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Honeybee health in Africa—a review

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Abstract – Honeybee (*Apis mellifera* L.) pathogens and parasites and the negative effects thereof on honeybee populations remain an issue of public concern and the subject of active research. Africa with its high genetic diversity of honeybee sub-species and large wild population is also exposed to various factors responsible for colony losses in other parts of the world. Apart from the current American foulbrood epidemic in the Western Cape of South Africa, no large-scale colony losses have been reported elsewhere on the continent. We discuss the presence of pathogens, parasites, pests and predators of African honeybees as well as the threats they face in relation to habitat changes arising from the impact of increased human populations. In addition, we discuss current efforts aimed at protecting and promoting the health of African honeybees.

honeybees / Africa / honeybee health / pathogens / parasites / pests / predators / habitat loss

1. INTRODUCTION

The crucial service and economic value of the majority of Apis and non-Apis pollinators have been reviewed and debated extensively (Aebi et al. 2012; Ollerton et al. 2012; Vanbergen et al. 2013). Honeybees (Apis mellifera L.), both wild and managed, are responsible for the pollination of numerous crops and plants, contributing not only to food security but also the economy (Klein et al. 2007; Allsopp et al. 2008; vanEngelsdorp and Meixner 2010). The decline in honeybee numbers is alarming given their important role in ecosystem services (Neumann and Carreck 2010; Vanbergen et al. 2013). Concern about the decline in colony numbers is warranted in light of the growing demand for crop pollination and added pressure for a sufficient supply of

Corresponding author: H. Human, hhuman@zoology.up.ac.za Manuscript editor: Marina Meixner honeybee colonies (Aizen and Harder 2009; Neumann and Carreck 2010; Goulson et al. 2015).

In recent years, there have been increased research efforts to understand and provide solutions for the large colony losses experienced in many parts of the world (Moritz et al. 2010a; Neumann and Carreck 2010; Smith et al. 2013). A combination of factors have been identified as possible drivers of these colony losses (Neumann and Carreck 2010; Potts et al. 2010; vanEngelsdorp and Meixner 2010; Smith et al. 2013; Pirk et al. 2014; McMenamin and Genersch 2015). One key driver is the international trade in honeybees and bee products, which serves as an active means for the introduction of non-native species and the consequential spread of pathogens, parasites and pests (e.g. recent introduction of small hive beetles in Italy) (Mutinelli 2011; Mutinelli et al. 2014). As experienced in other parts of the world, honeybee populations in Africa have also been affected by the introduction of novel pathogens, parasites and pests (Varroa destructor, American foulbrood, Nosema ceranae) as well as habitat loss (Hussein 2001a, b; Dietemann et al. 2009).

Despite the different threats, Africa seems fortunate as it contains a large endemic wild population of honeybees (Dietemann et al. 2009), which shows a significantly higher genetic diversity than other honeybee populations (Wallberg et al. 2014). In addition, African apiculture has room for growth since only a small proportion of honeybee colonies are commercially managed, with beekeeping in many countries still based on traditional practices (Johannsmeier 2001; Dietemann et al. 2009). Therefore, Africa's large wild population may still be able to adapt to new threats, like diseases, without human interference.

Here, we will focus on the diversity of African honeybees as well as the various problems they face including pathogens, parasites, pests, predators, pesticides and habitat transformation. Efforts currently in place aimed at protecting African honeybee health will also be highlighted.

2. HONEYBEES OF AFRICA

Globally, many A. mellifera L. sub-species (up to 30) have been described in the literature (Ruttner 1988, 1992; Hepburn and Radloff 1998; Bouga et al. 2011; da Silva et al. 2015). Sub-species are mainly classified based on various morphological characteristics, and more recently, molecular techniques have also been applied (Ruttner 1988; Meixner et al. 2013). Africa and Madagascar are home to 11 honeybee sub-species, namely Apis mellifera intermissa, Apis mellifera sahariensis, Apis mellifera lamarckii, Apis mellifera jemenitica (sometimes called Apis mellifera nubi, Apis mellifera sudanensis or Apis mellifera bandasii), Apis mellifera monticola, Apis mellifera litorea, Apis mellifera adansonii, Apis mellifera scutellata, Apis mellifera capensis and Apis mellifera unicolor (Hepburn and Radloff 1998; Engel 1999; Franck et al. 2001; Al-Ghamdi et al. 2013). Recently, Meixner et al. (2011) proposed Apis mellifera simensis as a new sub-species in Ethiopia based on morphometrical features. A. mellifera intermissa, A. mellifera sahariensis and A. mellifera lamarckii occur in the northern parts of Africa, while the remaining eight sub-species occupy the rest of the continent, with the exception of *A. mellifera unicolor* which is found in Madagascar (Ruttner 1988; Hepburn and Radloff 1998; Engel 1999). The conservation of African honeybees is fundamental to maintain the large wild population and high genetic diversity. They may be less susceptible to various pathogens, parasites, pests and predators, as a result of natural selection occurring due to a lack of human intervention.

3. PATHOGENS, PARASITES, PESTS AND PREDATORS OF AFRICAN HONEYBEES

Most of the pathogens and parasites affecting global honeybee colony health are present throughout Africa (Bradbear 1988; Matheson 1993, 1995; Allen and Ball 1996; Hepburn and Radloff 1998; Hussein 2001a, b; Swart et al. 2001; Ellis and Munn 2005; Mumoki et al. 2014). We discuss, summarise (Table I) and illustrate (Figures 1, 2 and 3) most of the pathogens, parasites, pests and predators known to be present on the mainland Africa and highlight potential consequences for these honeybee populations.

3.1. Bacteria

3.1.1. American foulbrood (Paenibacillus larvae)

American foulbrood (AFB) is widely distributed in many African countries, except the central region (Ellis and Munn 2005; Human et al. 2011; Mumoki et al. 2014). AFB, caused by *Paenibacillus larvae*, affects the larval stage (mostly after capping) and can be transmitted by adult honeybees within and between colonies (Lindström et al. 2008). AFB is a notifiable disease of the OIE (Office International des Epizooties/World Organisation for Animal Health). It has been suggested that African honeybees are less susceptible and more capable of dealing with most parasites and pathogens (Fries and Raina 2003), either by expressing stronger hygienic

Country	Bac	Bacteria	Fungi	Viruses	Ā	Mites			Pest	Pests and predators	dators			References ^a
	AFB	EFB			Varroa	Acarapis	Beetles	Flies	Moths	Ants	Wasps	Birds	Mammals	
Algeria	+	+	+	+	+	+		+	+	+	+	+		Hussein (2001a), Bradbear (1988), Allen and Ball (1996), Matheson (1993), Ellis and Munn (2005), Hepburn and Radloff (1998)
Angola		+			+	+	+	+	+		+	+	+	Hussein (2001b), Bradbear (1988), Matheson (1993), Ellis and Munn (2005), Hepburn and Radloff (1998), WAHID Interface (2015)
Benin			+	+	+		+		+	+	+	+	+	Amakpe et al. (2015), Mumoki et al. (2014), Hepburn and Radloff (1998), Paraïso et al. (2011)
Botswana		+			+		+	+	+	+	+		+	Hussein (2001b), Bradbear (1988), Matheson (1993), Ellis and Munn (2005), Hepburn and Radloff (1998), Allsopp (2006)
Burundi								+						Matheson (1995), Ellis and Munn (2005)
Cameroon CAR	+	+				+	+ +	+	+ +	+	+ +			Hepburn and Radloff (1998) Hussein (2001b), Bradbear (1988), Matheson (1993), Ellis and Munn (2005),
														Hepburn and Radloff (1998)
Congo						+	+	+	+	+	+			

Table I. Summary of pathogens, parasites, pests and predators associated with honeybees, reported to be present (+) in 35 African countries.

Table I (continued)	(manin													
Country	Bacteria	ĺ	Fungi	Viruses	N	Mites			Pest	Pests and predators	edators			References ^a
	AFB EI	EFB			Varroa	Acarapis	Beetles	Flies	Moths	Ants	Wasps	Birds	Mammals	
														Hussein (2001b), Bradbear (1988), Matheson (1993), Ellis and Munn (2005), Hepburn and Radloff (1998)
DRC						+	+	+				+	+	Hussein (2001b), Bradbear (1988), Ellis and Munn (2005), Hepburn and Radloff (1998)
Egypt			+	+	+	+	+	+	+	+	+	+		Hussein (2001a), Bradbear (1988), Allen and Ball (1996), Matheson (1993), Matheson (1995), Ellis and Munn (2005)
Eritrea	++	,					+							Ellis and Munn (2005)
Ethiopia			+		+	+	+	+	+	+		+	+	Hussein (2001a), Bradbear (1988), Matheson (1993), Ellis and Munn (2005), Hepburn and Radloff (1998), Begna (2014), Jatema and Abebe (2015)
Gambia	+						+							Ellis and Munn (2005)
Ghana	+		+		+		+	+	+	+	+			Hussein (2001a), Matheson (1993), Ellis and Munn (2005), Hepburn and Radloff (1998), Frazier et al. (2010)
Guinea- Bissau	+ +		+			+	+	+	+					Hussein (2001a), Bradbear (1988), Matheson (1993), Matheson (1995), Ellis and Munn (2005), Hepburn and Radloff (1998)

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Table I (continued)	inued)													
Country	Bac	Bacteria	Fungi	Viruses	Μ	Mites			Pests	Pests and predators	dators			References ^a
	AFB	EFB			Varroa	Acarapis	Beetles	Flies	Moths	Ants	Wasps	Birds	Mammals	
Côte d'Ivoire							+				+			Hepburn and Radloff (1998)
Kenya			+	+	+		+	+	+	+	+	+	+	Hussein (2001a), Muli et al. (2014), Bradbear (1988), Matheson (1993), Ellis and Munn (2005), Hepburn and Radloff (1998)
Libya	+	+	+	+	+						+	+		Hussein (2001a), Bradbear (1988), Matheson (1993), Ellis and Munn (2005), Haddad et al. (2015)
Malawi		+	+			+	+	+	+	+	+	+	+	Hussein (2001b), Matheson (1993), Ellis and Munn (2005), Hepburn and Radloff (1998)
Morocco	+	+	+	+	+	+	+	+	+	+	+	+		Hussein (2001a), Bradbear (1988), Matheson (1993), Ellis and Munn (2005), Hepburn and Radloff (1998), Haddad et al. (2015)
Mozambique					+	+	+	+	+	+	+		+	Hussein (2001b), Bradbear (1988), Ellis and Munn (2005), Hepburn and Radloff (1998), Allsopp (2006)
Namibia Niger			+		+	+	+	+						Ellis and Munn (2005) Ellis and Munn (2005)
Nigeria			+		+		+	+	+	+		+	+	Hussein (2001a), Ellis and Munn (2005), Mumoki et al. (2014), Hepburn and Radloff (1998)

AFB EFB Rwanda + Senegal + South Africa + Sudan + Swaziland + Tanzania +	Fungi	Viruses	Μ	Mites			Pest	Pests and predators	dators			References ^a
a Africa + ia	В		Varroa	A carapis	Beetles	Flies	Moths	Ants	Wasps	Birds	Mammals	
a Africa + + ia				+		+	+		+			Hussein (2001b), Bradbear (1988), Ellis and Munn (2005), Hepburn and Radloff (1998)
a Affrica + ia	+		+	+	+	+	+	+	+	+	+	Hussein (2001a), Bradbear (1988), Ellis and Munn (2005), Hepburn and Radloff (1998)
Africa + and ia					+	+			+		+	Hussein (2001a), Hepburn and Radloff (1998)
ia	+	+	+	+	+	+	+	+	+	+	+	Hussein (2001b), Allen and Ball (1996), Ellis and Munn (2005), Baxter (2009), Hepburn and Radloff (1998)
			+		+	+	+	+	+	+	+	Hussein (2001a), El-Niweiri (2004)
			+									Ellis and Munn (2005), Allsopp (2006)
	+		+		+	+	+	+	+	+	+	Hussein (2001a), Bradbear (1988), Ellis and Munn (2005), Hepburn and Radloff (1998), Mumbi et al. (2014)
Tunisia + +	+	+	+	+		+	+	+		+		Hussein (2001a), Bradbear (1988), Allen and Ball (1996), Matheson (1993), Matheson (1995), Ellis and Munn (2005), Hepburn and Radloff (1998)
Uganda		+	+		+	+	+	+			+	

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	References ^a	Beetles Flies Moths Ants Wasps Birds Mammals	Hussein (2001a), Kajobe et al. (2010), Bradbear (1988), Ellis and Munn (2005), Hepburn and Radloff (1998), Frazier et al. (2010)	 H Hussein (2001b), Bradbear (1988), Ellis and Munn (2005), Hepburn and Radloff (1998) 	 + + Hussein (2001b), Bradbear (1988), Ellis and Munn (2005), Hepburn and Radloff (1998), Allsopp (2006)
	edators	Wasps		+	
	Pests and predators	Ants			+
	Pes	Moths			
		Flies		+	+
		Beetles		+	+
	Mites	Varroa Acarapis			
	N	Varroa			+
	Viruses				
	Fungi				+
inued)	Bacteria	AFB EFB		+	
Table I (continued)	Country			Zambia	Zimbabwe

CAR Central African Republic, DRC Democratic Republic of the Congo $^{\rm a}$ Refer to the reference list for complete citations

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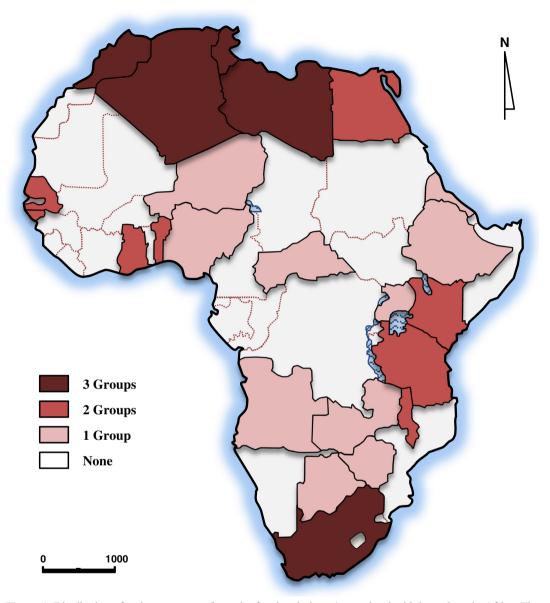


Figure 1. Distribution of pathogen groups (bacteria, fungi and viruses) associated with honeybees in Africa. The higher the numbers of groups present per country, the *darker the shade*; e.g. the *darkest colour* indicates the presence of bacteria, fungi and viruses. Countries depicted in *white* indicate no reported presence of pathogens or insufficient data (for detailed information, see Table I).

behaviour or reducing disease pressure by more frequent absconding (non-reproductive swarming; Hepburn and Radloff 1998 and references therein). However, currently in the Western Cape of South Africa, it seems that AFB and the lack of good beekeeping practices used in that region have overburdened the managed honeybee population resulting in

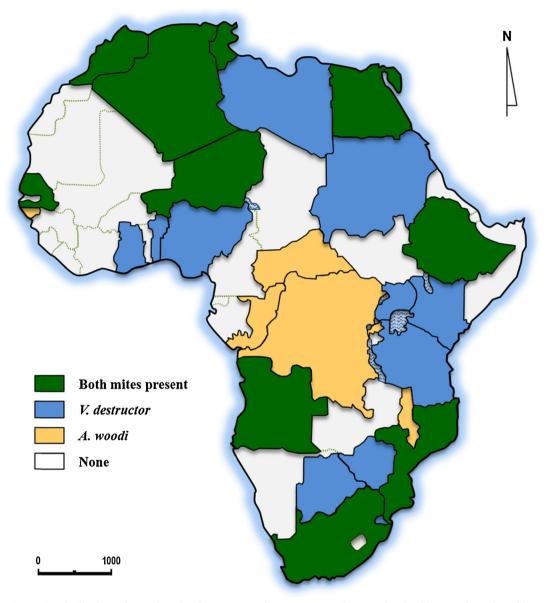


Figure 2. Distribution of parasites (*V. destructor* and *Acarapis woodi*) associated with honeybees in Africa. Countries depicted in *white* indicate no reported presence of parasites or insufficient data (for detailed information see Table I).

significant colony losses (Kriel 2015). The spread of this disease into the wild population, in particular in rural underdeveloped areas on the African continent, may have severe implications for pollination (Kasina et al. 2009).

3.1.2. European foulbrood (Melissococcus plutonius)

The other major bacterial disease of honeybees, European foulbrood (EFB), is caused by

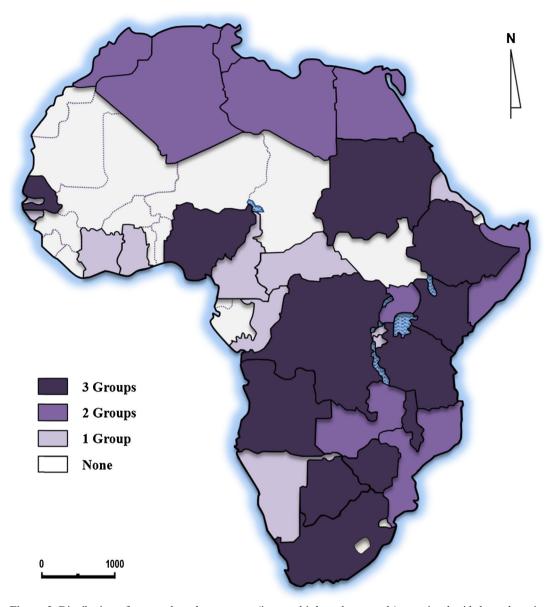


Figure 3. Distribution of pest and predator groups (insects, birds and mammals) associated with honeybees in Africa. The higher the numbers of groups present per country, the *darker the shade*; e.g. the *darkest colour* indicates the presence of insects, birds and mammals. Countries depicted in *white* indicate no reported presence of pests and predators or insufficient data (for detailed information, see Table I).

Melissococcus plutonius and is very prevalent in Africa (Matheson 1993; Hussein 2001a, b; Ellis and Munn 2005; Mumoki et al. 2014). EFB is also a notifiable disease of the OIE. EFB kills larvae before they are capped and disease outbreaks appear to be seasonal and stress related (Forsgren 2010). Even though this disease is considered to be less pathogenic than AFB, it may still result in economic colony losses (Forsgren et al. 2013). Despite the long history in Africa, significant losses have not been reported (Swart et al. 2001; Pirk et al. 2014).

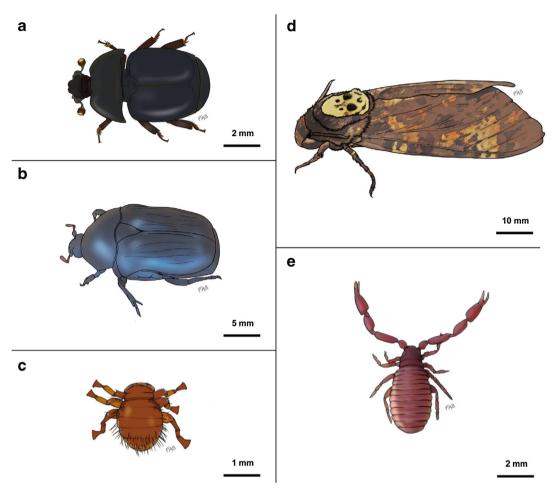


Figure 4. Drawings of interesting pests commonly found in South African colonies: **a** small hive beetle (*Aethina tumida*), **b** large hive beetle (*Oplostomus fuligineus*), **c** bee louse (*Braula coeca*), **d** death's head hawkmoth (*Acherontia atropos*), and **e** bee pseudoscorpion (*Ellingsenius* spp.). Drawings by Dr F. Démares (Adobe Photoshop CS2).

3.2. Fungi

3.2.1. Nosema apis and N. ceranae

There are many reports confirming the presence of *N. apis* (Hussein 2001a, b; Swart et al. 2001; Fries and Raina 2003; Ellis and Munn 2005; Strauss et al. 2013; Mumoki et al. 2014) in Africa, but there are only two reports of *N. ceranae* in colonies from Algeria and Benin (Higes et al. 2009; Cornelissen et al. 2011). *N. apis* and *N. ceranae* are microsporidian gut parasites that cause nosemosis in adult honeybees. Symptoms produced by *N. apis* in honeybees (most often in spring) include trembling, crawling, inability to fly and spotting (dysentery) (Sammataro and Avitabile 2011). In contrast, *N. ceranae* does not produce obvious symptoms and is commonly found throughout the year (Bourgeois et al. 2010). Both *Nosema* species affect colony mortality rates, as well as honey and brood production (Fries 2010; Fries et al. 2013). Evidence with regards to the virulence, seasonality and overall effect of both *N. apis* and *N. ceranae* infection in honeybee colonies is contradictory (Williams et al. 2014; Milbrath

et al. 2015; Natsopoulou et al. 2015). European honeybees have shown that the effects of both *Nosema* species depend on the honeybee subspecies and the strain of *Nosema* (Paxton et al. 2007; Martín-Hernández et al. 2011). Unfortunately, in Africa, there is limited knowledge of the occurrence and prevalence of both *Nosema* species; nevertheless, there is also a lack of reported negative impacts on African subspecies.

3.2.2. Chalkbrood (Ascosphaera apis)

Ascosphaera apis occurs in various countries in Africa, including Algeria, Tunisia, Egypt, Ethiopia, Nigeria and South Africa (Heath 1985; Hussein 2001a, b; Swart et al. 2001; Ellis and Munn 2005; Yohannes et al. 2009; Sanad and Mohanny 2011; Akinwande et al. 2013; Strauss et al. 2013). Chalkbrood is a fungal brood disease that affects larvae. The mummified larvae can easily be detected and vary in colour from white to black (reviewed in Aronstein and Murray 2010). In some cases, chalkbrood can cause a reduction in colony numbers and possibly colony losses (reviewed in Jensen et al. 2013). However, proper beekeeping practices (e.g. good ventilation) may limit the effects of this disease (Sammataro and Avitabile 2011).

3.3. Viruses

At present, there are at least 23 viruses associated with honeybee health (McMenamin and Genersch 2015), of which the presence of nine have been reported in many African countries. These viruses include Deformed wing virus (DWV), Black queen cell virus (BQCV), Varroa destructor virus 1 (VDV-1), Israeli acute paralysis virus (IAPV), Acute bee paralysis virus (ABPV), Chronic bee paralysis virus (CBPV), Apis mellifera filamentous virus (AmFV), Lake Sinai virus (LSV) and Sacbrood virus (SBV) (Allen and Ball 1996; Davison et al. 1999; Hussein 2001a; Kajobe et al. 2010; Loucif-Ayad et al. 2013; Strauss et al. 2013; Muli et al. 2014; Mumoki et al. 2014; Amakpe et al. 2015). Recently, five of the nine viruses mentioned above were extensively reviewed by Mumoki et al. (2014), and therefore, we will focus on the remaining four viruses namely, CBPV, VDV-1, AmFV and LSV. All four viruses appear to occur throughout the year and they mostly affect adult honeybees (de Miranda et al. 2013).

CBPV-infected honeybees can show either one of two distinct sets of symptoms: trembling, crawling, irregular wing position, stretched abdomens or black/greasy appearance (hairless) (Ribière et al. 2010). CBPV may affect all honeybee life stages and transmission of this virus is mostly horizontal with little information about vertical transmission routes (de Miranda et al. 2013).

VDV-1 is closely related to DWV and it has been suggested that VDV-1 can cause wing deformity in honeybees (Ongus 2006; Zioni et al. 2011). This virus affects larvae, pupae and adults, and transmission occurs through various pathways (de Miranda et al. 2013). The presence of this virus in Africa is of concern due to its known association with *V. destructor* (see Section 3.4.1).

AmFV does not cause noticeable symptoms in adult honeybees, but some of these honeybees when dissected may have white haemolymph (de Miranda et al. 2013). Although this virus has been reported all year round, it may be more prevalent during spring (de Miranda et al. 2013; Hartmann et al. 2015). Horizontal and vertical transmission routes exist and information with regards to its association with other pathogens (e.g. N. apis) is contradictory (Hartmann et al. 2015). The only positive confirmation of AmFV presence is from South Africa (Allen and Ball 1996); hence, the economic effect may be negligible. Furthermore, Hartmann et al. (2015) suggested that AmFV on its own should not have an impact at the colony level.

LSV has only recently been described in adult honeybees (Runckel et al. 2011) and was only found in three adult samples from Benin (Amakpe et al. 2015). The transmission routes and associations of this virus with other pathogens or parasites are unknown (de Miranda et al. 2013). For that reason, the economic importance of LSV in Africa requires further investigation but seems negligible at present.

In general, severe losses due to honeybee viruses have not been reported in Africa, but this may be due to a lack of knowledge, data collection/availability and virus primer specificity; the latter can be addressed by developing virus primers specifically for African honeybees. However, the presence of these viruses is of concern since they may cause stress which in combination with other factors (e.g. *V. destructor* or pesticides) may ultimately affect honeybee health.

3.4. Parasitic mites

3.4.1. Varroa destructor

V. destructor is one of the most well-known, economically important and widely distributed ectoparasites affecting honeybees (Rosenkranz et al. 2010) and is an OIE notifiable infestation. This mite was once confined to its natural host the Eastern honeybee, Apis cerana, but has since shifted its host to, among others, the Western honeybee (Donzé and Guerin 1994; Potts et al. 2010). V. destructor has been reported in many African countries (Hussein 2001a, b; Ellis and Munn 2005; Mumoki et al. 2014); however, this may be an underestimate due to the limited availability of data. Nonetheless, the reported presence of V. destructor in South Africa, Angola, Kenya, Egypt, Morocco, Senegal, Niger and Nigeria is distressing, as this indicates a wide geographical spread within the continent (Table I and Figure 2).

V. destructor mites feed on the haemolymph of honeybees (adults and developing brood) and reproduction takes place inside capped brood cells (Donzé and Guerin 1994). The duration of mite feeding during honeybee pupal development depends on the caste and sub-species (Rosenkranz et al. 2010). V. destructor mites have a preference for drone brood due to the longer post-capping stage, which allows for the production of a higher number of mated daughter mites (Fuchs 1990). Physiological parameters, flight behaviour and longevity of honeybees infested with mites during development or as adults can be negatively affected (Schneider and Drescher 1987; Bowen-Walker and Gunn 2001; Kralj and Fuchs 2006; Rosenkranz et al. 2010). In addition, V. destructor mites are capable of transmitting numerous viruses within and between colonies (Chen and Siede 2007; de Miranda et al. 2013).

Even though most of these viruses are present in Africa (see Section 3.3), there have been no reports of high colony losses directly linked to *V. destructor* mites and/or viruses (Muli et al. 2014; Pirk et al. 2014). The survival of African honeybee colonies in the presence of *V. destructor*, without chemical treatment, suggests that honeybees may not be as threatened in Africa or more resistant compared with other parts of the world.

3.4.2. Tracheal mites (Acarapis woodi)

The endoparasitic tracheal mite, Acarapis woodi, has been reported in most countries in Africa (Bradbear 1988; Hussein 2001a, b; Matheson 1993; Swart et al. 2001) and is an OIE notifiable infestation. Adult mites are found in the trachea of honeybees where they feed on haemolymph (Otis and Scott-Dupree 1992). Most of the damage attributed to these mites has been found in European sub-species of honeybees that overwinter, and include low honey production, increased mortality rates and reduced honeybee lifespans (Eischen et al. 1989; Otis and Scott-Dupree 1992; Sammataro et al. 2013). In Africa, overwintering does not occur at the same scale, and for that reason, mite infestations may not result in the same damage mentioned above. The continuous presence of newly emerged African honeybees may be ideal for these mite populations to grow. However, very little data exist on the effect and presence of these mites in African honeybee colonies, and more research is required to determine whether these mites may pose a threat. This also applies to other honeybee mites such as Tropilaelaps spp. (Asian origin). These mites have only been reported in Kenya (Kumar et al. 1993), but there are doubts as to whether the identification of the sample was accurate (Anderson and Roberts 2013).

3.5. Associated honeybee pests and predators

3.5.1. Coleoptera (beetles)

Small hive beetles (SHB) (Aethina tumida) The natural distribution of *Aethina tumida* (SHB) is

limited to sub-Saharan Africa, where SHB are considered to be a negligible pest (Lundie 1940; Hepburn and Radloff 1998) (Figure 4a). However, infestation with SHB is listed by the OIE as a notifiable infestation. Adult beetles and larvae reside within the honeybee colony and cause damage to brood, pollen and honey which they feed upon (Elzen et al. 1999). In North Africa, the introduction of SHB into Egypt did not have significant negative impacts, and SHB populations remain low (El-Niweiri et al. 2008) or absent (Hassan and Neumann 2008) in local honeybee colonies. Devastating effects have been reported in countries outside of Africa (Australia and the USA) where the beetles have been introduced (Neumann and Elzen 2004). From an African perspective, the beetles do not seem to pose a significant threat to beekeeping; however, the fact that they can act as vectors of honeybee viruses and bacteria should be of concern (Eyer et al. 2009; Schäfer et al. 2010). Since SHB are endemic to parts of Africa, it seems that honeybees have co-evolved with this particular pest.

Large hive beetles The African continent is home to numerous large hive beetles (Cetoniids, e.g. *Oplostomus fuligineus*, *Oplostomus haroldi*) that can invade honeybee colonies (Hepburn and Radloff 1998; Fombong et al. 2013) (Figure 4b). Adult beetles consume food stores as well as honeybee brood (Swart et al. 2001). These beetles can become problematic if present in large numbers, but in general, they are not considered to be serious pests of honeybee colonies in Africa.

3.5.2. Diptera (flies)

Tachinid fly (Rondanioestrus apivorus) In the family Tachinidae, *R. apivorus*, is the only species known to parasitise honeybees; specimens have been collected in southern Africa and Uganda (Knutson and Murphy 1990; Hepburn and Radloff 1998). Female flies deposit larvae on the abdomens of their hosts, which allows immediate penetration into the honeybee (Skaife 1920; Fletcher 1978). Larval growth inside the honeybee is quick, and after 4 weeks, the larva (with two distinctive black spiracles) is ready to emerge from the adult honeybee. Pupation occurs in the soil and adult flies are fully developed after approximately 10 days (Knutson and Murphy 1990). The distribution of these flies in Africa is limited, and according to Skaife (1920) and Anderson et al. (1983), only 3 and 5 % of adult honeybees are parasitised, respectively. However, in rare circumstances, infestation levels of up to 30 % have also been reported (Anderson et al. 1983). This fly seems to be of little economic importance for African honeybee health, due to the low parasite levels and a lack of recent data.

Bee conopid (Physocephala spp.) *Physocephala* is another fly genus (wasp-like appearance) that parasitises honeybees in a similar manner to *R. apivorus*, and they are also limited to southern Africa and Uganda (see above); the only difference being that larvae pupate inside the honeybee's abdomen (Anderson et al. 1983). Mature larvae and pupae can be distinguished from *R. apivorus* by their spike-like spiracles (Swart et al. 2001). These flies are only noticed occasionally and the levels of infestation vary; therefore, they seem to pose no threat to African honeybee health (Knutson and Murphy 1990).

Bee louse (Braula spp.) Braula, or the bee louse, is a tiny wingless fly (Hepburn 1978) which used to have a global distribution (Ellis and Munn 2005) (Figure 4c). In the past few decades, the chemical treatment of V. destructor has had a detrimental effect on bee louse populations (Kulincevic et al. 1991; Sammataro and Avitabile 2011) and may have reduced their distribution to areas such as Africa where mite treatment is not used (Hepburn and Radloff 1998; Hussein 2001a, b; Strauss et al. 2014). Bee lice usually attach themselves to an adult honeybee and steal food out of the mouths of their hosts (Knutson and Murphy 1990). Although opinions differ regarding the status of adult Braula as a parasite, some maintain that bee lice cause little or no harm to honeybee colonies apart from consuming honey and pollen stores (Hepburn 1978). However, bee lice have been reported to disfigure honey combs, cause paralysis or death of developing honeybees and decrease the queen's egg laying efficiency (Argo 1926; Hepburn 1978; Knutson and Murphy 1990; Marcangeli et al. 1993; Zaitoun and Al-Ghzawi 2008). At low infestation levels, the impact of *Braula* spp. is negligible in honeybee colonies and they should not affect colony health in Africa. However, their potential as vectors of viruses and other diseases still has to be evaluated.

3.5.3. Lepidoptera (moths)

Wax moth (Galleria mellonella and Achrola grisella) Galleria mellonella (greater wax moth) and Achrola grisella (lesser wax moth) are common in honeybee colonies throughout Africa, with the greater wax moth being more prevalent and damaging (Hepburn and Radloff 1998; Hussein 2001a, b; Swart et al. 2001; Lawal and Banjo 2007; Oyerinde and Ande 2009). Wax moth larvae are considered to be "hive cleaners" since they consume all the remaining comb and stores once the honeybees have absconded (Fletcher 1978). However, larvae can cause destruction when they tunnel through the brood and honey comb and wooden parts of the hive (Hepburn and Radloff 1998). In addition to the physical damage caused, larval tunnelling can result in galleriasis and bald brood (Ellis et al. 2013). Wax moth damage is most pronounced in weak or stressed colonies, and therefore, good management practices are essential to minimise damage and colony losses (Swart et al. 2001). So far, they are not a threat to African honeybees and it is unlikely that they may become a threat.

Death's head hawkmoth (Acherontia atropos) Acherontia atropos is found throughout Africa and the adult moth is easily identified by the distinct skull design on its thorax (Hepburn and Radloff 1998; Picker et al. 2004; Lawal and Banjo 2007; Zagorinsky et al. 2012) (Figure 4d). They are known to invade honeybee colonies in search of honey (Moritz et al. 1991; Kitching 2003). The unique characteristics of these moths are their ability to not only imitate the piping sounds of the queen but also to use chemical camouflage which prevent them from being attacked by workers (Moritz et al. 1991). Compared to the wax moths (see above), death's head hawkmoths only consume honey/nectar and do not cause any obvious damage in the colony (Swart et al. 2001). As a result, they are not considered to be harmful or of any economic importance.

3.5.4. Hymenoptera (ants, wasps and honeybees)

Ants Various ant species (e.g. Anoplolepis custodiens, Linepithema humile, Pheidole megacephala, Dorylus fulvus), either native or introduced to Africa, have been reported in honeybee colonies (Hepburn and Radloff 1998; Hussein 2001a, b; Swart et al. 2001; Begna 2007). Ants are known to enter honeybee colonies and remove food stores and brood, and their continued disturbance can cause colonies to abscond (Swart et al. 2001). The invasion of colonies by ants has the potential to cause serious economic losses to the beekeeper: both through the loss of hive products and most importantly the colony itself.

Wasps Bee pirates (*Palarus latifrons*, *Philanthus triangulum*)

Palarus latifrons (banded bee pirate) and *Philanthus triangulum* (yellow bee pirate) can be found in Africa (Hepburn and Radloff 1998; O'Neill 2008). They are considered to be active predators that capture honeybees either as a food source for themselves or provisioning for their young (Fletcher 1978; Swart et al. 2001). *Palarus latifrons* hunt honeybees at the hive entrance, while *Philanthus triangulum* capture them while they are foraging (Anderson et al. 1983). The aggressive behaviour of the wasps can prevent honeybees from leaving the hive to forage, and this may affect colony productivity and reduce honeybee numbers (O'Neill 2008).

German yellow jacket (Vespula germanica)

Vespula germanica, is native to northern Africa, but has been introduced into the western parts of South Africa (Archer 1998; Tribe and Richardson 1994). These social wasps are opportunistic predators that feed on a range of invertebrates, including honeybees, as well as nectar and honey (Masciocchi et al. 2010). They have been observed to feed on dead honeybees and typically

only carry bee body parts back to their nests (Coelho and Hoagland 1995). It seems as though they do not pose a significant risk to honeybee numbers, but they can threaten other native wasp species when competing for nesting areas and food (Tribe and Richardson 1994).

3.5.5. Honeybees

Apis mellifera capensis social parasite A unique problem facing South African beekeepers is the human-facilitated invasion of A. mellifera capensis into the natural range of the other subspecies, A. mellifera scutellata (Hepburn and Allsopp 1994; Hepburn and Radloff 1998; Oldroyd 2002). Upon entering A. m. scutellata colonies, A. m. capensis workers, which have the predisposition to become social parasites (Zheng et al. 2010), compete for reproduction. A. m. capensis workers are able to lay diploid eggs and produce queen-like signals (Onions 1912; Martin et al. 2002; Neumann and Moritz 2002; Pirk et al. 2012). These A. mellifera capensis social parasites do not contribute to the work force and their offspring do not replace the host workers, but these social parasites and their clonal offspring just reproduce which then results in the collapse of the host colony (Hillesheim et al. 1989; Neumann et al. 2001; Moritz 2002; Neumann and Hepburn 2002). This parasite is spread by migratory beekeepers during pollination and has resulted in large-scale colony losses with significant economic implications for the South African beekeeping industry (Allsopp and Crewe 1993; Johannsmeier 1994; Moritz 2002; Kryger et al. 2003; Dietemann et al. 2006; Pirk et al. 2014). The problem is still ongoing after 25 years.

Dwarf honeybee (Apis florea) A. florea, native to Asia, was first detected in Khartoum, Sudan, in 1985 (Lord and Nagi 1987; Mogga and Ruttner 1988; Radloff et al. 2011). *A. florea* has gradually expanded its distribution to the whole of Sudan (Moritz et al. 2010b) and to neighbouring countries such as Ethiopia (Bezabih et al. 2014). Since the climate and floral conditions are similar to their natural distribution range (Radloff et al. 2011), the species may easily colonise the whole continent. With respect to pollination, the competition for pollen between the native *A. mellifera sudanensis* and *A. florea* seems to be limited, suggesting that the impact on native *Apis* species will be minor (El Shafie et al. 2002; Bezabih et al. 2014).

3.5.6. Bee pseudoscorpion (Ellingsenius spp.)

Bee pseudoscorpions (Class: Arachnida) are widely distributed throughout Africa with eight species described (Judson 1990) (Figure 4e). Bee pseudoscorpions (not true scorpions) are small in size with large pincers (Judson 1990). Their diet is restricted to biological detritus (Thapa et al. 2013), and thus, they are considered to be harmless in honeybee colonies (Allsopp et al. 2003).

3.5.7. Birds and mammals

Various birds and mammals (e.g. humans, honey badgers, baboons, monkeys, mice), associated with or damaging to honeybee colonies, are common throughout Africa (Crane 1999; Hepburn and Radloff 1998; Hussein 2001a, b).

The most well-known birds associated with honeybees are bee-eaters (Meropidae), honeyguides (Indicatoridae) and drongos (Dicruridae). Honey-guides are widely known for guiding animals (e.g. baboons and honey badgers) to honeybee nests (Crane 1999). They do not feed on honeybees but consume wax that remains after the nest has been robbed and/or damaged by the guided mammal (Swart et al. 2001). Bee-eaters and drongos prey on honeybees and remove the sting/venom prior to ingestion, and severe predation by these birds can cause honeybees to stop foraging (Hepburn and Radloff 1998). Among these birds, bee-eaters are considered to be the most damaging to honeybee colonies since a single bird can devour up to 600 honeybees on a daily basis (Hepburn and Radloff 1998).

Of the mammals, the most destructive are honey badgers and humans. Honey badgers (*Mellivora capensis*) are nocturnal mammals with powerful claws that they use for digging, climbing and breaking hives open (Hepburn and Radloff 1998). Their destructive behaviour results in the loss of colonies. Damage caused by humans includes total destruction of colonies (e.g. traditional honey hunting), vandalism, fire, theft and even intentional poisoning of honeybee colonies (Crane 1999; Hussein 2001a, b; Swart et al. 2001; Dietemann et al. 2009).

4. PESTICIDES

The increased demand for food security in developing countries has resulted in increased crop production and subsequently a greater use of agrochemicals. Pesticides, in particular, can have a negative and harmful impact on the behaviour and physiology of honeybees that can directly influence the overall health of the colony (Yang et al. 2008; Di Prisco et al. 2013; Williamson and Wright 2013; Smith et al. 2013). These negative effects can become even more pronounced when honeybees are simultaneously exposed to multiple stressors, i.e. pathogens or parasites (Vidau et al. 2011; Köhler et al. 2012). Pettis et al. (2012) reported a higher infection of Nosema species in honeybees exposed to neonicotinoids, while Aufauvre et al. (2012) demonstrated the impact of multiple exposure to both parasites and pesticides. However, under field conditions, Retschnig et al. (2015) found no interactions between N. ceranae and neonicotinoid pesticides, and therefore, more studies under natural situations are necessary before definitive conclusions can be made.

Limited studies are available on the impacts of pesticides on African honeybees. In addition, the focus tends to be on pesticides used for agricultural crops, but in Africa, the use of pesticides to control mosquitoes (malaria vectors) may also affect honeybees negatively (Munyuli 2011). Most of the studies on pesticide use in Africa are laboratory based. In South Africa, Human et al. (2014) investigated the influence of nicotine (non-synthetic pesticide) on A. mellifera scutellata brood and found no negative impact. In adult A. mellifera scutellata, however, Köhler et al. (2012) found that multiple stressors (nicotine and Escherichia coli) affected survival despite them showing active detoxification (du Rand et al. 2015). Al Naggar et al. (2015) found that while pesticides are widely used in Egypt, they show little or no effect on the local honeybee population. The reported low levels of pesticide residues in comb and bee bread found in Kenya compared to those of colonies in the USA suggest that pesticide use may still be less intense in Africa (Muli et al. 2014). The effects of pesticides and the role they play in colony losses of honeybees in Africa need to be investigated further.

5. FLORAL RESOURCES AND HABITAT TRANSFORMATION

Hepburn and Radloff (1998) gave a detailed description of bee plants, floral resources, altitude and vegetation types on the African continent. For example, in southern Africa, 80 % of its extremely rich flora is endemic and hosts an impressive diversity of pollinators (Cowling et al. 1997). A large number of these plants are important for honeybees (Hepburn and Radloff 1998).

Africa's unique biodiversity may be at risk due to an increase in the human population that results in higher rates of deforestation and substantial changes in natural landscapes (Norris et al. 2010; Abrol 2012). Reasons for deforestation include urbanisation (building of infrastructure), mining and agricultural development (including plantations, logging and crop production) (Duveiller et al. 2008; Munyuli 2011). All the abovementioned causes can result in habitat loss and fragmentation that may affect various pollinators, including honeybees (Donaldson et al. 2002; Brown and Paxton 2009; Dietemann et al. 2009; Munyuli 2011; Goulson et al. 2015). In particular, the transition from natural to agricultural farmland and the planting of monocultures change floral diversity and may impact the nutritional requirements and fitness of honeybees (Johannsmeier and Mostert 2001; Murray et al. 2009; Goulson et al. 2015). Indeed, genetic diversity of the honeybee population is reduced in agricultural vs. natural areas (Jaffé et al. 2010). Even in agriculturally utilised land, pollination success is dependent on pollinator diversity (Carvalheiro et al. 2011). Moreover, honeybees actively regulate their nutritional intake (Altaye et al. 2010; Pirk et al. 2010). If they are unable to meet their nutritional demands, due to deficient pollen and nectar resources, worker survival, colony health and development may be negatively affected (Brodschneider and Crailsheim 2010; Goulson et al. 2015).

6. CONCLUSION

The recent decline in honeybee populations and the demand for sustainable pollination to ensure food security have resulted in increased awareness of the need to protect honeybee populations, especially in Africa (Dietemann et al. 2009). There is a need to initiate an African database (similar to that of the OIE) for the presence of pathogens, parasites, pests and predators.

Increased research has to focus on the underlying mechanisms of potential resistance of African honeybees. To ensure a healthy honeybee population, early identification of possible threats is vital. One of the recent outcomes is the establishment of the African Reference Laboratory for Bee Health, situated at the International Centre of Insect Physiology and Ecology (*icipe*) in Kenya to improve knowledge of honeybee health in East Africa (AU-IBAR Press Release 2014).

Moreover, active efforts to continually monitor pollinators are very important in the prevention of a pollination calamity (Goulson et al. 2015) and will help to reduce knowledge gaps on pollinator systems in Africa (Archer et al. 2014). Research on the role and importance of pollination systems in Africa is lacking, especially when compared with global data (Archer et al. 2014). We also need to prevent further introduction of any biological agents that may negatively affect natural honeybee and other pollinator populations (Dietemann et al. 2009; Munyuli 2011). Furthermore, education of the general public on the conservation of honeybee plants and nesting sites is of utmost importance. More specifically, beekeepers (commercial, developmental and hobbyist) need to be properly trained in beekeeping management and hive biology, ultimately resulting in the minimisation of colony stress (Dietemann et al. 2006, 2009).

Honeybee populations in Africa may have a natural mechanism of resilience against many of the introduced pathogens and parasites (Pirk et al. 2014). Compared to European honeybees, African populations are genetically diverse (due to the large wild population), have higher swarming rates and smaller colonies and are less commercialised (Hepburn and Radloff 1998; Schneider et al. 2004; Dietemann et al. 2009; Wallberg et al. 2014). In addition, colonies in Africa are known for their absconding behaviour in response to unfavourable conditions, continued disturbance and the presence of pathogens, parasites, pests or predators (Fletcher 1978; Hepburn and Radloff 1998; Fries and Raina 2003). All of these factors may contribute to reducing the impact of stressors on honeybee health in Africa. Even though African honeybee populations have not been impacted by the losses as recorded in Europe and the USA (vanEngelsdorp and Meixner 2010; Pirk et al. 2014), there is a need to take precautionary measures to protect and conserve them and their habitat.

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Apidae / Afrique / pathogène / ravageur / prédateur / perte d'habitats

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Honigbienen / Afrika / Bienengesundheit / Krankheitserreger / Parasiten / Schädlinge / Prädatoren / Habitatverlust

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