhere in the world, with a few exceptions, substantial losses have not been reported in Africa (71, 88). In South Africa, the introduction of varroa mites resulted in a period of high colony losses, but within six to seven years, losses stabilized at approximately 5%, similar to pre-varroa levels (6). However, significant colony losses due to an outbreak of American foulbrood have recently been reported in South Africa (88). Colony losses due to varroa mites have also been reported on Madagascar (92). The subspecies *A. m. unicolor* (111) is unique to these islands and is possibly more susceptible compared to mainland subspecies. In Egypt, Yahya et al. (123) report declining colony numbers beginning in 1990, with a 50% decrease between 2005 and 2016. They cite the introduction of varroa mites (first reported in 1983), loss of agricultural land, overuse of pesticides, in-hive chemical use, and the introduction of alien plant species as contributing factors.

5.2. Pests and Predators

Both small (*A. tumida*) and large (*O. fuligineus* and *Oplostomus haroldi*) hive beetles are endemic to parts of Africa. All hive beetles can do damage to colonies by consuming nectar, pollen, and brood (118). Even though they are not considered serious pests of African honey bees, they can be a seasonal problem in some places if present in large numbers and are known to cause colonies to abscond (118). The small hive beetle *A. tumidae* has been reported as a serious pest on the island of Mauritius, where beekeepers report heavy losses (70). Mauritius also has a recent history of European subspecies importations (112). These beetles have had devastating effects on colonies outside Africa, where they have been introduced (78).

The greater (*G. mellonella*) and lesser (*A. grisella*) wax moths are also ubiquitous across Africa and are considered by many to be the most serious insect pests of honey bees (43–45). This is particularly the case in movable-frame beekeeping, where comb is stored and reused to maximize honey production. Infestations can result in absconding where colonies are weak (32). However, these moths are also considered hive cleaners, since they consume all remaining comb and stores in colonies that have absconded. This has likely aided in reducing pathogen and pesticide buildup in free-living populations.

The honey badger, *Mellivora capensis*, is the most serious predator of honey bee colonies in Sub-Saharan Africa and is one reason why hives are placed high up in trees or suspended on tree branches. African beekeepers also face considerable challenges with theft and vandalism, fire, and even intentional poisoning of honey bee colonies (23, 45, 46).

5.3. Habitat Loss

Deforestation and landscape fragmentation is well documented in Africa (11, 55). An increasing human population is likely to compound these losses (1, 82). However, parts of the continent are home to charismatic wildlife, which support economically vital tourism. In this context, large and substantial efforts are being made to protect and conserve landscapes for wildlife. Conservation of honey bee populations should be part of these efforts.

5.4. Climate Change

A recent survey of beekeepers in Tanzania found that, while experienced beekeepers were accustomed to climate-induced fluctuations in honey yields, newly trained beekeepers were more likely to abandon beekeeping in years following low honey production caused by drought (116). Africa is no stranger to drought. However, recent climate change models predict that parts of Africa will experience more frequent droughts that last longer in the future (74). Lack of rainfall would reduce plant bloom and survival, which would negatively impact honey yields but also reduce colony buildup and reproduction (43). Likewise, higher rainfall predicted in some areas could limit the ability of bees to forage. These changes in climate would also presumably limit the availability of food resources for migrating colonies. The overall effect would be fewer colonies seeking nesting cavities. Since African beekeepers are almost universally dependent on the availability of these wild bees to stock their hives, beekeeping and honey production would certainly be severely negatively impacted. Further negative impacts would be expected on the pollination of food crops and wild flora, possibly creating a demand for managed pollinators.

6. BEEKEEPING

Commercially kept western honey bees are highly managed to meet the economic demands placed upon them. The desire for large honey crops, the pollination of monocultures, and the increased production of bees and queens to meet the demand for replacement colonies have put pressure on these bees, with significant consequences. Larger colonies are capable of increased honey hoarding (31). The desire for larger colonies has driven interventions such as swarm prevention, stimulatory feeding, and chemocentric disease and parasite control (25). However, application of disease and parasite control measures prevents the evolution of honey bee resistance or tolerance to diseases and parasites (100). Swarm prevention by expanding hive size allows for large, continuously breeding colonies, thereby increasing the availability of brood for ongoing parasite reproduction within colonies (59). Movable-frame hives and management practices encourage the continual reuse of comb, which allows buildup of pathogens and pesticides in wax (72). In addition, a high concentration of hobby beekeepers in urban areas, crop pollination, package bee production, and queen breeding programs all concentrate large numbers of colonies in confined areas, allowing for the free flow of pathogens and parasites and competition for limited food resources (22, 81, 100). In Europe, these anthropogenic factors, especially in combination, have not only driven losses (69), but also put locally adapted subspecies at risk (64). We have greatly benefited from the products and services of honey bees, but they are now considered to be in decline (77, 89). In some industrialized countries, there is a growing recognition that the industrial beekeeping model is driving honey bee decline. In Europe, there is a call to conserve geographically adapted subspecies (64). There is also growing support for movements that promote a less industrialized form of beekeeping, including natural beekeeping (20), Darwinian beekeeping (99), survivor stock, and sustainable beekeeping. However, this is likely to be a hard sell to commercial beekeepers and large commercial crop growers now dependent on the industrial beekeeping model.

In contrast, the hands-off approach of traditional beekeeping in Africa appears to have far-reaching benefits for the bees. Honey yields from individual colonies remain relatively low, but the bees appear healthier (71, 88). Across most of Sub-Saharan Africa, colony densities are low, and swarming and absconding are frequent. Swarming results in a broodless period interrupting parasite reproduction (59, 94), and colonies in small nests that swarm more often have lower varroa infestation rates and less disease (59). Newly established colonies from swarms and migrating colonies start with low mite infestation levels (62, 94, 100). During dearth, colonies are allowed to abscond and migrate, so supplemental feeding is not necessary. While there are benefits to traditional beekeeping, there is much room for improvement. New hive materials, such as plastics and concrete, are being tried given the realization that the use of log and bark hives, which results in the death of large trees, is not sustainable (18). Clearly, there is a need for more basic research aimed at a deeper understanding of the unique ecology and biology of these bees, and their management requires an indigenous approach that reflects that knowledge base, as well as the economics and needs of local communities and markets.

7. CONCLUSION AND FUTURE DIRECTIONS

The diversity of African honey bees reflects the diversity of ecosystems that they inhabit and the communities of organisms with which they evolved. Quantifying the behavioral and biological differences between subspecies will require further investigation. However, it is clear that African honey bees are distinct when compared to bees from other parts of the world, including the ubiquitous European honey bee stocks. Honey bees in Africa exhibit behaviors and biology that are likely adaptations to the cycle of dry and wet seasons and predation found in tropical and subtropical climates. They are more prone to swarming and migration. They are also likely to form amalgamations while migrating or during swarming. The aggression of African honey bees is well appreciated and seems to be an adaptation to the predators, including human honey hunters, that these bees encounter in their natural environment. African bees also seem to be somewhat resistant to disease, and they exhibit hygienic behavior. More research is needed to understand how common hygienic behavior is and to what degree it confers resistance.

However, African honey bees share challenges with *Apis* subspecies in other parts of the world, both managed and unmanaged. Endemic hive beetles and introduced wax moths can have devastating effects on colonies. Unique to Africa is the destructive power of honey badgers, which are reported by beekeepers to be a major vertebrate predator of honey bees. Introduced pathogens and pests, like varroa mites, are ongoing concerns. However, there is evidence that continental African bees are able to withstand and perhaps evolve in response to these introduced challenges, underscoring the need to maintain wild-living populations. Many smallholder beekeepers do not seem to be affected by widespread pesticide use, but more research is needed to identify the extent of pesticide effects. The main concern in the twenty-first century is habitat destruction coupled with climate change. As forage habitat becomes more fragmented with increased urbanization and agricultural intensification, bee populations are likely to decline, as has been seen in other parts of the world.

In recognition of their value and their vulnerability, protecting pollination populations has become a global concern (90). Going forward, it will be critical to preserve existing African honey bee populations and the unique benefits of these adapted subspecies. Ultimately successful beekeeping that contributes significantly to an individual's livelihood, as well as ongoing ecosystem services provided by honey bees, depends first and foremost on the availability of healthy bee populations.

Our successful management of European bees relies on our understanding of their biology. This level of understanding is lacking for African bees. More basic research is necessary to develop management systems based on a deeper understanding of the biology of African honey bees in the context of their environment. In addition, it will be critical to understand the factors that have contributed to their success in the presence of environmental challenges to preserve these and factor them into management systems.

Bommarco et al. (12) suggested a model for ecological intensification to meet global food demands while minimizing agriculture-induced environmental impacts. In Africa, maintaining biodiversity as the human population triples will be a major challenge. This will also have to be done within the context of increased weather extremes and continued challenges with soil fertility and erosion. Economic growth will create greater wealth in the broader society but will also put the burden of agricultural production on a smaller proportion of the population. Paramount is the requirement that high-quality scientific research be supported and conducted to meet these significant challenges and an informed and increasingly productive agricultural sector be created.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

LITERATURE CITED

1. Abrol DP. 2012. The role of pollination in improving food security and livelihoods. In *Pollination Biology: Biodiversity Conservation and Agricultural Production*, ed. DP Abrol, pp. 737–70. Berlin: Springer
2. Adjare SO. 1990. *Beekeeping in Africa*. FAO Agric. Serv. Bull. 68/6, Food Agric. Org. U. N., Rome
3. Aidoo SK. 1997. Honey quality and marketing in Ghana. In *Perspectives for Honey Production in the Tropics*, ed. MJ Sommeijer, J Beetsma, JW Boot, EJ Roberts, R De Vries, pp. 103–16. Utrecht, Neth.: NECTAR
4. Ajao AM, Oladimeji Y. 2015. Structure, production and constraints of honey hunting and traditional beekeeping returns in Patigi, Kwara State, Nigeria. *Egypt. Acad. J. Biol. Sci.* 8(1):41–52
5. Allsopp M. 2004. Cape honeybee (*Apis mellifera capensis* Eshscholtz) and varroa mite (*Varroa destructor* Anderson & Trueman) threats to honeybees and beekeeping in Africa. *Int. J. Trop. Insect Sci.* 24:87–94
6. Allsopp M. 2006. *Analysis of* Varroa destructor *infestation of southern African populations*. MSc thesis, Univ. Pretoria, S. Afr.
7. Allsopp MH, deLange WJ, Veldtman R. 2008. Valuing insect pollination with cost of replacement. *PLOS ONE* 3:e3128
8. Amulen DR, D'Haese M, Ahikiriza E, Agea JG, Jacobs FJ, et al. 2017. The buzz about bees and poverty alleviation: identifying drivers and barriers of beekeeping in sub-Saharan Africa. *PLOS ONE* 12:e0172820
9. Anand S, Sisay G. 2011. Engaging smallholders in value chains: creating new opportunities for beekeepers in Ethiopia. *Oxfam Policy Pract. Agric. Food Land* 11:74–88
10. Berg S. 1996. *Investigations to increase the attractiveness of the Malawi standard hive for natural colonization through bee swarms*. Rep., Dept. Natl. Parks Wildl., Rumphi, Malawi
11. Bogaert J, Bamba I, Koffi KJ, Sibomana S, Djibu JPK, et al. 2008. Fragmentation of forest landscapes in Central Africa: causes, consequences and management. In *Patterns and Processes in Forest Landscapes: Multiple Use and Sustainable Management*, ed. R Lafortezza, G Sanesi, J Chen, TR Crow, pp. 67–87. Berlin: Springer
12. Bommarco R, Kleijn D, Potts SG. 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol. Evol.* 28(4):230–38

13. Bradbear N. 2009. *Bees and Their Role in Forest Livelihoods: A Guide to the Services Provided by Bees and the Sustainable Harvesting, Processing and Marketing of Their Products*. Non-Wood For. Prod. 19. Rome: Food Agric. Org. U. N.
14. Carroll T, Kinsella M. 2013. Livelihood improvement and smallholder beekeeping in Kenya: the unrealized potential. *Dev. Pract.* 23:332–45
15. Chakuya J, Gandiwa E, Muboko N, Muposhi VK. 2022. A review of habitat and distribution of common stingless bees and honeybees species in African savanna ecosystems. *Trop. Conserv. Sci.* 15:194008292210996
16. Chandler MT. 1976. The African honeybee—*Apis mellifera adansonii*: the biological basis of its management. In *Proceedings of the First International Conference on Apiculture in Tropical Climates, London*, pp. 61–68. Cardiff, Wales: Int. Bee Res. Assoc.
17. Cheruiyot SK, Lattorff HMG, Kahuthia-Gathu R. et al. 2018. Varroa-specific hygienic behavior of *Apis mellifera scutellata* in Kenya. *Apidologie* 49:439–49
18. Clause B, Clause R. 1991. *Zambian Beekeeping Handbook*. Lusaka, Zambia: Beekeep. Div. For. Dept.
19. Commonw. Secr. 1979. *Beekeeping in rural development*. Rep., Commonw. Nations, London
20. Conrad R. 2013. *Natural Beekeeping: Organic Approach to Modern Apiculture*. London: Chelsea Green Publ. 2nd ed.
21. Crane E. 1983. *The Archaeology of Beekeeping*. London: Gerald Duckworth Co.
22. Crane E. 1990. *Bees and Beekeeping: Science, Practice and World Resources*. London: Heinnmann Newness
23. Crane E. 1999. *The World History of Beekeeping and Honey Hunting*. London: Gerald Duckworth Co.
24. Davison S, Govan D, Leat V, Allsopp MH. 1999. Bee diseases in South Africa I: EFB, AFB, chalkbrood and bee viruses. *S. Afr. Bee J.* 71:84–87
25. Delaplane KS. 1997. Practical science—research helping beekeepers 2. Colony manipulations for honey production. *Bee World* 78:5–11
26. Desalgne P. 2012. *Ethiopian honey: accessing international markets with inclusive business and sector development*. Rep., SNV Neth. Dev. Org., The Hague
27. Dietemann V, Pirk CWW, Crewe RM. 2009. Is there a need for conservation of honeybees in Africa? *Apidologie* 40:285–95
28. Dogantzis KA, Tiwari T, Conflitti IM, Dey A, Patch HM, et al. 2021. Thrice out of Asia and the adaptive radiation of the western honey bee. *Sci. Adv.* 7:eabj2151
29. Drescher W, Crane E. 1982. *Technical cooperation activities: beekeeping a directory and guide*. Rep., Ger. Agency Tech. Coop. (GTZ), Eschborn, Ger.
30. Endalamaw TF. 2015. *Dynamics in the management of honey production in the forest environment of southwest Ethiopia: interactions between forests and bee management*. MSc thesis, Wageningen Univ., Neth.
31. Farrar C. 1937. The influence of colony populations on honey production. *J. Agric. Res.* 54:945–54
32. Fletcher DJC. 1978. The African bee *Apis mellifera adansonii* in Africa. *Annu. Rev. Entomol.* 23:151–71
33. Fletcher DJC, Johannsmeier MF. 1987. The status of beekeeping in South Africa. *S. Afr. Bee J.* 50:5–20
34. Fletcher DJC, Tribe GD. 1977. Swarming potential of the African bee *Apis mellifera adansonii* L. In *African Bees*, ed. DCJ Fletcher, pp. 25–34. Pretoria, S. Afr.: Apimondia
35. Frazier M, Muli E, Conklin T, Schmehl D, Torto B, et al. 2010. A scientific note on *Varroa destructor* found in East Africa; threat or opportunity? *Apidologie* 41:463–65
36. Fries I, Raina S. 2003. American foulbrood and African honey bees (Hymenoptera: Apidae). *J. Econ. Entomol.* 96:1641–46
37. Fuller ZL, Niño EL, Patch HM, Bedoya-Reina OC, Baumgarten T, et al. 2015. Genome-wide analysis of signatures of selection in populations of African honey bees (*Apis mellifera*) using new web-based tools. *BMC Genom. Electron. Resour.* 16:518
38. Gebremedhn H, Estifanos A. 2013. On farm evaluation of Kenyan Top bar hive (KTBH) for honey production in Tigray Region, Northern Ethiopia. *Livestock Res. Rural Dev*. 25(5):86
39. Getachew A, Assefa A, Gizaw H, Adgaba N, Assefa D, et al. 2015. Comparative analysis of colony performance and profit from different beehive types in southwest Ethiopia. *Glob. J. Anim. Sci. Res.* 3:178–85
40. Gichora M. 2003. *Towards realization of Kenya's full beekeeping potential: a case study of Baringo District*. PhD thesis, Rheinische Friedrich-Wilhems-Univ. Bonn, Ger.

41. Guy RD. 1976. Whence the Cape bee? *S. Afr. Bee J.* 48:9–11
42. Harbo JR, Harris JW. 2009. Responses to *Varroa* by honey bees with different levels of Varroa Sensitive Hygiene. *Bee World* 48:156–61
43. Hepburn HR, Radloff SE. 1998. *Honeybees of Africa*. Berlin: Springer
44. Human H, Pirk CWW, Crewe RM, Ditemann V. 2011. The honeybee disease American foulbrood—an African perspective. *J. Entomol. Soc. S. Afr.* 19:551–57
45. Hussein MH. 2001. Beekeeping in Africa. *Apiacta* 1–2:32–48
46. Hussein MH. 2001. Beekeeping in Africa: II—central, southern African countries and islands. In *Proceedings of the 37th International Apiculture Congress, Durban, South Africa*. Rome: Apimondia
47. Ilyasov RA, Lee ML, Takahashi JI, Kwon HW, Nikolenko AG. 2020. A revision of subspecies structure of western honey bee *Apis mellifera*. *Saudi J. Biol. Sci.* 27:3615–21
48. Ingram VJ, Njikeu J. 2011. Sweet, sticky and sustainable social business. *Ecol. Soc.* 16(1):37
49. Jenkins GP, Miklyaev M. 2014. *Honey production in Ethiopia: a cost-benefit analysis of modern versus traditional beekeeping technologies*. Dev. Discuss. Pap. 2013–17, JDI Exec. Progr., Kingston, Can.
50. Kalanzi F, Nansereko S, Buyinza J, Kiwuso P, Turinayo Y, et al. 2015. Socio-economic analysis of beekeeping enterprise in communities adjacent to Kalinzu forest, Western Uganda. *Int. J. Res. Land-Use Sustain.* 2:81–90
51. Karicha JM, Akaranga SI, Musili TKM. 2021. Secularization of marriage ritual among the Ameru in Kenya. *East Afr. J. Tradit. Cult. Relig.* 3(2):52–57
52. Kasina M, Kraemer M, Martius C, Wittmann D. 2009. Farmers' knowledge of bees and their natural history in Kakamega district, Kenya. *J. Apicult. Res.* 48:126–33
53. Kidd AD, Schrimpf B. 2009. Bees and bee-keeping in Africa. In *The Origins and Development of African Livestock: Archaeology, Genetics, Linguistics and Ethnography*, ed. R Blench, K MacDonald, pp. 503–26. London: UCL Press
54. Kiiti MK. 2013. *Socio-economic, cultural and institutional factors influencing modern box hives adoption in Kitui County, Kenya*. MA thesis, Kenyatta Univ., Nairobi, Kenya
55. Kouassi JL, Gyau A, Diby L, Bene Y, Kouame C. 2021. Assessing land use and land cover change and farmers' perceptions of deforestation and land degradation in south-west Côte d'Ivoire, West Africa. *Land* 10:429
56. Kritsky G. 2017. Beekeeping from antiquity through the Middle Ages. *Annu. Rev. Entomol.* 62:249–64
57. Kuboja NM, Kilima FTM, Isinika AC. 2020. Absconding of honeybee colonies from beehives: underlying factors and its financial implications for beekeepers in Tanzania. *Int. J. Agric. Sci. Res. Technol. Ext. Educ. Syst.* 10:185–93
58. Lalika MCS, Machangu JS. 2008. Beekeeping for income generation and coastal forest conservation in Tanzania. *Bees Dev.* 88:4–6
59. Loftus CJ, Michael SL, Seeley T. 2016. How honey bee colonies survive in the wild: testing the importance of small nests and frequent swarming. *PLOS ONE* 1(3):e0150362
60. Lowore J, Bradbear N. 2015. Understanding forest beekeeping in Africa as an efficient forest-resource harvesting system and not a rudimentary system in need of modernization. In *Proceedings of the XIV World Forestry Congress, Durban, South Africa*. Rome: Food Agric. Org. U. N.
61. Marlowe FW, Berbesque JC, Wood B, Crittenden A, Porter C, Mabulla A. 2014. Honey, Hadza, hunter-gatherers, and human evolution. *J. Hum. Evol.* 71:119–28
62. McMenamin A, Mumoki F, Frazier M, Kilonzo J, Mweu B, et al. 2017. The impact of hive type on the behavior and health of honey bee colonies (*Apis mellifera*) in Kenya. *Apidologie* 48:703–15
63. McNally LC, Schneider SS. 1992. Seasonal cycles of growth, development and movement of the African honeybee, *Apis mellifera scutellata*, in Africa. *Insect. Soc.* 39:167–79
64. Meixner MD, Costa C, Kryger P, Hatjina F, Bouga M, et al. 2010. Conserving diversity and vitality for honey bee breeding. *J. Apic. Res.* 49(1):85–92
65. Meixner MD, Leta MA, Koeniger N, Fuchs S. 2011. The honey bees of Ethiopia represent a new subspecies of *Apis mellifera—Apis mellifera simensis* n. ssp. *Apidologie* 42:425–37
66. Meixner MD, Sheppard WS, Dietz A, Krell R. 1994. Morphological and allozyme variability in honey bees from Kenya. *Apidologie* 25:188–202

67. Melin A, Rouget M, Midgley J, Donaldson JS. 2014. Pollination ecosystem services in South African agricultural systems. *S. Afr. J. Sci.* 110(11/12):2014-0078
68. Mogga J, Ruttner F. 1988. *Apis florea* in Africa: source of the founder population. *Bee World* 69:100–3
69. Moritz RFA, de Miranda JR, Fries I, Le Conte Y, Neumann P, Paxton RJ. 2010. Research strategies to improve honeybee health in Europe. *Apidologie* 41:227–42
70. Muli E, Okwaro LA, Kilonzo J, Ali N, Monthy GT. 2018. *Varroa destructor*—free islands in the South West Indian Ocean. *Bee World* 95:122–23
71. Muli E, Patch H, Frazier M, Frazier J, Torto B, et al. 2014. Evaluation of the distribution and impacts of parasites, pathogens, and pesticides on honey bee (*Apis mellifera*) populations in East Africa. *PLOS ONE* 9:e94459
72. Mullin CA, Frazier M, Frazier JL, Ashcraft S, Simonds R, et al. 2010. High levels of miticides and agrochemicals in North American apiaries: implications for honey bee health. *PLOS ONE* 5:e9754
73. Mumoki FN, Fompong A, Muli E, Muigai AWT, Masiga D. 2014. An inventory of documented diseases of African bees—a review. *J. Entomol. Soc. S. Afr.* 22:473–87
74. Nangombe S, Zhou T, Zhang W, Wu B, Hu S, et al. 2018. Record-breaking climate extremes in Africa under stabilized 1.5 C and 2 C global warming scenarios. *Nat. Clim. Change* 8:375–80
75. Ndamage J. 2018. *Beekeeping Modernization and Community Livelihoods*. Kampala, Uganda: ARCOS Netw.
76. Ndiaye M. 1976. Beekeeping development in Senegal. In *Apiculture in Tropical Climates*, ed. E Crane, pp. 171–79. London: IBRA
77. Neumann P, Carreck NL. 2010. Honey bee colony losses. *J. Apic. Res.* 49:1–6
78. Neumann P, Elzen PJ. 2004. The biology of the small hive beetle (*Aethina tumida*, Coleoptera: Nitidulidae): gaps in our knowledge of an invasive species. *Apidologie* 35:229–47
79. Neumann P, Hepburn R. 2002. The Cape honeybee (*Apis mellifera capensis*): from laying workers to social parasites. *Apidologie* 33:165–92
80. Newman RJS, Marchant R, Enns C, Capitani C. 2021. Assessing the impacts of land use and climate interactions on beekeeping livelihoods in the Taita Hills, Kenya. *Dev. Pract.* 31(4):446–61
81. Nolan MP, Delaplane KS. 2017. Distance between honeybee *Apis mellifera* colonies regulates populations of *Varroa destructor* at a landscape level. *Apidologie* 48:8–16
82. Norris K, Asase A, Collen B, Gockowksi J, Mason J, et al. 2010. Biodiversity in a forest-agriculture mosaic: the changing face of West African rainforests. *Biol. Conserv.* 143:2341–50
83. Nuru A, Amssalu B, Hepburn HR, Radloff SE. 2002. Swarming and migration in the honey bees (*Apis mellifera*) of Ethiopia. *J. Apic. Res.* 41:35–41
84. Otis GW. 1982. Weights of worker honeybees on swarms. *J. Apic. Res.* 21:88–92
85. Oziona EJ, Okaka ANC. 2019. Herbal medicines in African traditional medicine. In *Herbal Medicine*, ed. PF Builders. London: InTechOpen. **https://doi.org/10/5772/intechopen.80348**
86. Pager H. 1973. Rock paintings in Southern Africa showing bees and honey hunting. *Bee World* 54:61–68
87. Pirk CW, Human H, Crewe RM, van Engelsdorp D. 2014. A survey of managed honey bee colony losses in the Republic of South Africa—2009 to 2011. *J. Apic. Res.* 53:35–42
88. Pirk CW, Strauss U, Yusuf AA, Demares F, Human H. 2015. Honeybee health in Africa—a review. *Apidologie* 47:276–300
89. Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25:345–53
90. Potts SG, Imperatriz-Fonseca V, Ngo HT, Aizen MA, Biesmeijer JC, et al. 2016. Safeguarding pollinators and their values to human well-being. *Nature* 540:220–29
91. Rain SK. 2007. *A Practical Guide for Raising and Utilization of Silkmoths and Honey Bees in Africa*. Nairobi, Kenya: icipe
92. Rasolofoarivao H, Clémencet J, Ravaomanarivo LHR, Razafindrazaka D, Reynaud B, Delatte H. 2013. Spread and strain determination of *Varroa destructor* (Acari: Varroidae) in Madagascar since its first report in 2010. *Exp. Appl. Acarol.* 60(4):521–30
93. Rothenbuhler WC. 1964. Behaviour genetics of nest cleaning in honey bees. I. Responses of four inbred lines to disease-killed brood. *Anim. Behav.* 12:578–83
94. Royce LA, Rossignol PA, Burgett DM, Stringer BA. 1991. Reduction of tracheal mite parasitism of honeybees by swarming. *Philos. Trans. R. Soc. Lond. B.* 331:123–29

95. Ruttner F. 1978. Biometrical-statistical analysis of the geographic variability of *Apis mellifera* L. *Apidologie* 9:363–81
96. Ruttner F. 1988. *Biogeography and Taxonomy of Honeybees*. Berlin: Springer
97. Schneider SS, DeGrandi-Hoffman G, Smith DR. 2004. The African honeybee: factors contributing to a successful biological invasion. *Annu. Rev. Entomol.* 49:351–76
98. Seeley T. 1985. *Honeybee Ecology*. Princeton, NJ: Princeton Univ. Press
99. Seeley T. 2017. Darwinian beekeeping: an evolutionary approach to apiculture. *Am. Bee J.* 157:277–82
100. Seeley TD, Smith ML. 2015. Crowding honeybee colonies in apiaries can increase their vulnerability to the deadly ectoparasite *Varroa destructor*. *Apidologie* 46:716–27
101. Shackleton C, Shackleton S, Buiten S, Bird N. 2007. The importance of dry woodlands and forests in rural livelihoods and poverty alleviation in South Africa. *For. Policy Econ.* 9:558–77
102. Silberrad REM. 1976. *Bee-Keeping in Zambia*. Pretoria, S. Afr.: Apimondia
103. Smith FG. 1960. *Beekeeping in the Tropics*. London: Longmans
104. Smith FG. 1966. Bees more vicious in East Africa. *S. Afr. Bee J.* 38:14
105. Smith KM, Loh EH, Rostal MK, Zambrana-Torrelio C, Mendiola L, Daszak P. 2013. Pathogens, pests, and economics: drivers of honey bee colony declines and losses. *Ecohealth* 10:434–45
106. Stein K, Coulibaly D, Stenchly K, Goetze D, Porembski S, et al. 2017. Bee pollination increases yield quantity and quality of cash crops in Burkina Faso, West Africa. *Sci. Rep.* 7:17691
107. Steiner WE. 2017. A scientific note on the arrival of the dwarf honeybee, *Apis florea* (Hymenoptera: Apidae), in Djibouti. *Apidologie* 48:657–59
108. Strauss U, Human H, Gauthier L, Crewe RM, Dietemann V, Pirk CWW. 2013. Seasonal prevalence of pathogens and parasites in the savannah honeybee (*Apis mellifera scutellata*). *J. Invertebr. Pathol.* 114:45–52
109. Taylor LR. 1986. The four kinds of migration. In *Insect Flight*, ed. W Danthanarayana, pp. 265–80. Berlin: Springer
110. Taylor OR. 1977. The past and possible future spread of Africanized honey bees in the Americans. *Bee World* 58:19–30
111. Techer MA, Clémencet J, Simiand C, Preeaduth S, Azali HA, et al. 2017. Large-scale mitochondrial DNA analysis of native honey bee *Apis mellifera* populations reveals a new African subgroup private to the South West Indian Ocean islands. *BMC Genet*. 18:53
112. Techer MA, Clemencet J, Simiand C, Turpin P, Garnery L, et al. 2017. Genetic diversity and differentiation among insular honeybee populations in South West Indian Ocean likely reflect old geographical isolation and modern introductions. *PLOS ONE* 12(12):e0189234
113. Towsend GF. 1969. *Beekeeping possibilities and requirements in East Africa*. Rep., Univ. Guelph, Can.
114. Tsafack Matsop AS, Mulu Achu G, Kamajou F, Ingram V, Vabi Boboh M. 2011. Comparative study of the profitability of two types of bee farming in the North West Cameroon. *Tropicultura* 29:3–7
115. vanEngelsdorp D, Meixner MD. 2010. A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. *J. Invertebr. Pathol.* 1:S80–95
116. Wagner K, Meilby H, Cross P. 2019. Sticky business—why do beekeepers keep bees and what makes them successful in Tanzania? *J. Rural Stud.* 66:52–66
117. Wallberg A, Schöning C, Webster MT, Hasselmann M. 2017. Two extended haplotype blocks are associated with adaptation to high altitude habitats in East African honey bees. *PLOS Genet*. 13(5):e1006792
118. Wambua B, Muli E, Kilonzo J, Ngángá J, Kanui T, Muli B. 2019. Large hive beetles: an emerging serious honeybee pest in coastal highlands of Kenya. *Bee World* 96(3):1–2
119. Whitfield CW, Behura SK, Berlocher SH, Clark AG, Johnston JS, et al. 2006. Thrice out of Africa: ancient and recent expansions of the honey bee, *Apis mellifera*. *Science* 314:642–45
120. Winston ML. 1980. Swarming after swarming and reproductive rate of unmanaged honeybee colonies (*Apis mellifera*). *Insect. Soc.* 27:391–98
121. Winston ML. 1987. *The Biology of the Honey Bee*. Cambridge, MA: Harvard Univ. Press
122. Winston ML, Gard WO, Orley RT Jr. 1979. Absconding behaviour of the Africanized honeybee in South America. *J. Apic. Res.* 18:85–94
123. Yahya AN, Codling G, Giesy JP, Safer A. 2018. Beekeeping and the need for pollination from an agricultural perspective in Egypt. *Bee World* 95(4):107–12

Annual Review of Entomology

Volume 69, 2024

Contents

Errata

An online log of corrections to *Annual Review of Entomology* articles may be found at http://www.annualreviews.org/errata/ento